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The endemic “sugar canes” of Madagascar (Poaceae, Saccharinae: Lasiorrhachis) are close relatives of sorghum

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10 **The endemic “sugar canes” of Madagascar (Poaceae, Saccharinae: *Lasiorrhachis*) are close relatives**
11 **of sorghum**
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14 Running title: Malagasy *Lasiorrhachis*
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11 Crop wild relatives are important but often poorly known. This is the case for subtribe Saccharinae
12 (Poaceae: Andropogoneae) which includes sugarcane (*Saccharum*) and sorghum (*Sorghum*). We
13 present a phylogenetic and taxonomic account of the Malagasy endemic genus *Lasiorhachis*,
14 previously included in *Saccharum*. New plastome and nuclear sequences were assembled from
15 genome skimming data. Phylogenetic analyses of whole plastomes place *Lasiorhachis* as sister to
16 *Sorghum* and only distantly related to the interbreeding *Saccharum* complex. This is also supported
17 by analyses of nuclear ITS and partial assemblies for eight low-copy regions. Some nuclear regions
18 suggest that *Lasiorhachis* is closer to *Sorghum* section *Sorghum* than other *Sorghum* spp. sometimes
19 segregated as *Vacoparis*. We present a full taxonomic treatment of *Lasiorhachis* with an
20 identification key, synonymy, typification, descriptions, drawings, and a distribution map of the
21 three species, all endemic to the central highlands of Madagascar. *Lasiorhachis* species occupy
22 contrasting ecological niches and at least one of them, *L. viguieri*, has significance for ecosystem
23 function. As crop wild relatives of sorghum, *Lasiorhachis* species should be included in germplasm
24 collections.
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36 KEYWORDS
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38 Andropogoneae – crop wild relative – grass – lectotype – phylogenetics – Malagasy – nuclear genes
39 – plastome – *Saccharum* – shotgun sequencing – taxonomy – typification
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12 INTRODUCTION

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15 The value of wild relatives of crop species is increasingly acknowledged. Besides their interest for
16 comparative studies of domestication and traits related to productivity or stress resistance, they
17 provide an important genetic reservoir that may be harnessed through traditional breeding or
18 genetic engineering for sustainable agriculture (Brozynska, Furtado & Henry, 2016; Castañeda-
19 Álvarez *et al.*, 2016; Dempewolf *et al.*, 2017; Zhang *et al.*, 2017). In many cases however, these wild
20 relatives are insufficiently known, rare, narrow in distribution or threatened, and they are often not
21 represented in germplasm collections; poorly resolved taxonomy of many groups impedes targeted
22 collection, curation and conservation of crop wild relatives (Castañeda-Álvarez *et al.*, 2016).

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25 Poaceae subtribe Saccharinae [Panicoideae: Andropogoneae; including Sorghinae as defined by
26 Kellogg (2015) and Soreng *et al.* (2017)] comprise important food and biofuel crops, valued for their
27 rapid growth in tropical and subtropical climates, partly due to their C₄ photosynthetic pathway
28 (Kellogg, 2015). Outstanding among them is sugarcane, i.e. the three cultivated species of
29 *Saccharum* L. and their commercial hybrid cultivars. In 2017, the world produced 1.8 billion tonnes
30 of sugarcane, far outstripping any other single crop (FAOSTAT, 2019). Sorghum, *Sorghum bicolor* (L.)
31 Moench, is an important grain and fodder crop with > 57 million tonnes annual production
32 (FAOSTAT, 2019). Species of *Miscanthus* Andersson, which also grow in cooler regions, have
33 attracted increasing interest due to their potential use as second-generation biofuel (Heaton,
34 Dohleman & Long, 2008; Brosse *et al.*, 2012; Sacks *et al.*, 2013; Zhuang *et al.*, 2013). Underlining this
35 importance as crops, the genome sequence of *S. bicolor* was made available in 2009 (Paterson *et al.*,
36 2009) and was followed more recently by *M. sinensis* Andersson (Energy Biosciences Institute and
37 Joint Genome Institute, 2017) and the highly polyploid genome of sugarcane (Garsmeur *et al.*, 2018),
38 “probably the most complex of all plant crops” (Aitken, Berkman & Rae, 2016).
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10 Andropogoneae, including Saccharinae, have been recognized as among the most morphologically
11 complex groups of grasses (Clayton & Renvoize, 1986). The evolutionary history of Saccharinae is just
12 beginning to be untangled, and the taxonomic delimitation is being reconsidered as our
13 understanding of the evolutionary history of the group develops. Phylogenetic evidence for their
14 monophyly is contradictory (Hodkinson *et al.*, 2002; Kellogg, 2013; Hawkins *et al.*, 2015; Saarela *et*
15 *al.*, 2018), and there are no obvious morphological synapomorphies (Kellogg, 2015). The
16 classification by Kellogg (2015) included 16 genera, with 177 species, whereas Soreng *et al.* (2017)
17 accepted 26 genera.

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24 Several genera of Saccharinae, including some potentially allied to *Saccharum*, e.g. *Eulalia* Kunth, are
25 highly polyphyletic (Kellogg, 2015). *Saccharum* s.s. includes only six species, and several others
26 traditionally included are either closer to *Miscanthus* or entirely unrelated (Hodkinson *et al.*, 2002;
27 Kellogg, 2013, 2015; Evans *et al.* 2019). The *Saccharum* complex, as originally defined for plant
28 breeders by Mukherjee (1954) and expanded by Daniels & Daniels (1975), included *Saccharum*,
29 *Erianthus* Michx. section *Ripidium* Henrard, *Miscanthus* and *Sclerostachya* (Andersson ex Hackel)
30 A.Camus and *Narenga* Bor (both now part of *Miscanthus*). *Erianthus* section *Ripidium* is now treated
31 as a separate genus, *Tripidium* H.Scholz, not directly related to either *Saccharum* or *Erianthus* Michx.
32 (Welker *et al.*, 2015; Evans *et al.*, 2019; Welker *et al.*, 2019). Evans *et al.* (2019) updated the
33 definition of the *Saccharum* complex to include all groups interbreeding in the wild: *Miscanthus*,
34 *Miscanthidium* Stapf, *Saccharum* and New World *Erianthus*. Outside this complex, *Sorghum* is
35 polyphyletic, and *Sarga* Ewart now includes around half of the former *Sorghum* spp. (Spangler, 2003;
36 Hawkins *et al.*, 2015; Kellogg, 2015). Reticulate evolution with frequent allopolyploidization, as in
37 many other Andropogoneae (Estep *et al.*, 2014), probably characterizes Saccharinae and leads to
38 genes with diverging histories (Kellogg, 2013; Welker *et al.*, 2015). Identifying and preserving wild
39 relatives of sugarcane, sorghum and *Miscanthus* is therefore non-trivial. For example, the World
40 Collection of Sugarcane and Related Grasses (WCSRGR at the USDA-ARS Subtropical Horticulture
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10 Research Station in Miami, Florida) includes a wide array of species of Saccharinae for which
11 relationships are not yet fully understood (Todd *et al.*, 2017).
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14 Species of Saccharinae endemic to Madagascar remain poorly known and have so far not been
15 included in germplasm collections due to the sparseness of scientific links and difficulties in
16 accessing material. The first awnless endemic species was described by Hackel (1885) as *Andropogon*
17 *hildebrandtii* Hack. and placed in the new *Andropogon* section *Lasiorhachis* Hack., named after the
18 soft woolly texture of its synflorescence. *Andropogon* section *Lasiorhachis* was raised to the rank of
19 subgenus (Hackel, 1889) and then to genus (Stapf, 1927). Stapf (1927) noted that “the structure of
20 the panicle and of the spikelets has more in common with *Sorghum* than with any other genus”. The
21 other two species have awns and were originally described in *Erianthus* (Camus, 1924), moved to
22 *Miscanthidium* (Camus, 1959) and brought together with the awnless *L. hildebrandtii* (Hack.) Stapf in
23 *Lasiorhachis* (Hack.) Stapf by Bosser (1968). The genus was then incorporated into *Saccharum* by
24 Clayton (1981), even though “its true position lies between *Saccharum* and *Hemisorghum*” (Clayton,
25 1981). The first DNA sequence data for *Lasiorhachis* were not published until Hackel *et al.* (2018):
26 the plastid markers *ndhF*, *rbcl* and *trnk-matK* placed the three species, with *Eulalia villosa* (Spreng.)
27 Nees, close to *Sorghum*, but with weak support. A plastome sequence of the type species *L.*
28 *hildebrandtii* was published by Piot *et al.* (2018) and strongly supported the species as sister to
29 *Sorghum bicolor*.
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41 We present an account of *Lasiorhachis*, comprising three species endemic to Madagascar that were
42 previously classified in *Saccharum*, but are now accepted as a separate genus again (Kellogg, 2015;
43 Soreng *et al.*, 2017; Vorontsova *et al.*, 2018). A full taxonomic treatment is given alongside new
44 plastome and nuclear genetic data to reassess their phylogenetic position. We confirm that
45 *Lasiorhachis* is the sister genus of *Sorghum*, which helps further clarify the taxonomy of Saccharinae
46 and brings new relevance to this genus of crop wild relatives.
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52 MATERIAL AND METHODS

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10 ACCESSIONS AND TAXONOMY

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12 Collection trips were conducted across Madagascar during the period 2011 – 2018. Ten occurrences
13 of *Lasiorrhachis* were seen in the wild and collections were made (Fig. 1). Cultivation of *Lasiorrhachis*
14 *perrieri* (A.Camus) Bosser was attempted at the Parc Botanique et Zoologique de Tsimbazaza, but
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16 without success. A full taxonomic analysis of the 76 collections held at the K, P and TAN herbaria was
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18 carried out. Descriptive morphological terms such as “inflorescence” are used for recognition and
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20 communication purposes only, and further research will be required to align these to
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22 developmentally correct terminology such as “synflorescence”, as reviewed by Kellogg (2015). This
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24 study focuses on macromorphological characters and does not attempt to examine
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26 micromorphology or anatomy.
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28 SEQUENCING AND MARKER ASSEMBLY

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30 Genomic DNA from two *Lasiorrhachis* specimens (*L. hildebrandtii* LRK2008 and *L. perrieri* NOP140)
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32 was extracted and shotgun-sequenced on a HiSeq machine as described in Besnard *et al.* (2013),
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34 producing 125-bp paired-end reads. The full *L. hildebrandtii* plastid genome (plastome) has been
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36 published by Piot *et al.* (2018), and we assembled the plastome of *L. perrieri* as described therein.
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38 We also assembled partial nuclear ribosomal DNA (nrDNA) containing the internal transcribed spacer
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40 regions (ITS) for both accessions. For this, reads were mapped to *S. bicolor* 5.8S nrDNA sequence
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42 (MH762138.1) in Geneious v. 8.0.5 (Biomatters Ltd.), using the built-in mapping algorithm with
43
44 default parameters, and mapping again to a 75% majority consensus sequence for ten iterations.
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46 Coverage for nrDNA was >1000x in both accessions. Partial coding sequences (CDS) were further
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48 assembled for eight low-copy nuclear regions for which sufficient homologues from Andropogoneae
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50 were available in GenBank: the aberrant panicle organization 1 gene (*apo1*); the DELLA-encoding
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52 protein gene *dwarf8* (*dwarf8*); *floricaula/leafy-like* (*floricaula*); the granule-bound starch synthase 1
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54 gene (GBSSI or *waxy*); *erect panicle 2* exons 7 and 8 (*ep2-7* and *ep2-8*); the phytochrome B gene
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56 (*phyB*); and *retarded palea 1* (*rep1*). For assembly, reads were mapped to the exon sequences from
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10 the *S. bicolor* genome (GCF_000003195.3) in Geneious. A 75% majority consensus sequence was
11 then called and sites with total base phred quality <30 or not covered were coded as N. Assembled
12 exons were finally merged, not using exons with >50% ambiguous bases. Mean coverage per exon
13 ranged from 0.9 to 4.7x. The sequencing reads have been submitted to the Sequence Read Archive
14 (BioProject No. [to be added]), assembled plastome and nrDNA sequences to GenBank (accession
15 numbers MF563371.1 and [to be added], and [to be added] and [to be added], respectively), and the
16 incomplete low-copy gene assemblies are available as supplementary file **XX**.
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23 PHYLOGENETIC ANALYSIS

