

On the Validity of the Saccharum Complex and the Saccharinae Subtribe: A Re-assessment

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Abstract

The ‘Saccharum Complex’ represents an hypothetical collective of species that were supposedly responsible, through interbreeding, for the origins of sugarcane. Though recent phylogenetic studies have cast doubt on the veracity of this hypothesis, it has cast a long shadow over the taxonomics of the Andropogoneae and the Saccharinae subtribe. Though evidence suggests that *Saccharum* s.s. is comprised of only three true species, according to Kew’s GrassBase there are as many as 34 species in *Saccharum* s.l. Our recent work has shown that many of these species are millions of years divergent from *Saccharum*. As the *Saccharum* complex represents the species that sugarcane breeders attempt to introgress into sugarcane, and as the Saccharinae, in its current form, covers almost 12 million years of Andropogoneae evolution an update on the extents of the Taxonomic and customary groupings is much needed. Based on the latest sequence based phylogenies and the inclusion of traditional taxonomics we develop an integrated view of the Saccharinae + *Saccharum* complex species in the context of the major groupings within the Andropogoneae. We use this phylogeny to re-circumscribe the limits of both the Saccharinae subtribe and the *Saccharum* complex group of interbreeding species.

Introduction

The Saccharinae subtribe is part of the Andropogoneae tribe of the PACMAD clade of Poaceae (true grasses). The Andropogoneae were defined by Dumortier (1824). Though the Saccharinae was first coined in 1815 by Knuth (1815). However, his definition was deemed invalid and, formally the Saccharinae were defined by Grisebach (1846). They type species for the Saccharinae is *Saccharum officinarum* L.

Though the ‘*Saccharum* complex’ is an informal definition initially intended to represent those species thought to have contributed to the origins of sugarcane, it has had such an undue influence on taxonomics that the origins and development of the concept needs to be understood. Muckergee (1957) first coined the term ‘*Saccharum* complex’ where he pointed out that the four genera

Saccharum, *Erianthus*, *Sclerostachya* and *Narenga* constituted a closely related inter-breeding group concerned in the origin of sugarcane. Daniels et al. (1975) included *Miscanthus* section *Diandra* to the 'Saccharum complex' as it was thought to be involved in the origin of *Saccharum*. This concept was further refined by Clayton and Renvoize (1986) who extended the subtribe Saccharinae to include the genera: *Erianthus* Michaux, *Eriochrysis* P. Beauv., *Eulalia* Knuth, *Eulaliopsis* Honda, *Homozeugos* Stapf, *Imperata* Crillo, *Lophopogon* Hack, *Microstegium* Nees, *Miscanthus* Andersson, *Pogonatherum* P. Beauv., *Polliniopsis* Hayata, *Polytrias* Hack, *Saccharum* and *Spodiopogon* Trin. (as a result many of these genera have been re-classified as *Saccharum* and genus *Saccharum* now comprises between 35 and 40 species, mostly from the tropics and sub-tropics). The suggestion being, that all these genera are closely allied to *Saccharum* and were actually involved in the evolution of sugarcane's ancestors. This paper has had considerable taxonomic influence and, for example, both the New World and Old World genera of *Erianthus* as well as *Narenga porphyrocoma* are now all included within *Saccharum sensu lato*.

This definition has also significantly influenced the delimiting of genus *Saccharum* itself, with many authorities also treating *Saccharum* in a broader sense (*Saccharum sensu lato*). For example, Kew's GrassBase currently recognizes 36 species within *Saccharum* (<http://www.kew.org/data/grasses-db/sppindex.htm#S>) and Tropicos presents 189 distinct species names under the *Saccharum* genus (<https://www.tropicos.org/name/Search?name=Saccharum>) though many of these names are synonyms. Indeed, the circumscription of *Saccharum* remains highly controversial and has changed significantly over the past century. Several phenetic studies have indicated strong molecular differentiation between *Saccharum* and *Erianthus* (Besse et al., 1998; Nair et al., 2005; Selvi et al., 2006). Conversely, a phylogenetic analysis based on the internal transcribed spacer (ITS) of the nuclear ribosomal DNA (Hodkinson et al., 2002) found no support for this division, even though this study suggested that *Saccharum s.l.* is polyphyletic. Even the taxonomic delimitation between *Saccharum* and *Miscanthus* is not clear, with intergeneric hybrids occurring between them (Clayton & Renvoize, 1986; Hodkinson et al., 2002).