24 The plastome sequences were combined with 54 other full plastomes, including representatives of
25 Andropogoneae selected from recent studies (Burke *et al.*, 2016; Arthan *et al.*, 2017) and all
26 plastomes of *Eulalia*, *Miscanthus*, *Miscanthidium*, *Saccharum*, *Sarga* and *Sorghum* that are available
27 on GenBank. After excluding the second inverted repeat region, they were aligned using the default
28 MAFFT v. 7.407 (Kato & Standley, 2013) algorithm. CDS and non-coding regions were extracted
29 from the alignment and phylogenetic trees inferred separately using Bayesian estimation in MrBayes
30 v. 3.2.6 (Ronquist & Huelsenbeck, 2003; Altekar *et al.*, 2004) with a GTR+ γ substitution model,
31 running two analyses with four chains until the standard deviation of splits was <0.01. We also re-
32 estimated a phylogeny based on *ndhF-rbcl-trnk/matK* for Saccharinae and selected outgroup taxa.
33 For this, we combined the data used by Hackel *et al.* (2018) with the respective regions extracted
34 from the full plastomes, aligned each marker set using the MAFFT *G-INS-i* algorithm, trimmed
35 alignment ends with >90% missing data and concatenated the three alignments. A phylogenetic tree
36 was produced from the concatenated alignment using MrBayes as described above, partitioning by
37 gene. We also compared topologies with the monophyly of *Lasiorrhachis* constrained or not via a
38 likelihood ratio test in RAxML v. 8.2.12 for the *ndhF-rbcl-trnk/matK* alignment. Finally, for ITS and
39 the low-copy nuclear genes, we retrieved homologous sequences for Andropogoneae via *blastn*
40 searches (Camacho *et al.*, 2009) against GenBank, retaining only the longest matching sequence per
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10 NCBI taxon for ITS and the longest among identical sequences for the low-copy genes. Each set of
11 sequences was then aligned with the *Lasiorchachis* assemblies using MAFFT-G-INS-i, alignment ends
12 trimmed and trees inferred using MrBayes as described above. We used *Arthraxon* P.Beauv. for
13 rooting the plastome tree given its early-diverging position in Andropogoneae s.s. based on the
14 plastome analyses of Arthan *et al.* (2017). Sequences of *Arthraxon* were not available for all nuclear
15 markers and we chose *Arundinella* Raddi, which was consistently available, as a less closely related
16 lineage outside Andropogoneae s.s. for rooting.
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22 RESULTS

23 TAXONOMY

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27 A visual examination of specimens, spikelet dissections and living plants suggested the presence of
28 three clearly distinct species with different morphologies and ecological niches in Madagascar. None
29 of these has been recorded outside the island. None of the previously published treatments of these
30 species by Bosser (1968, 1969) and Clayton (1981) included parallel descriptions and identification
31 keys. The first full taxonomic treatment of *Lasiorchachis* is presented below.
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36 PHYLOGENETIC ANALYSIS

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39 Plastome sequences strongly supported *L. perrieri* NOP140 and *L. hildebrandtii* LRK2008 as sister to
40 each other and placed both as sister to *Sorghum* (represented by *S. bicolor* and *S. mekongense*
41 A.Camus), with *Sarga timorensis* (Kunth) Spangler being the next closest relative (Figs 2, S1).
42
43 *Lasiorchachis* thus fell in Andropogoneae subtribe Saccharinae (*fide* Kellogg, 2015, Soreng *et al.*,
44 2017) but was clearly distinct from the *Saccharum* complex. Support was generally higher for the
45 tree inferred from non-coding parts of the plastome alignment, but CDS supported the same
46 position for *Lasiorchachis* and recovered most of the other clades. The plastid *ndhF-rbcL-trnK/matK*
47 tree did not resolve relationships among *Sarga*, *Sorghum* and *Lasiorchachis*, despite more species
48 being sampled (Fig. 3). It also placed two accessions of *Eulalia villosa* in *Lasiorchachis* with weak
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10 support; a likelihood ratio test, however, did not reject the monophyly of *Lasiorhachis* compared to
11 an unconstrained topology ($p=0.23$, logL difference -0.005).
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14 The trees for ITS and the eight low-copy regions, containing between 47 and 320 tips, received only
15 weak support for the backbone of Andropogoneae (Figs 3, S1 A-I). However, all trees grouped
16 *Lasiorhachis* with *Sorghum* spp., distinct from the species of the *Saccharum* complex and a *Sarga*
17 clade (= *Sorghum* sections *Stiposorghum* and *Parasorghum*). In four trees (*apo1*, *dwarf8*, *ep2-7*, *ep2-*
18 *8*) in which *Sorghum laxiflorum* F.M.Bailey and *S. macrospermum* E.D.Garber (*Sorghum* sections
19 *Chaetosorghum* and *Heterosorghum*, respectively) are represented, their sequences are placed sister
20 to or paraphyletic with respect to *Lasiorhachis* (Fig. 4 A, B, D, E), which is thus closer to a clade
21 corresponding to *Sorghum* section *Sorghum* [*Sorghum arundinaceum* (Desv.) Stapf, *S. bicolor*, *S.*
22 *halepense* (L.) Pers. and/or *S. propinquum* (Kunth) Hitchc.; also including sequences identified as
23 *Polytrias indica* (Houtt.) Veldkamp in *rep1*; Fig. S2 I]. *Cleistachne sorghoides* Benth. was placed with
24 either *Sarga* or *Sorghum*. The seven nuclear trees that included *Eulalia villosa* (ITS, *dwarf8*, *ep2-7*,
25 *ep2-8*, GBSSI, *phyB* and *rep1*) placed it clearly distant from *Lasiorhachis*, *Sarga* and *Sorghum*.
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35 DISCUSSION

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37 The phylogenetic analysis presented here confirms *Lasiorhachis* spp. as close relatives of *Sorghum*,
38 as recognized by Stapf (1927). *Lasiorhachis* is closer to *Sorghum* s.s. than the species segregated
39 from it as *Sarga* (Spangler, 2003), and it is clearly distinct from sugarcane and its relatives in the
40 *Saccharum* complex. This confirms the result of Piot *et al.* (2018), who included only *L. hildebrandtii*
41 in their plastome analysis. A coalescent analysis of nuclear genome-wide markers also supports *L.*
42 *hildebrandtii* as sister to *S. bicolor* and suggests a dominant nuclear signal for this position (Bianconi
43 *et al.*, unpublished data). Limited available nuclear sequence data for *S. laxiflorum* and *S.*
44 *macrospermum* included in our analysis suggest that these species (segregated as *Vacoparis*
45 Spangler; Spangler, 2003) may be more distant from *Sorghum* s.s. (i.e. *Sorghum* section *Sorghum*)
46 than *Lasiorhachis*. Paraphyly of sequences of these two species with regard to *Lasiorhachis* may
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10 indicate an allopolyploidy event before the origin of *Lasiorchachis* and *Sorghum*. The single known
11 chromosome count in *Lasiorchachis* is $2n = 20$ (recorded on the herbarium specimen *Tateoka 3514*,
12 P02643315 of *L. hildebrandtii*), suggesting that it is diploid based on the Andropogoneae base count
13 of $x = 10$ (Kellogg, 2015); due to the shallow sequencing and our assembly method, potential
14 paralogous genes resulting from any allopolyploidy could not be distinguished.
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19 Taken together, the results strongly support *Lasiorchachis* as sister to *Sorghum* s.s. (= *Sorghum*
20 section *Sorghum*) and may warrant the recognition of *Vacoparis* as separate genus. It is also possible
21 that following more comprehensive analyses *Lasiorchachis* may become part of the broader *Sorghum*.
22 Additional data from all species of *Sorghum* and *Lasiorchachis*, especially from more variable plastid
23 markers (or entire plastomes), are needed. Clearly, plastid *ndhF* + *rbcl* + *trnK/matK* are insufficient
24 to resolve relationships (see Fig. 3), and we expect the placement of *Eulalia villosa* in *Lasiorchachis* in
25 the three-gene tree to change with more data, especially since all nuclear trees including this species
26 place it in a distant position.
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33 Macromorphological characters traditionally used in keys and taxonomic treatments do not provide
34 enough data for a clear differentiation of clades or genera in *Lasiorchachis* and its relatives, as
35 evidenced by the multiple alternative taxon delimitations discussed above. The variability in male
36 and female expression and development, of both sessile and pedicellate spikelets, were cited as a
37 distinguishing characteristic of *Lasiorchachis* by Stapf (1927) and Bosser (1968), but it does also occur
38 across Andropogoneae as pointed by Clayton (1981) and Kellogg (2015). Hackel (1885, 1889)
39 described *L. hildebrandtii* as having glabrous lodicules and an apically pilose ovary, and Stapf (1927)
40 corrected these to apically pilose lodicules and a glabrous ovary; we have also recorded pilose
41 lodicules and a glabrous ovary, although anatomical data needs confirmation through a more
42 detailed study. This study did not confirm the presence of the ovary appendage in *L. hildebrandtii*
43 recorded by Watson, Macfarlane & Dallwitz (1992 onwards) and Kellogg (2015): this could be due to
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10 our focus on macromorphology and a lack of detailed micromorphological examination. Critical
11 micromorphological and anatomical study of fresh material is still necessary for all three species.
12

13 Functional traits of dominant C₄ Poaceae determine ecosystem function in the subtropical grasslands
14 and savannas of Madagascar (Solofondranohatra *et al.*, 2018), which cover at least 65% of the land
15 area (Moat & Smith, 2007). *Lasiorchachis* makes a non-trivial contribution to ecosystem function: the
16 most abundant species, *L. viguieri* (A.Camus) Bosser, dominates flammable rocky grasslands
17 alongside *Panicum andringitrense* A.Camus at c. 2200 m elevation on the granite plateau of
18 Andringitra National Park (site 6; Vorontsova *et al.*, 2016). Its woody rhizomes and thick culm bases
19 persist during fires and form the ground cover in several highland ecosystems (Vorontsova M.S.,
20 pers. obs.). *Lasiorchachis hildebrandtii* occupies a contrasting shady niche and is one of the few C₄
21 plants to be found under forest canopy, at somewhat lower elevations. The niche of *Lasiorchachis*
22 *perrieri* is different again: the larger size of its tussocks restricts its habitats to those with a ready
23 source of running water. Occurrence of *Sorghum* in Madagascar is still poorly recorded, but there
24 are both native and introduced, wild, food and fodder species; these tend to occupy habitats at
25 lower elevations than *Lasiorchachis*, often found close to human dwellings and in disturbed areas.
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27 Divergence in morphology and ecological niche in *Lasiorchachis* suggests a long evolutionary history.
28 The median stem age estimate of Hackel *et al.* (2018) for the two *Lasiorchachis* clades of between
29 2.5–4.0 Mya was modelled on a more poorly resolved tree topology. Bianconi *et al.* (unpublished
30 data), using genome-level data, dated the median split between *S. bicolor* and *L. hildebrandtii* at 4
31 Mya under a “younger” calibration scenario. This suggests that the diversification of *Lasiorchachis* in
32 Madagascar occurred during the Pleistocene or, potentially, the Late Miocene. Although the
33 majority of the grass flora of Madagascar probably dispersed from Africa, *Lasiorchachis* was
34 estimated by Hackel *et al.* (2018) to have an Asian–Australasian origin, albeit based on a weakly
35 supported topology. If the relationship of the Australasian “*Vacoparis*” as sister to Malagasy
36 *Lasiorchachis* and Asian-African *Sorghum s.s.* proves to be correct, this would support an Australo-
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10 Asian origin of the group followed by dispersal to Africa and Madagascar. Any conclusion on the
11 origin and timing of *Lasiorchachis* and its diversification will require studies at the population level as
12 well as a better understanding of the whole of the enigmatic Saccharinae.
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15 No accessions of *Lasiorchachis* have been successfully cultivated to date, despite of their horticultural
16 potential due to their beautiful inflorescence colours: snow-white in *L. hildebrandtii*, golden brown
17 in *L. perrieri* and a vivid pink-purple in *L. viguieri*. No seed collections have been made. No tests for
18 potentially useful alleles have been carried out. As well as providing a missing piece of the evolution
19 puzzle of Saccharinae, *Lasiorchachis* remains a mysterious knowledge gap in its own right.
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25 TAXONOMIC TREATMENT

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27 ***Lasiorchachis*** (Hack.) Stapf in Hooker's Icon. Pl. 32: t. 3124. 1927 as '*Lasiorrhachis*' ≡ *Andropogon*
28 section *Lasiorchachis* Hack. in Flora 68: 142. 1885 ≡ *Andropogon* subgenus *Lasiorchachis* (Hack.) Hack.
29 in Monogr. Phan. [A.DC. & C.DC.] 6: 471. 1889.
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33 *Type: Lasiorchachis hildebrandtii* (Hack.) Stapf (*Andropogon hildebrandtii* Hack.).
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35 Coarse long-lived densely tufted perennials with short thick woody rhizomes and erect flowering
36 culms. All leaves basal. Ligule membranous to coriaceous. Auricles absent or deltoid. Leaf blades
37 thick, linear to narrow-lanceolate, with a pronounced white midrib. Inflorescences silky terminal
38 panicles with primary and secondary branching from the main culm. Spikelets paired. Internodes
39 apically cupulate. Internodes and pedicels villous. Callus truncate. Sessile spikelet lower floret sterile,
40 upper floret hermaphrodite. Glumes chartaceous to coriaceous, convex. Upper lemma bilobed,
41 ciliate at the apex, with or without an awn. Lodicules with apical hairs. Anthers three. Pedicelled
42 spikelets the same as sessile spikelets and hermaphrodite, or somewhat reduced in size and male.
43 Sometimes the pedicel and the pedicelled spikelet reduced or absent on some branches.
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51 *Notes:* The three species of this genus are clearly distinct and easy to identify. Flowering culms are
52 generated, grow rapidly prior to flowering and dehisce shortly after flowering. Photosynthate seems
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10 to be stored primarily in the woody rhizomes and the lowermost culm internodes. *Lasiorhachis*
11 *viguieri* frequently loses aboveground biomass to fires; leaves and culms regrow after fire from
12 lower parts of the plant. No signs of burning were noted on *L. hildebrandtii* or *L. perrieri*.
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16 The presence, size, and reproductive functionality of the pedicelled spikelet varies between
17 different parts of the inflorescence and between plants. Complete absence of the pedicellate
18 spikelet is rare and has only been noted in some lowermost inflorescence branches of *L.*
19 *hildebrandtii*. The most common condition is a male pedicellate spikelet (*L. perrieri*) or a bisexual
20 pedicellate spikelet (*L. hildebrandtii*, *L. viguieri*). The dispersal unit is most commonly a single
21 spikelet which detaches as the spikelet callus is separated from the cupular apex of the internode.
22
23 When the pedicellate spikelet is male, sterile or absent, the sessile hermaphrodite spikelet often falls
24 off together with its pedicel and the pedicellate spikelet. It also seems common for a section of an
25 inflorescence branch with c. 2-20 spikelets to detach as a whole. The relative roles of the
26 indumentum (thick in all species) and the awns (present in two of three species) in seed dispersal are
27 not clear. No seed dispersal agents are known.
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35 KEY TO *LASIORHACHIS*:
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- 37 1. Inflorescences snow-white in colour; inflorescence branches loose and pendent; awns absent.
38 **1. *L. hildebrandtii***
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41 1. Inflorescences tinged brown or pink or purple; inflorescence branches erect; awns present.. 2
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43 2. Flowering culms 1.5-2.0 m tall; inflorescences tinged brown; sessile spikelets 3.0-4.0(-4.5) mm
44 long **2. *L. perrieri***
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46 2. Flowering culms 0.50-1.15(-1.45) m tall; inflorescences tinged pink or purple; sessile spikelets (5-
47)6-9 mm long **3. *L. viguieri***
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10 1. *Lasiorchachis hildebrandtii* (Hack.) Stapf in Hooker's Icon. Pl. 32: t. 3124. 1927 \equiv *Andropogon*
11 *hildebrandtii* Hack. Flora 68: 141. 1885 \equiv *Saccharum hildebrandtii* (Hack.) Clayton Kew Bull. 35(4):
12 818. 1981. Type: MADAGASCAR, Antananarivo, Andrangolaoka, Nov 1880, *J.M.Hildebrandt 3755*
13 (Lectotype designated here: W [W1916-0028387] (photograph!), isolectotypes: JE [JE00012628,
14 JE00012629] (photograph!), K [K000244592]!, P [P00450367, P00450368, P00450369]!, W [W1889-
15 0039830, W1916-0028386] (photograph!)).

20 Tufted perennial 0.6-1.5(-2.0) m. Flowering culm 2.5-5.0 mm diameter at base. Nodes dark,
21 glabrescent. Culms and leaves glabrescent. Basal leaf sheaths smooth, shiny. Ligule coriaceous,
22 truncate, 1 mm long. Auricles deltoid, acute to rounded, dark, 1-2 mm long, ciliate when young. Leaf
23 blades pseudopetiolate, flat, 7-13 mm wide, the margins serrulate. Inflorescences 15-33 cm long, lax,
24 densely covered in white indumentum, the branches loose and pendent, with secondary branching,
25 the internodes and pedicels somewhat shorter or longer than the spikelets, the spikelets usually not
26 overlapping. Sessile spikelets 3.5-4.5(-6.0) mm long, ovate, hermaphrodite, villous. Callus hairs 1-2
27 mm long. Lower glume with two keels, five- to seven-nerved, with cross-veins visible on the inner
28 surface. Upper glume five- to seven-nerved. Anthers 2.5 mm long. Awns absent. Pedicellate spikelets
29 the same as sessile spikelets, hermaphrodite or smaller and male. Sometimes the pedicel and the
30 pedicellate spikelet reduced or absent on some branches. (Figs. 1B, 5).

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40 *Distribution*: northern and central parts of the Malagasy highlands, with a single record from the
41 northern wet forests (Fig. 8).

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44 *Habitat*: shaded understory of wet forest, gallery forest and sometimes seasonal forest or tapia,
45 often by the sides of streams; on laterite or granite; 700-1600m (the northernmost outlier record
46 *Humbert & Capuron 21951* is recorded from 400-600m which could represent an error).