As the Saccharum complex/Saccharinae comprises the gene pool that sugarcane breeders use when attempting to introgress useful characteristics into sugarcane the true relationship of these genera and species to each other, as determined by molecular techniques is of considerable import and relevance. This is especially the case, as modern molecular techniques do not support the concept of a 'saccharum complex' (D'Hont et al. 2008). Moreover, there is increasing evidence that *Saccharum* is a well-defined lineage that diverged over a long evolutionary period from the lineages leading to the New World *Erianthus* and Old World *Miscanthus* genera (Grivet et al. 2004; Estep et al. 2014; Lloyd Evans & Joshi, 2016).

Kellogg (2013) also added *Euclasta*, *Spathia*, *Lophopogon* and *Leptatherum* to the Saccharinae. However, the most recent treatment of the Saccharinae is that of Soreng et al. (2017) where the Saccharinae subtribe is circumscribed to include the following genera: *Agenium*, *Asthenochloa* (introduced as a member of the Sorghinae), *Cleistachne*, *Erianthus*, *Eriochrysis* (syn *Lepidosaccharum*), *Euclasta* (syn *Indochloa*), *Eulalia*, *Hemisorghum*, *Homozeugos*, *Imperata*, *Lasiorhachis*, *Leptatherum* (syn *Polliniopsis*), *Miscanthidium*, *Miscanthus*, *Narenga*, *Polytrias*, *Pseudodichanthium*, *Pseudopogonatherum*, *Pseu-*

dosorghum, *Saccharum*, *Sclerostachya*, *Sorghastrum*, *Sorghum*, *Trachypogon*, *Tripidium*, *Veldkampia*.

Some of these genera are clearly not closely related to *Saccharum*. Indeed, recent phylogenetic studies indicate that *Tripidium* is over 11 million years divergent, from *Saccharum* with *Eriochrysis* being even more divergent (Lloyd Evans et al., 2019). Low copy number phylogenetics indicates that genus *Sorghum* is not monophyletic (Estep et al. 2014, Lloyd Evans et al. 2019) and ITS phylogenetics demonstrates that *Microstegium* is not monophyletic (Snyman et al. 2018). Chloroplast-based phylogenetics diverges from low copy number phylogenetics and ITS-based phylogenetics (Lloyd Evans et al. 2019, Snyman et al. 2018) demonstrating that reticulate (network) evolution is commonplace in the Andropogoneae and the Saccharinae. As a result, the current circumscription of the Saccharinae is in dire need of review and updating based on the latest phylogenetics.

Other examples of clearly misplaced taxa are *Saccharum* (*Lasiorrhachis*) *hildebrandtii*, which whole chloroplast analysis clearly places within *Sorghum* (Piot et al. 2018). Extended ITS phylogenetics places both *Saccharum hildebrandtii* and *Saccharum perrieri* (Lloyd Evans and Hughes 2020) within *Sorghum*.

Other species are not well studied, but are probably the most closely related to *Saccharum*. These include *Narenga*, *Saccharum longisetosum* (syn *Erianthus rockii*), *Miscanthus nepalensis*, *Miscanthus nudipes*, *Erianthus fulvus* and *Narenga fallax*. Some workers (Welker et al. 2015) place the South American *Erianthus* species, as exemplified by the type, *Erianthus giganteus* (Walter) P. Beauv. within *Saccharum*, though the case is not yet proven.

It is clear that the extent of the Saccharum complex requires a new circumscription. We present an ITS-based phylogeny that places the species most closely related to *Saccharum* in their taxonomic context. We also employ a text searching and community based approach to analyze the taxonomic placement of those genera currently placed in *Saccharum* and develop a consensus phylogeny based on a combination of ITS and nuclear low copy number gene phylogenetics leading to the most comprehensive molecular view of the relationships between purported members of the Saccharinae subtribe developed to date.

Results

ITS-based Phylogeny

The ITS-based phylogeny (Figure 1) places the species most closely related to *Saccharum* within their taxonomic context. *Miscanthus* (along with *Pseudosorghum*) forms an outgroup to *Saccharum* and its allies. The remaining species are sister to *Saccharum s.s.* and can be divided into four distinct groupings. The outgroup for this clade is a novel clade formed from *Narenga*, *Miscanthus* and *Erianthus* species. Sister to this grouping are the *Erianthus* species from the Americas. Sister to *Erianthus* are the African *Miscanthidium* species and a novel grouping of *Narenga porphyrocoma*, *Erianthus rockii* and *Miscanthus fuscus*.

Combined Text search, Taxonomic and Phylogenetic Analysis.