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50 *Notes*: Easy to recognize by its silky snow-white inflorescences with pendent branches (Fig. 1B) and
51 no awns. It is the only species of the genus fully lacking awns, a feature that could be related to its
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10 forest understory habitat. Of the two original annotated sheets from Hackel's herbarium, the chosen
11 lectotype W1916-0028387 has the best flowering material. $2n = 20$ (*Tateoka* 3514).
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14 *Specimens examined: Madagascar. Antananarivo:* Ambatolaona, 4 September 1956, *Descoings, B.*
15 *1773* (TAN); Ambatolaona, *Morat, P. 552* (TAN); Ambatolaona, 11 November 1912, *Viguiet, R. &*
16 *Humbert, H. 1196* (P); Ambohitantely, *Peltier, J. & Peltier, M. 4349b* (TAN); Analabe, Betsitra,
17 October 1905, *D'Alleizette, C. 1280* (P); Angavokely, May 1956, *Bosser, J.M. 9579* (TAN); Angavokely,
18 April 1959, *Bosser, J.M. 12727* (TAN); Angavokely, October 1960, *Bosser, J.M. 14648* (P, TAN);
19 Angavokely, December 1960, *Bosser, J.M. 14983* (P); Angavokely, 27 April 1947, *Humbert, H. 20880*
20 (P); Angavokely, 28 October 1970, *Keraudren-Aymonin, M. & Aymonin, G.G. 25229* (P); Angavokely,
21 28 October 1970, *Keraudren-Aymonin, M. & Aymonin, G.G. 25201* (P); Angavokely, 14 January 1960,
22 *Leandri, J. 2552* (P); Angavokely, October 1960, *Leandri, J. 3219* (P); Angavokely, 10 January 1919,
23 *Perrier de la Bâthie, H. 12926* (P,P,TAN); Angavokely, 25 June 1964, *Tateoka, T. 3514* (P, TAN);
24 Antananarivo, 1960, *Keraudren-Aymonin, M. 18* (P); Manankazo, September 1913, *Perrier de la*
25 *Bâthie, H. 10726* (P). **Antsiranana:** Lokoho, 1948, *Humbert, H. & Capuron, R. 21951*(P). **Fianarantsoa:**
26 Andohantanimenaha, Itremo, 25 February 2013, *Vorontsova, M.S. et al. 1004* (K,TAN);
27 Antsirakambiaty, Itremo, 12 March 2012, *Vorontsova, M.S. et al. 739* (K,TAN); Itremo,
28 Andohatanimenaha, 19 February 2014, *Nanjarisoa, O.P. et al. 146* (K,TAN). **Toamasina:** Andasibe, 9
29 January 1911, *Perrier de la Bâthie, H. 10830* (P); Andrangovallo, October 1937, *Humbert, H. & Cours,*
30 *G. 17946* (P); Ankarakaoka, October 1937, *Humbert, H. & Cours, G. 17534* (P); Lac Alaotra, *Herbier de la*
31 *Station Agricole de l' Alaotra 34* (TAN); Lac Alaotra, *Herbier du Jardin Botanique de Madagascar 3415*
32 (P); Moramanga, Anosibe, September 1953, *Bosser, J.M. 6600* (P); Moramanga, August 1953, *Bosser,*
33 *J.M. 6618* (P); Nonokambo, 21 August 1937, *Jardin Botanique de Tananarive 2851* (P); Sahamalaza,
34 Manakambahiny Est, *Dequaire, J. 27854* (P); Sahatandra, 16 October 1912, *Viguiet, R. & Humbert, H.*
35 *764* (P); Sandrangato, December 1954, *Descoings, B. 218* (P, TAN); Ambatovy, 24 November 2011,
36 *Bernard, R. et al. 1836* (P).
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10 2. *Lasiorhachis perrieri* (A.Camus) Bosser in *Adansonia sér.* 2, 8: 515. 1968 \equiv *Erianthus perrieri*
11 A.Camus in *Bull. Soc. Bot. France* 71: 1182. 1925 \equiv *Miscanthidium perrieri* (A.Camus) A.Camus in *Bull.*
12 *Soc. Bot. France* 106: 339. 1959 \equiv *Saccharum perrieri* (A.Camus) Clayton in *Kew Bull.* 35(4): 818. 1981.
13
14 Type: MADAGASCAR, Antananarivo, Betafo, Oct 1913, *H.Perrier de la Bâthie 10723* (Lectotype
15 designated here: P [P00450374]!, isolectotype: P [P03370850]!).
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19 Tufted perennial 1.5-2.0 m. Flowering culm 5-10 mm diameter at base. Nodes dark, glabrescent.
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21 Culms and leaves glabrescent. Basal leaf sheaths smooth, hardened. Ligule coriaceous, truncate,
22 reddish, 2-4 mm long. Auricles absent or rounded, dark, up to 1 mm long, glabrous. Leaf blades flat,
23 10-15 mm wide, the margins serrulate. Inflorescences 20-30 cm long, dense, with brownish
24 indumentum, the branches close together and largely erect, with secondary branching, the
25 internodes and pedicels somewhat shorter than the spikelets, the spikelets overlapping. Sessile
26 spikelets 3.0-4.0(-4.5) mm long, ovate, hermaphrodite, loosely hirsute to glabrous. Callus hairs 1-2
27 mm long. Lower glume with two keels, seven- to nine-nerved, with cross-veins visible on the inner
28 surface. Upper glume three- to five-nerved. Anthers 2.8 mm long. Awns present, geniculate, twisted,
29 7-12 mm long, glabrous. Pedicellate spikelets similar to sessile spikelets but smaller, usually male
30 with no awns, sometimes hermaphrodite with awns. (Figs. 1C-E, 6).
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38 *Distribution:* restricted area of the Central Highlands in the Antananarivo and Fianarantsoa
39 provinces. Known from five localities only. (Fig. 8).
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42 *Habitat:* open rocky habitats near streams, on basalt or gneiss, 1300-1900 m (Fig. 1C).
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45 *Notes:* The rarest member of the genus. Poor documentation of this species could be related to
46 infrequent flowering, and the difficulty of identification in the vegetative state. A population of *L.*
47 *perrieri* was recorded from Antsirakambiaty, Itremo, for the first time in 2014 (Fig. 1C-E) despite the
48 fact that this commonly visited area has been the subject of numerous previous botanical surveys,
49 including by the first author. Cultivation of this species has so far been unsuccessful. It is likely this
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10 species requires a reliable water supply; the population in Antsirakambiaty is found on the edge of a
11 permanent stream. The lectotype sheet chosen here was previously marked as a holotype before
12 the second duplicate was found; it is more extensively annotated and contains superior quality
13 material.
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17 *Specimens examined: Madagascar. Antananarivo:* Betafo, laves de l'lantsifitra, 25 December 1928,
18 *Humbert, H. 7138* (P); Tritriva, May 1912, *Perrier de la Bâthie, H. 10849* (P). **Fianarantsoa:**
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20 Ambatofinandrahana, January 1953, *Bosser, J.M. 5082* (TAN); Ambatofinandrahana, 25 January
21 1975, *Croat, T.B. 29502* (TAN); Ambositra, January 1964, *Bosser, J.M. 18996* (P, TAN, WAG);
22
23 Antsirakambiaty, Itremo, 18 February 2014, *Nanjarisoa, O.P. et al. 140* (K,TAN); Antsirakambiaty,
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25 Itremo, 19 May 2014, *Vorontsova, M.S. & Nanjarisoa, O.P. 1530* (TAN).
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28 **3. *Lasiorhachis viguieri*** (A.Camus) Bosser in *Adansonia sér. 2, 8: 515. 1968* \equiv *Erianthus viguieri*
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30 A.Camus in *Bull. Soc. Bot. France 71: 1182. 1925* \equiv *Miscanthidium viguieri* (A.Camus) A.Camus in *Bull.*
31 *Soc. Bot. France 106: 339. 1959* \equiv *Saccharum viguieri* (A.Camus) Clayton in *Kew Bull. 35(4): 818. 1981.*
32
33 Type: MADAGASCAR, Antananarivo, Ambatolampy, pentes herbeuses sur le flanc ouest de
34 l'Ankaratra, entre Ambatofotsy et le Tsiafajavona, 27 Nov 1912, *R.Viguiet & H.M.Humbert 1721*
35 (Holotype: P [P00450376]!, isotypes: P [P00450375, P00450377, P02356437]!).
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39 = *Miscanthidium antsirabense* A.Camus in *Bull. Soc. Bot. France 106: 338. 1959.* Type:
40
41 MADAGASCAR, Antananarivo, environs d'Antsirabe, Jan 1914, *H.Perrier de la Bâthie 10753* (Holotype:
42
43 P [P00450370]!, isotypes: P [P00450371, P00450372]).
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45 Tufted perennial 0.50-1.15(-1.45) m. Flowering culm 1.5-4.0 mm diameter at base. Nodes villous.
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47 Culms and leaves glabrescent. Basal leaf sheaths smooth, shiny, sometimes breaking down into
48 fibres. Ligule membranous, truncate, 1-4 mm long, surrounded by auricular hairs. Auricles absent.
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50 Leaf blades usually rolled, 3-11 mm wide, the margins smooth. Inflorescences 8-16 cm long, lax, with
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52 indumentum which is purple when fresh, the branches largely erect, usually branched only once,
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10 with limited secondary branching, the internodes and pedicels 1/2-3/4 as long as the spikelets, the
11 spikelets overlapping. Sessile spikelets (5-)6-9 mm long, ovate, hermaphrodite, villous to almost
12 glabrous. Callus hairs 1-3 mm long. Lower glume with two keels, seven- to nine-nerved, with cross-
13 veins visible on the inner surface. Upper glume three- to five-nerved. Anthers 2.8-3.6 mm long. Awns
14 present, geniculate, twisted, 8-20 mm long, glabrous. Pedicelled spikelets the same as sessile
15 spikelets, hermaphrodite; sometimes reduced in size, male, with no awns. (Figs 1A, 7).
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21 *Distribution:* central to southern highlands. (Fig. 8).
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23 *Habitat:* open canopy montane grassy ecosystems, often associated with rocky outcrops and
24 streams, often with *Erica* L.; (1500-)1700-2500 m (Fig. 1A).
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27 *Notes:* This is the most common and abundant *Lasiorhachis* sp., dominating a range of higher
28 elevation flammable C₄ habitats, including the rocky plateau grassland at Andringitra National Park
29 (plot 6; Vorontsova *et al.*, 2016). Found in drier and more open habitats than *L. hildebrandtii* and *L.*
30 *perrieri*, frequently those prone to fire. Charred leaf sheaths are frequently seen on herbarium
31 specimens. Adaptations to drier habitat could include its smaller height, and leaf blades that are
32 usually rolled; specimens with flat leaves could represent individuals growing in more humid
33 environments. The holotype sheet of *Erianthus viguieri* is the only one directly annotated by Aimée
34 Camus. The holotype sheet of *Miscanthidium antsirabense* shows signs of several annotates by
35 Aimée Camus, including pencil marks linking it to *Miscanthidium viguieri*.
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43 *Specimens examined:* **Madagascar. Antananarivo:** Ambatolampy, Ankaratra, February 1957, *Bosser,*
44 *J.M. 10748* (G, K, MO, P); Anjozorobe, December 1958, *Bosser, J.M. 12401a* (TAN); Ankaratra,
45 November 1955, *Bosser, J.M. 8665* (P,TAN); Antananarivo, May 1962, *Bosser, J.M. 16304* (P);
46 Antananarivo, *Gillard s.n.* (P); Antanifotsy, Ambohimandroso, December 1955, *Bosser, J.M. 8900* (P,
47 TAN); Antsampanrano, Ankaratra, December 1963, *Bosser, J.M. 18490* (P, TAN); Antsirabe, May
48 1913, *Perrier de la Bâthie, H. 15797* (P); Behenjy, May 1962, *Bosser, J.M. 15427* (P, TAN); Carion,
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10 December 1958, *Bosser, J.M. 12401b* (P); Carion, October 1959, *Bosser, J.M. 13256b* (P); Faratsiho,
11 entre Ambatondradama et Ambatofotsy, 26 December 1912, *Viguiier, R. & Humbert, H. 1624* (P);
12 Iaranandriana, January 1954, *Bosser, J.M. 7198* (P); Iaranandriana, January 1954, *Bosser, J.M. 7202*
13 (P,TAN); Manjakatombo, 19 December 1950, *Benoist, R. 475* (P); PK 28 route du sud, April 1962,
14 *Bosser, J.M. 15572* (P); PK 39 route du sud, May 1962, *Bosser, J.M. 15474* (P); Tsiafajavona, February
15 1957, *Bosser, J.M. 10760* (P); Ibity, June 1967, *Morat, P. 2864* (P, TAN). **Fianarantsoa:** Andringitra,
16 1924, *Humbert, H. 3647* (P); Andringitra, 28 November 2013, *Nanjarisoa, O.P. et al. 77* (K, P, TAN);
17 Andringitra, 13 December 2013, *Vorontsova, M.S. et al. 1245* (TAN); Andringitra, 13 December 2013,
18 *Vorontsova, M.S. et al. 1248* (TAN); Andringitra, 13 December 2013, *Vorontsova, M.S. et al. 1259*
19 (TAN); Andringitra, Andohariana, 13 January 1971, *Guillaumet, J.L. 3745* (P); Andringitra, 28
20 November 2013, *Nanjarisoa, O.P. et al. 76* (K,TAN); Fandriana, Miarinavaratra, January 1953, *Bosser,*
21 *J.M. 5071* (P); Manandriana, Ivato, January 1964, *Bosser, J.M. 18791* (P); Pic Boby, Andringitra, April
22 1964, *Bosser, J.M. 19441* (P, TAN); Andringitra, 25 November 2009, *Couch, C. et al. 589* (K, P);
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41 LABX-0041) and LABEX "CEBA" (ANR-10-LABX-25-01). Curators of the Muséum National d'Histoire
42 Naturelle herbarium (P) and Parc de Tsimbazaza herbarium (TAN) made specimens available. Lucy
43 Smith made the beautiful drawings, and Sarah Ficinski created the distribution map. We are grateful
44 to Cassiano Welker (Universidade Federal de Uberlândia), Michael R. McKain (University of Alabama)
45 and Elizabeth Kellogg (Donald Danforth Plant Science Center) for discussion on Andropogoneae
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10 evolution and the genus *Eulalia*. Thanks also to Emmet Judziewicz and an anonymous reviewer
11 whose comments improved this manuscript.
12

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12 FIGURE LEGENDS

13 **Figure 1.** Field photographs of *Lasiorchachis*. A, *Lasiorchachis viguieri* in Andringitra National Park,
14 *Nanjarisoa et al. 77*; B, *Lasiorchachis hildebrandtii* in Alaotra-Mangoro; C-E *Lasiorchachis perrieri* in
15 Itremo Protected Area, *Vorontsova et al. 1530*. Photographs by M.S. Vorontsova except B by Romer
16 Rabarijaona at www.inaturalist.org.
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21 **Figure 2.** Bayesian phylogenetic tree estimated for non-coding regions of 56 Andropogoneae
22 plastomes, including two *Lasiorchachis* spp. (in bold). Subtribe Saccharinae and the *Saccharum*
23 complex are highlighted. Filled circles at nodes indicate a posterior clade support of 0.95 and higher
24 with both non-coding plastome regions and coding regions; open circles indicate support only with
25 coding regions. See Figure S1 for precise node support values and plastome accession numbers.
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30 **Figure 3.** Bayesian phylogenetic tree estimated for the plastid regions *ndhF*, *rbcl* and *trnK/matK* for
31 Saccharinae species, including four *Lasiorchachis* accessions (in bold), and outgroup taxa. The
32 *Saccharum* complex is highlighted. Circles at nodes indicate a posterior clade support of 0.7 and
33 higher (open circles) or 0.95 and higher (filled circles).
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37 **Figure 4.** Schematic representation of Bayesian phylogenetic trees estimated for Andropogoneae
38 sequences of ITS (A) and eight low-copy nuclear regions (B-I). *Lasiorchachis* (arrow) and other clades
39 of interest of Saccharinae are highlighted. Triangle size is not proportional to the number of
40 collapsed tips. Sequences for two *Lasiorchachis* accessions were assembled from low-coverage
41 genome skims. All trees were rooted with *Arundinella*. The scale bar indicates 0.05 substitutions per
42 site, and circles at nodes indicate posterior support of 0.7 and higher (open) or 0.95 and higher
43 (filled).
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49 **Figure 5.** *Lasiorchachis hildebrandtii*. A, habit; B, junction between the leaf sheath and the left blade,
50 lateral view; C, ligule; D, inflorescence branch; E, spikelet pair; F – M, sessile spikelet; F, lower glume,
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10 ventral surface; G, lower glume, dorsal surface; H, upper glume, ventral surface; I, upper glume,
11 dorsal surface; J, lower lemma, ventral surface; K, lower lemma, dorsal surface; L, upper lemma,
12 ventral surface; M, upper lemma, dorsal surface. Scale bar: A = 4 cm, B, C = 4 mm, D = 5 mm, E = 2
13 mm, F – M = 1.6 mm. Drawn from *Descoings 218 (K)* by Lucy T. Smith.
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17 **Figure 6.** *Lasiorchachis perrieri*: A, habit at base; B, flowering habit, culm continued from A; C, ligule;
18 D, inflorescence branch; E, spikelet pair; F – R, sessile spikelet; F, lower glume, ventral surface; G,
19 lower glume, dorsal surface; H, upper glume, ventral surface; I, upper glume, dorsal surface; J,
20 spikelet with the glumes removed, lateral view; K, lower lemma, ventral surface; L, lower lemma,
21 dorsal surface; M, lower palea, ventral surface; N, lower palea, dorsal surface; O, upper lemma,
22 ventral surface; P, upper lemma, dorsal surface; Q, lodicules; R, immature caryopsis. Scale bar: A, B =
23 4 cm, C, D = 5 mm, E = 2.2 mm, F – R = 2 mm. Drawn from *Bosser 1899b (K)* by Lucy T. Smith.
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30 **Figure 7.** *Lasiorchachis viguieri*. A, habit; B, ligule; C, inflorescence branch; D, spikelet pair; E – N,
31 sessile spikelet; E, lower glume, ventral surface; F, lower glume, dorsal surface; G, upper glume,
32 ventral surface; H, upper glume, dorsal surface; I, spikelet with the glumes removed, lateral view; J,
33 lower lemma, ventral surface; K, lower lemma, dorsal surface; L, upper lemma; M, lodicule; N,
34 gynoecium; O – T, pedicelled spikelet; O, lower glume, ventral surface; P, lower glume, dorsal
35 surface; Q, upper glume, ventral surface; R, upper glume, dorsal surface; S, lower lemma; T, upper
36 lemma. Scale bar: A = 4 cm, B = 1.6 mm, C = 7 mm, D – T = 2.2 mm. Drawn from *Nanjarisoa 76 (K)* by
37 Lucy T. Smith.
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44 **Figure 8.** Distribution of *Lasiorchachis* including occurrence records from the specimens studied here
45 and field observations. Administrative province boundaries are marked in grey.
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48 **Appendix 1.** Sequences assembled as part of this study. [to be added after review]
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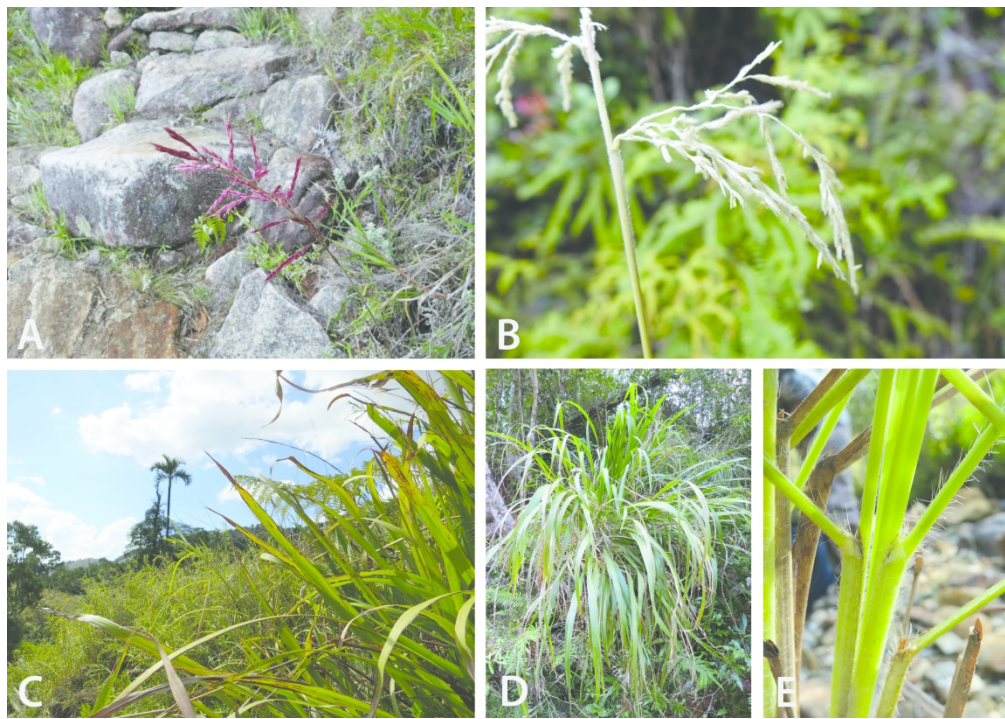
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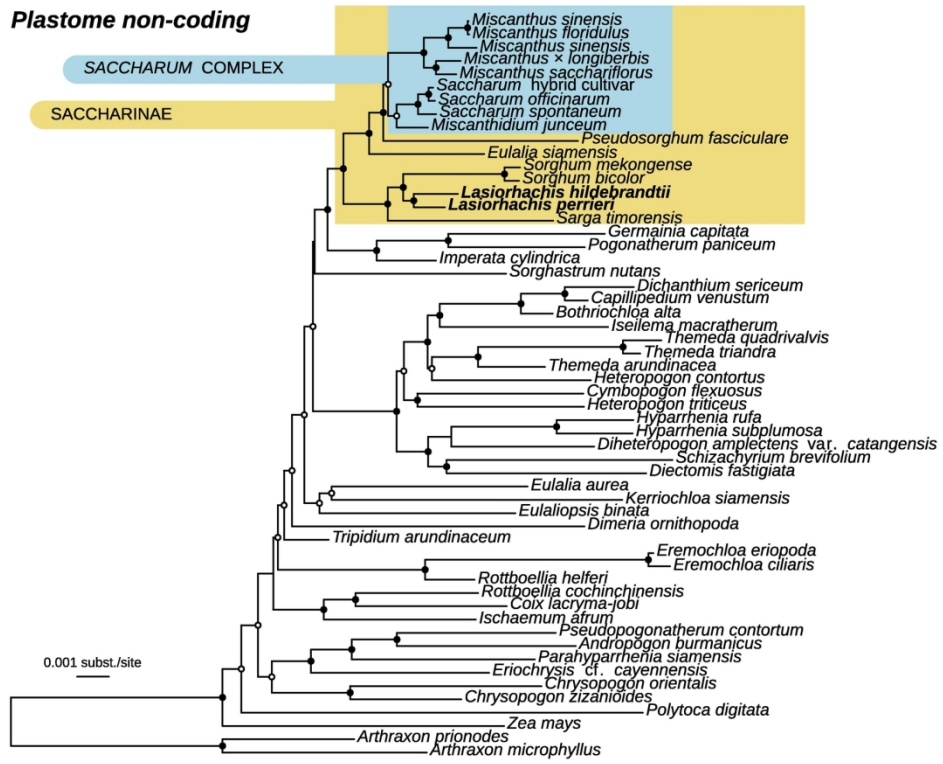
10 **Figure S1.** Detailed versions of Bayesian phylogenetic trees estimated for coding (A) and non-coding
11 plastome regions, with Bayesian posterior support values at nodes and plastome accession numbers.

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14 **Figure S2.** Detailed versions of Bayesian phylogenetic trees estimated for ITS (A) and eight low-copy
15 nuclear regions (B-I), with Bayesian posterior support values at nodes and accession numbers.
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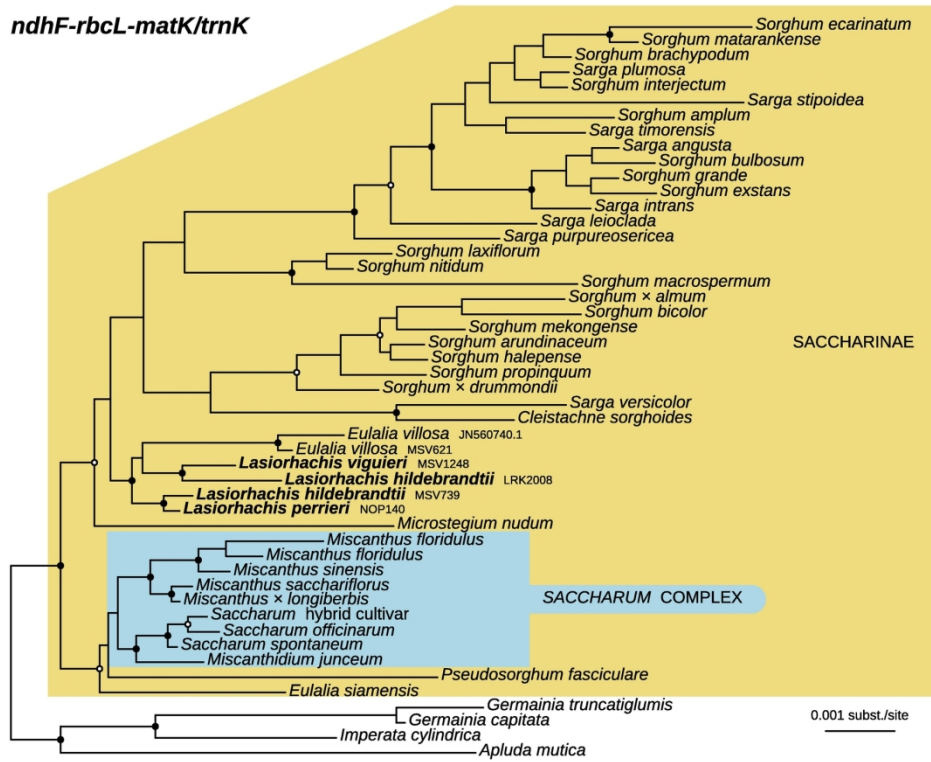
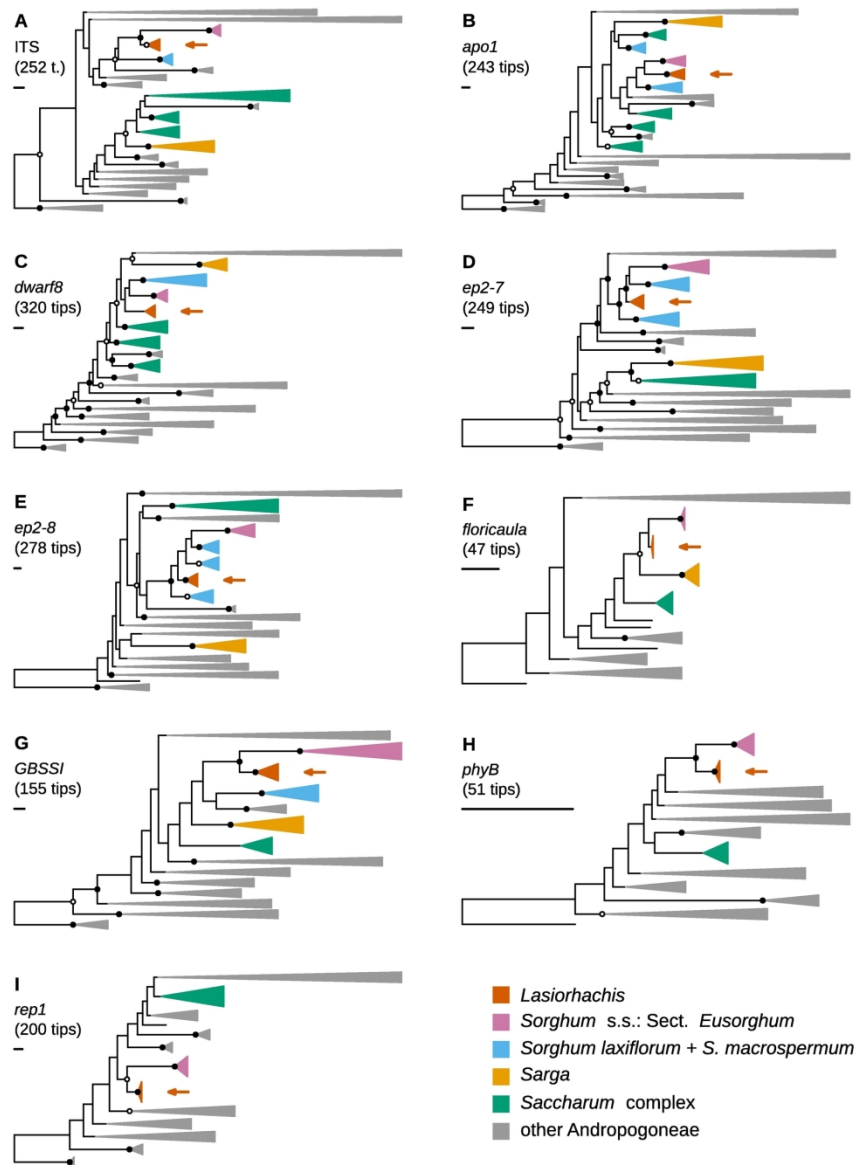