***Euclasta*:** *Euclasta* was introduced into the Saccharinae by Soreng et al. (2017) as a member of the Sorghinae. However, the The ITS phylogeny of Sk-

endzic et al. (2007) places *Euclasta* as sister to *Bothriochloa*. This is a member of the Andropogoninae and last shared a common ancestor with *Saccharum*

***Pseudodichanthium*:** No taxonomy could be found, but the closest ally is *Dichanthium* and some workers consider *Dichanthium serrafalcoides* (T.Cooke & Stapf) Blatt. & McCann a synonym for *Pseudodichanthium serrafalcoides* (T. Cooke & Stapf) Bor. *Pseudodichanthium* was removed from *Dichanthium* as *Pseudodichanthium* differed from other *Dichanthium* species in appearance, texture and disposition of the glumes, in the pedicellate spikelet being larger than the sessile, and in the winged glumes. It resembles the genus *Dichanthium* only in the imbricate spikelets of which the lower two or three are homogamous. Tiwar and Chrogha (2019) in their lectotypification of *Pseudodichanthium* placed the genus as closer to *Heteropogon*. However, *Heteropogon* and *Dichanthium* are allies, some 10.3 million years divergent from *Saccharum*.

***Pseudopogonatherum*:** In a whole chloroplast phylogeny, Arthan et al. (2017) placed *Pseudopogonatherum contortum* (as *Eulalia contorta*) within a clade containing *Andropogon burmanicus* and *Parahyparrhenia siamensis* that was sister to *Eriochrysis* and therefore last shared a common ancestor with *Saccharum* about 12 million years ago.

***Pseudosorghum*:** Estep et al. (2014) placed *Pseudosorghum* within the *Miscanthus* clade in their low copy number gene phylogeny. However, Arthan et al. (2017) in their whole chloroplast phylogeny placed *Pseudosorghum* as sister to *Eulalia* which would make it 10.1 million years divergent from *Saccharum*. The ITS phylogeny presented in this paper also supports *Pseudosorghum* as being sister to *Miscanthus*. It would therefore appear, as is the case for many Andropogoneae arose as the result of reticulate evolution, with differing genomic and plastome signals it may be appropriate to retain it within the Saccharinae.

***Veldkampia*:** The taxonomic position of *Veldkampia* is uncertain, though the original authors tentatively placed this single-species genus within *Saccharum* (Ibaragi & Kobayashi 2007). The reduction of the pedicellate spikelet to just the pedicel hints that this genus might be related to *Cleistachne*, though karyotype information would be required for confirmation.

***Spathia*:** Morphological studies place *Spathia* in a clade with *Eulalia* and *Germainia* (Kellogg and Watson 1992). However, recent molecular evidence does not support monophyly of and *Eulalia*+*Germainia* clade. If *Spathia* is closer to *Germainia*, then it is not within the Saccharinae. If it is more closely allied to *Eulalia* then it belongs to a group that is sister to the core Saccharinae.

***Erianthus*:** Typically, it is members of *Erianthus* sect *Ripidium* that are included in the *Saccharum* complex and not *Erianthus* as a whole. However, recently sufficient data has become available to examine the three main branches of *Erianthus*: *Erianthus* sect *Ripidium*, *Erianthus* species from the Americas (currently part of *Saccharum sensu lato*) and the trans-Himalayan *Erianthus* species (as exemplified by *Erianthus rockii* [syn *Saccharum longisetosum* and *Erianthus fulvus*]). Our recent analysis of *Erianthus* sect *Ripidium* demonstrated that *Erianthus* is polyphyletic and that members of *Erianthus* sect *Ripidium* more properly belong to genus *Tripidium* which is 12 million years divergent from *Saccharum* and is more closely related to *Phacelurus* (a genus of African and Eurasian grasses), (Lloyd Evans et al. 2018). *Erianthus* species from the Americas form a distinct clade that is sister to African *Miscanthidium* species and *Narenga* (including *Erianthus rockii*. The trans-Himalayan species (including *Erianthus fulvus* form an outgroup to all the other clades (Figure 1, Figure 2).

Eriochrysis: this genus is even more divergent from *Saccharum* than *Tripidium* and should be excluded from the *Saccharum* complex as it cannot naturally inter-breed with *Saccharum* (Lloyd Evans et al. 2019). The genus should also be excluded from the Saccharinae.

Eulalia: is sister to *Sorghastrum* and forms an outgroup to the core Saccharinae. At over 7 million years divergent from *Saccharum* it must be excluded from the *Saccharum* complex (Welker et al 2014). However, being in a grouping sister to the Saccharinae it might still be included in this sub-tribe.