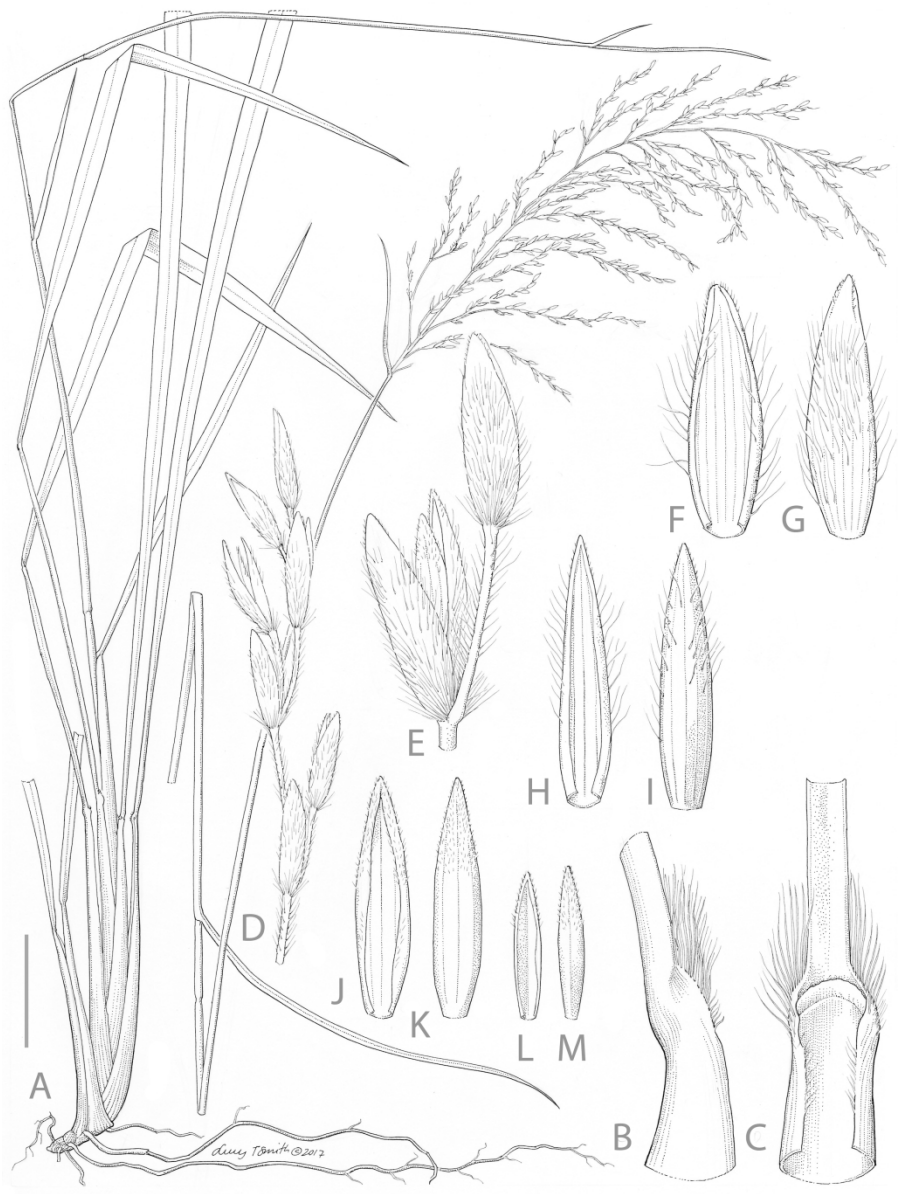
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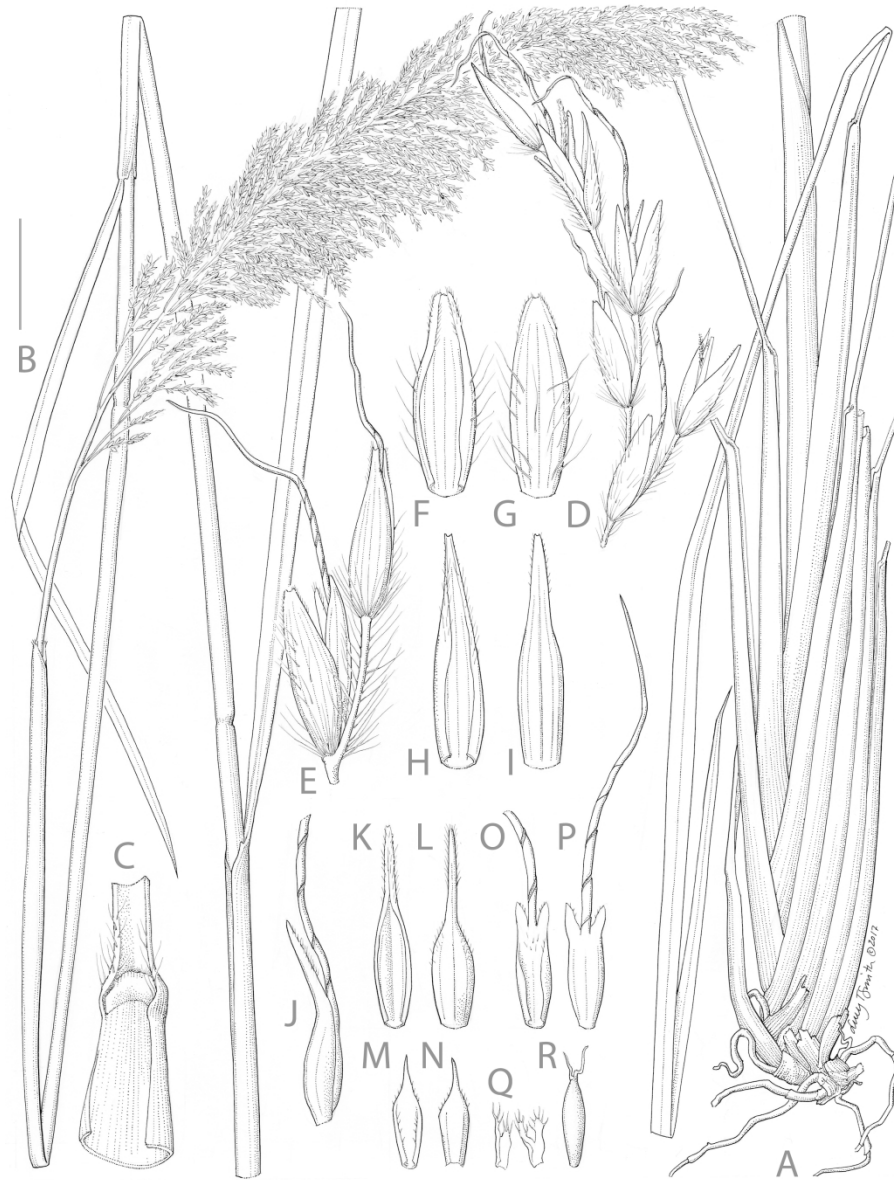
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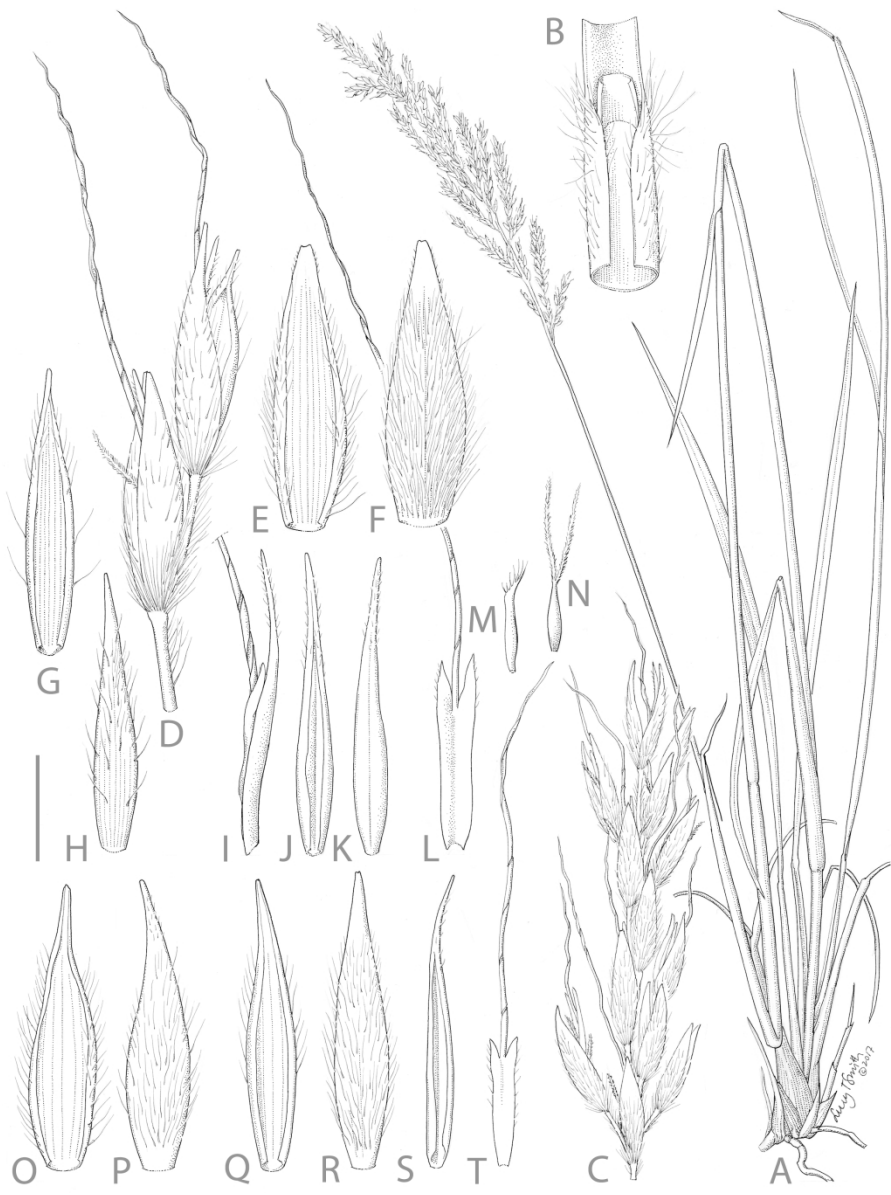
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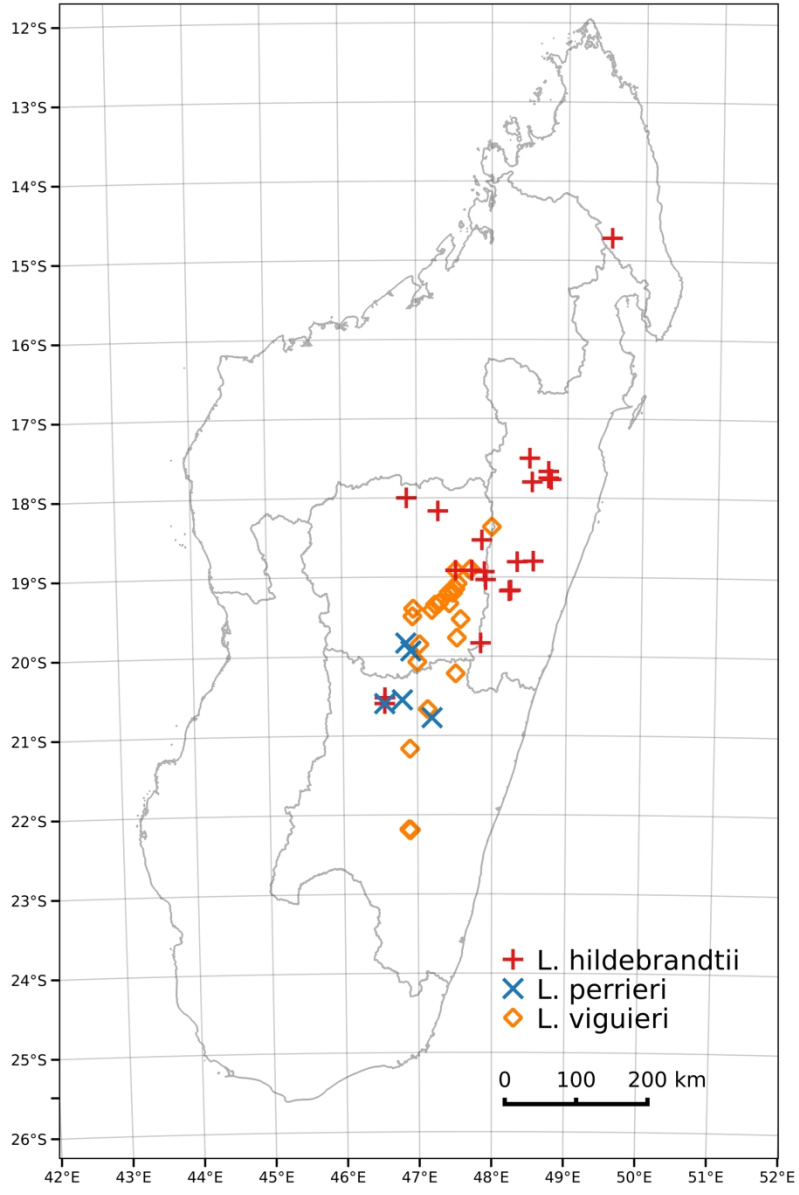


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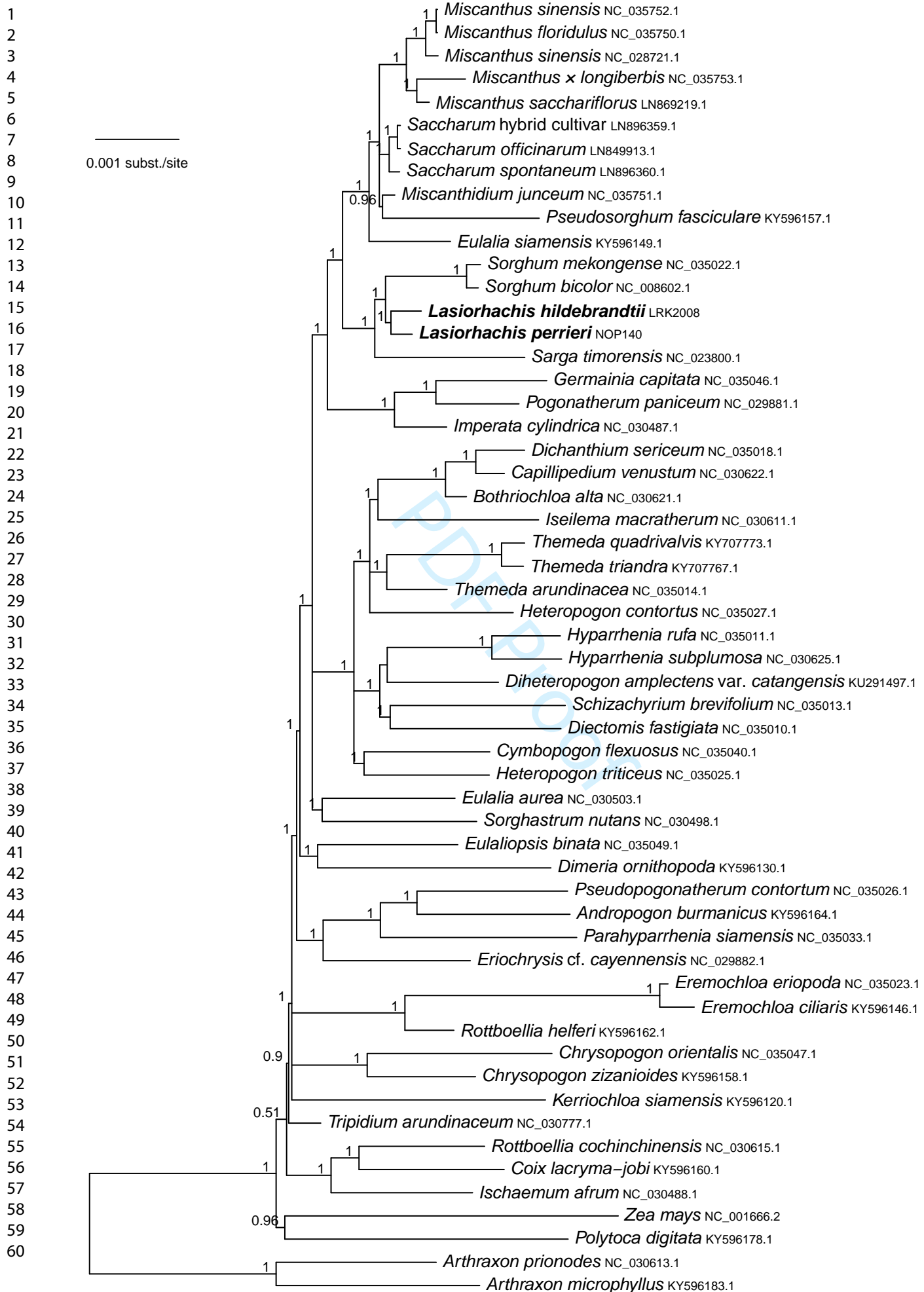


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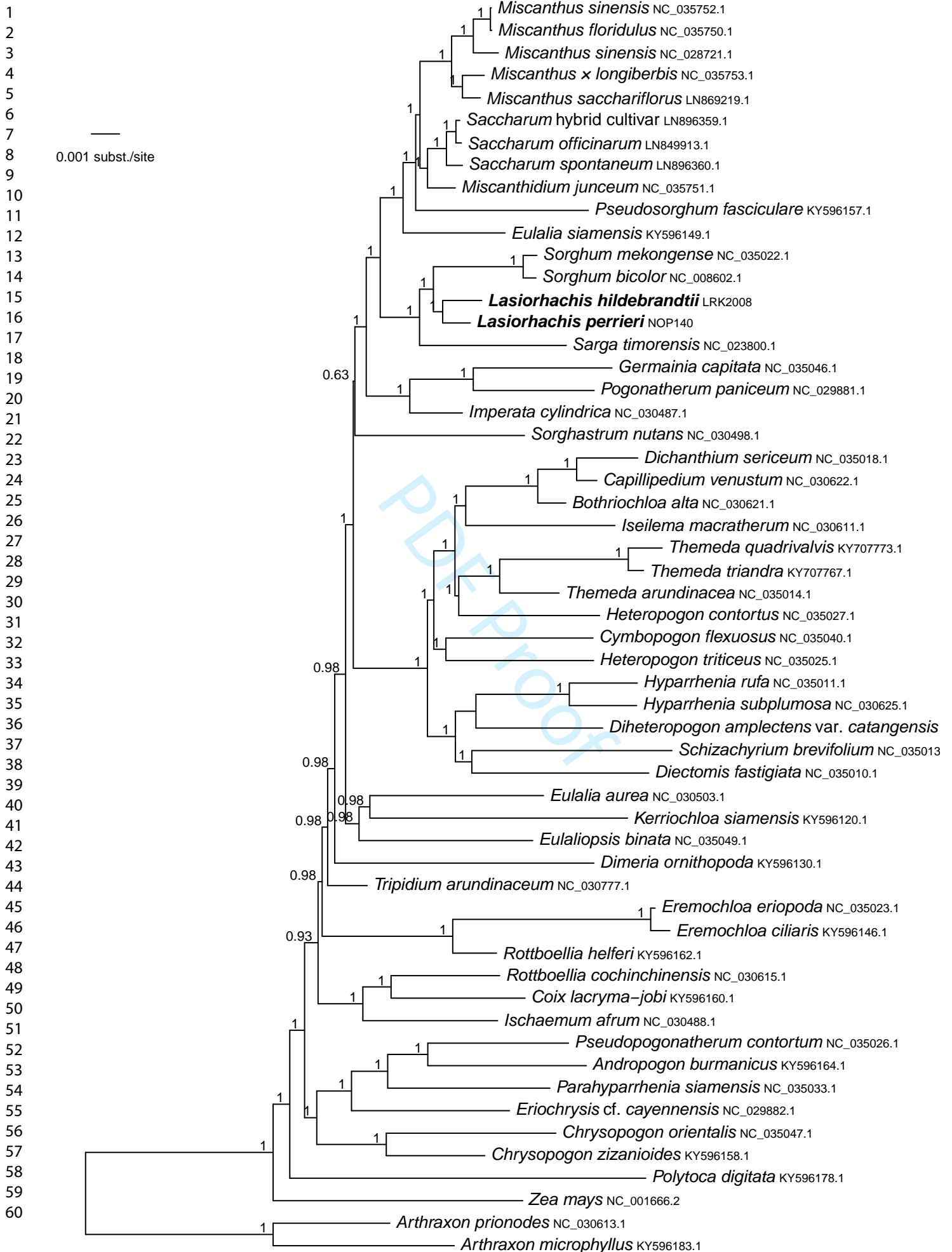