Microstegium: *Microstegium* is not monophyletic. One part of the genus is related to *Germainia*, whilst *Microstegium vimineum* groups with *Polytrias* and *Eulalia*. More research is needed, but ITS phylogenies place these as the immediate ancestors of the core Saccharinae. However, they are not within the natural hybridization window with *Saccharum* and should be excluded from the core Saccharinae and the *Saccharum* complex (Snyman et al. 2018; Lloyd Evans and Hughes 2020).

Polytrias: Like *Microstegium*, to which they are related, *Polytrias* species emerge as sister to *Microstegium vimineum* and the core Saccharinae, at least based on chloroplast analyses. However, ITS phylogenies place this genus as more distal to *Saccharum* (Lloyd Evans et al. 2019, Lloyd Evans and Hughes 2020).

Imperata: *Imperata* is an ancient hybrid. Its chloroplast phylogeny places it as sister to *Pogonatherum*, thus forming an outgroup to *Sorghum*. However, its genomic sequences (low copy number genes and ITS region) is much more divergent (at least 14 million years divergent from *Saccharum*) (Estep et al 2014; Lloyd Evans et al. 2018; Lloyd Evans and Hughes 2020).

Pogonatherum: Chloroplast phylogeny places *Pogonatherum* as sister to *Imperata* (Lloyd Evans et al. 2019).

Polliniopsis: (Now included in *Microstegium*, but see *Microstegium*, above). As no sequence data exists in NCBI for this genus, its position in Figure 1 is captured taxonomically as part of *Microstegium s.s.* and sister to *Apocypis* and *Germainia*.

Spodiopogon: Low copy number gene and ITS phylogenies place *Spodiopogon* as ancestral to *Sorghum* and the core Andropogoneae (Estep et al. 2014; Lloyd Evans and Hughes 2020).

Eulaliopsis: From whole chloroplast phylogenetic analysis *Eulaliopsis* is sister to *Dimeria* with this grouping last sharing a common ancestor with *Saccharum* 11.6 million years ago (Lloyd Evans et al. 2016) as a result it should be excluded from the Saccharinae and the *Saccharum* complex.

Homozeugos: No sequence data are currently available for this genus of African species. However, work by Gula II (1998) clearly placed *Homozeugos* as sister to *Trachypogon* and did not place this genus within the Saccharinae. *Trachypogon* is sister to *Germainia* and therefore a member of the Germainiinae and not the Saccharinae; the same holds true for *Homozeugos* (Kellogg and Birchler 1993). As ITS regions (NCBI: DQ005006) were available for *Trachypogon plumosus* these were added to the phylogeny of Snyman et al. 2018. The relative position of *Trachypogon* within the phylogeny was mapped to Figure 2 and the sister relationship of *Trachypogon* and *Homozeugos* was captured.

Lophopogon: No sequence data are currently available for this genus however, this genus of Indian plants is now placed within the Germainiinae (at least 11 million years divergent from *Saccharum*).

***Sorghum* and *Sarga*:** Based on whole chloroplast and chloroplast region phylogenetics, these genera were clustered as *Eusorghum* and *Parasorghum*, respectively. However, low copy number gene analyses and ITS analyses place *Sorghum* as sister to the core Andropogoneae and *Sarga* as sister to the core Saccharinae. When the core Andropogoneae and Saccharinae diverged some 7.5 million years ago hybridization events occurred between ancestral *Sarga* and *Sorghum* species. *Sarga* gained the *Sorghum* chloroplast type but retained its saccharinae-type genome (Estep et al 2014; Snyman et al 2017, Lloyd Evans et al. 2019, Lloyd Evans and Hughes 2020).

***Miscanthus*:** though this genus only diverged from *Saccharum* about 3.4 million years ago (Lloyd Evans and Joshi 2016) is clearly separate and divergent from *Saccharum* (with a base chromosome number of 19 as opposed to 10). It does, however, lie just within the window where wild hybridization with *Saccharum* is possible (Lloyd Evans and Joshi 2016). Chromosome analysis, however, indicate that only certain polyploid forms of *Miscanthus floridulus* are compatible with *Saccharum* hybridization (ref).

***Miscanthidium*:** Originally included within *Miscanthus*, there is now broad agreement that *Miscanthidium* forms a distinct and separate genus of African species (Hodkinson 2002). This genus is much more closely related to *Saccharum* (about 2 million years divergent) than *Miscanthus*. *Miscanthidium* should be included in a new definition of the Saccharinae.