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A – Plastome CDS

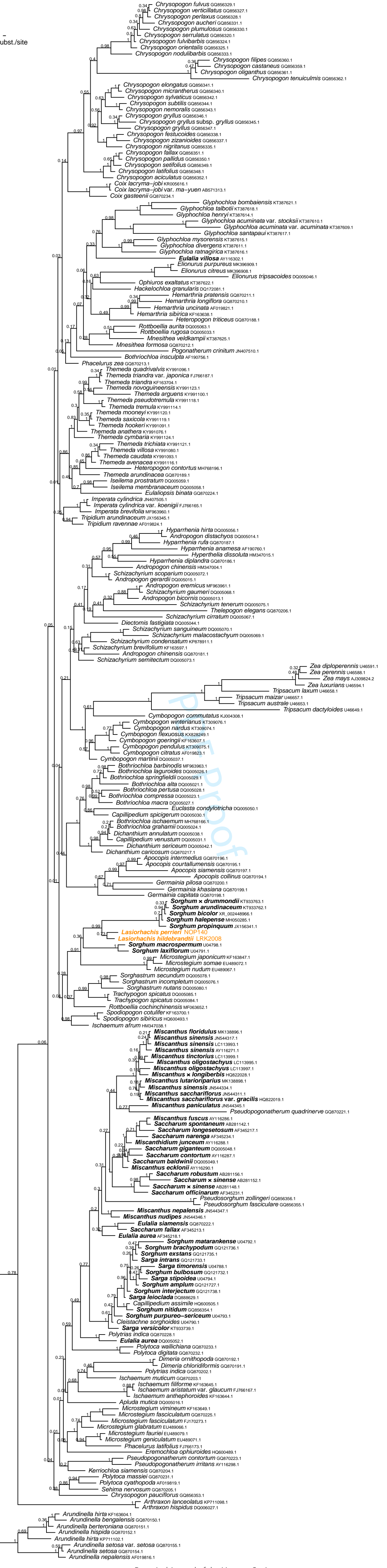


B – Plastome non-coding



A - ITS

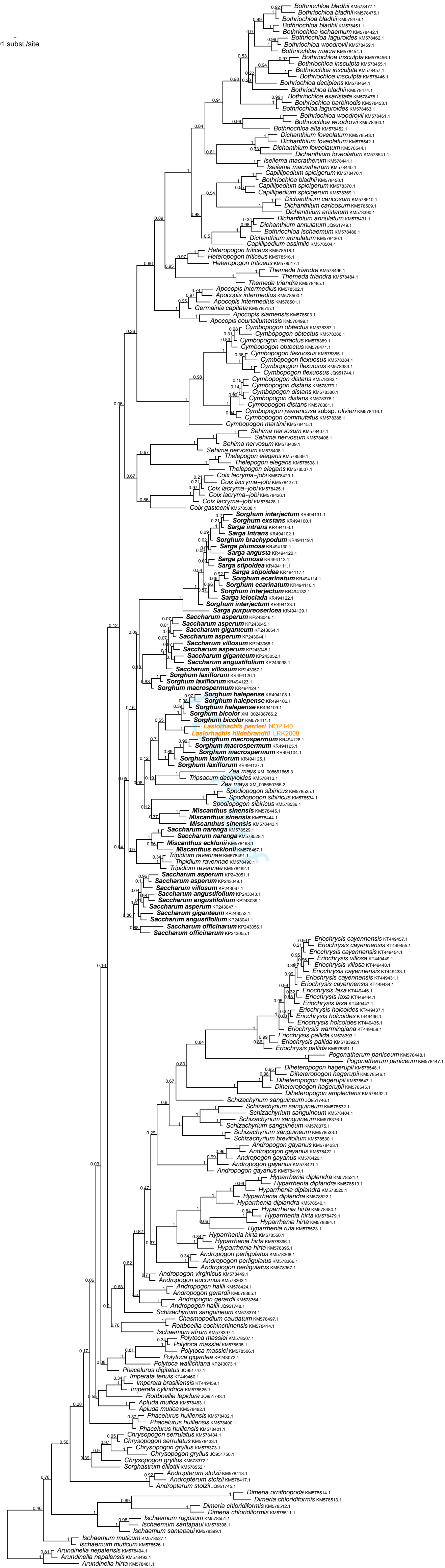
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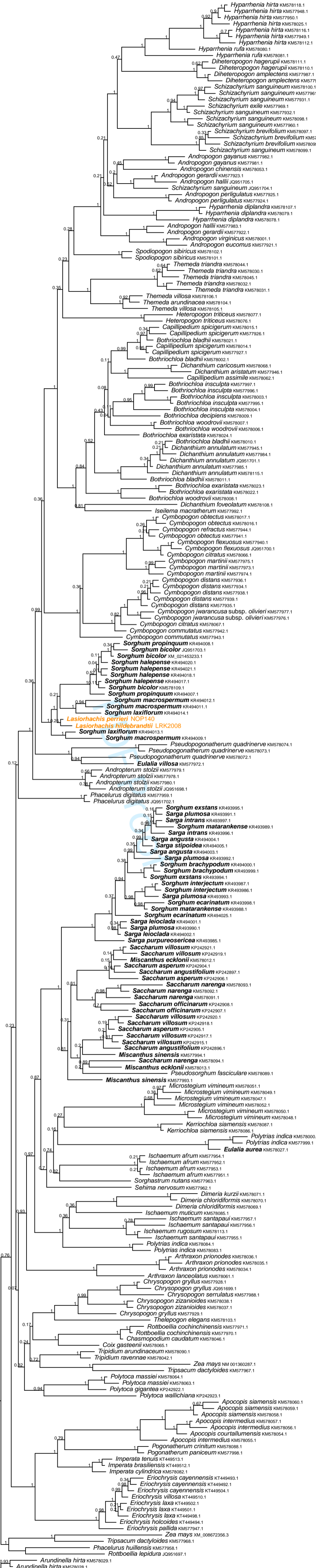
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D - ep2-7

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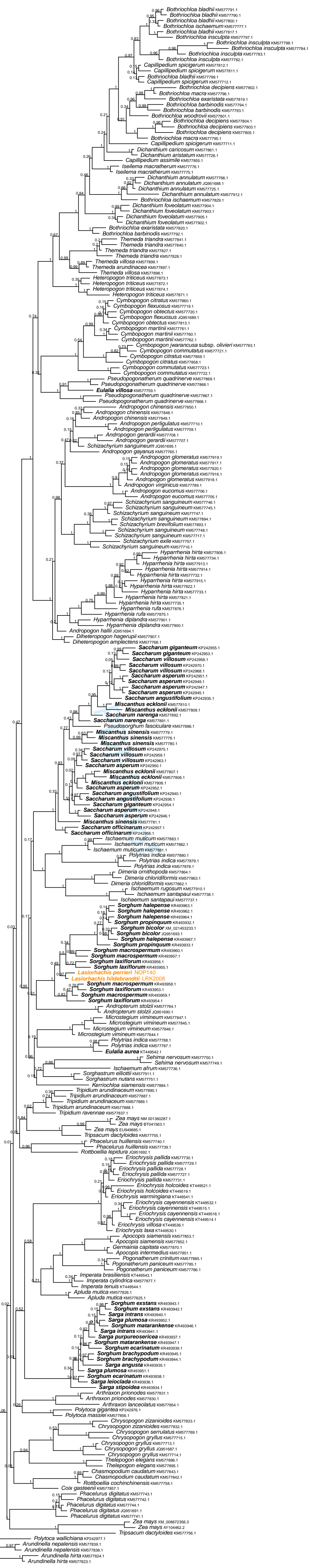
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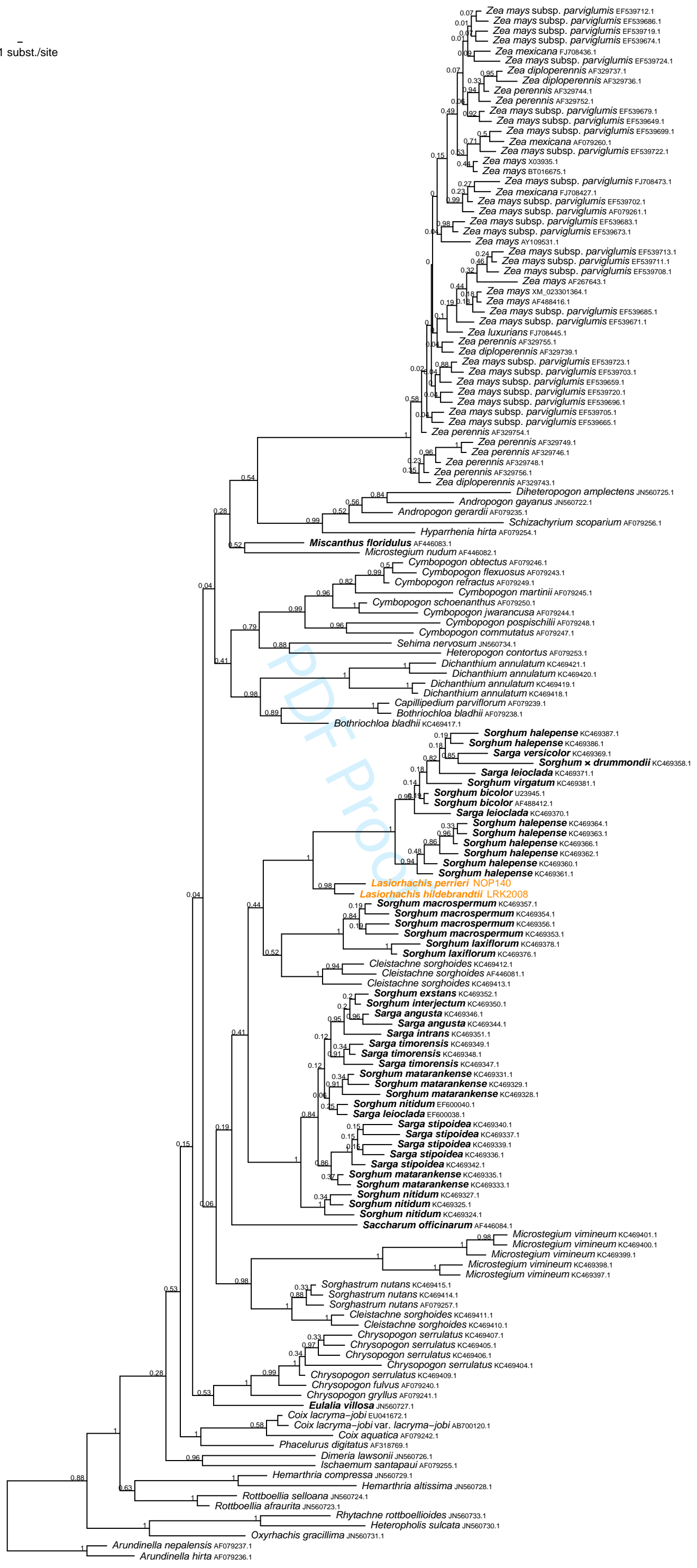
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