***Narenga*:** *Narenga porphyrocoma* is the species that, from chloroplast analyses, is most closely related to *Saccharum*. Low copy number gene evidence indicates that it hybridized with an ancestral *Saccharum* species about 2 million years ago (Lloyd Evans et al. 2019). ITS phylogenetics (Figure 1) places this genus within a clade of genera with a base chromosome number of 15. Thus it is a member of the *Saccharum* complex but should probably be excluded from *Saccharum s.s.*

Sorghastrum, *Kerriochloa*, *Sehima*, *Ischaemum*, *Dimerium* (along with with *Microstegium vimineum* and *Polytrias indica* all form a clade (in low copy number gene phylogenies) that is sister to the Saccharinae. Whether these are members of the Saccharinae (or form a separate subtribe separate from it) is a matter of debate. What is clear is that these genera are more closely related to *Saccharum* than the majority of the genera described above, however these genera were never included in the *Saccharum* complex.

Discussion

Based on the phylogenies presented in this paper we can place all the purported members of the *Saccharum* complex in their proper phylogenetic position. Given a 3.4–4.2 million year window where hybridization between members of the Andropogoneae is possible in the wild (Lloyd Evans and Joshi 2016) (shaded in Figure 2), this means that the genera *Tripidium* (*Erianthus* sect *Ripidium*), *Eriochrysis*, *Imperata*, *Polliniopsis*, *Homozeugos*, *Lophopogon* and *Microstegium* (but see below for *Microstegium vimineum*) can be excluded from the *Saccharum* complex as they cannot naturally inter-breed with *Saccharum*. *Eulalia* can be excluded as it is sister to the core Andropogoneae and it is generally held that the core Andropogoneae form the division between species that are part of the Saccharinae and those which are not (Kellogg 2013). The positions of *Microstegium*

vimineum, *Pogonatherum* and *Imperata* are more unclear. Both chloroplast and nuclear phylogenetics place *Microstegium vimineum* as an outgroup to the core Saccharinae (but outside the wild hybridization window) whilst the exact phylogenetic positions of *Pogonatherum* and *Imperata* as complex ancient hybrids requires more work. What can be said definitely is that they should be excluded from the Saccharum complex, but their position as ancestral to the Saccharinae remains in question. Indeed, Comparing low copy number gene phylogenies with whole chloroplast and ITS phylogenies reveals that many of these genera are complex reticulate hybrids and that further analysis is required to elucidate the true taxonomic placement of these genera. However, taking nuclear phylogenies as representing the 'true' phylogenetic placement, what is clear is that they are neither members of *Saccharum* nor members of the Saccharum complex.

The revelation that *Sarga* species are an hybrid and that their nuclear phylogenetic signals place them as a natural outgroup to the Saccharinae is a major finding (Estep et al. 2014, Snyman et al. 2018, Lloyd Evans and Hughes 2020). Thus, a genus that was not even considered as being closely related to *Saccharum* emerges as being more closely related than $\frac{3}{4}$ of the purported members of the Saccharum complex.

Taxonomically, *Sarga* species (and this includes *Cleistachne sorghoides* are the most distal member of the Saccharinae subtribe. Within the core Saccharinae we have *Miscanthus*, *Miscanthidium*, *Narenga*, *Erianthus*, a trans-Himalayan grouping and *Saccharum* itself (Figure 1), (Lloyd Evans and Hughes 2020).

Pseudosorghum emerges as sister to *Miscanthus* (Lloyd Evans and Hughes 2020) and should also be included in the Saccharinae.

Thus, the Saccharinae subtribe has a true biological meaning and can be confirmed to contain at least four core genera, with the exact positioning of the two clades within *Erianthus* requiring further work (though they are part of the Saccharinae). As an outgroup, *Sarga*, *Asthenochloa* and *Cleistachne* should also be included within the Saccharinae whilst the potential inclusion of *Microstegium vimineum*, *Pogonatherum* and *Imperata* will require further study.

Our ITS-based phylogeny (Figure 1) positions several new species within the Saccharinae (see Figure 2 for a legend). We have a novel clade that is sister to *Saccharum sensu stricto*. This clade includes *Erianthus*, *Narenga*, *Miscanthidium* and a novel clade that contains Trans-Himalayan species and which warrants further investigation. Interestingly, the base chromosomal count for the majority of this group is 15 (Jensen et al. 1989; Sreenivasan & Sreenivasan 1989; Hoshino & Davidse 1988). The exception being the trans-Himalayan outgroup with a base chromosome count of 10 (Mehra & Sharna 1975). There is some evidence that many of the members of this clade are themselves hybrids (Lloyd Evans et al. 2018; Lloyd Evans & Hughes 2020). Thus the different base chromosome number and separate hybrid origins of this grouping would seem to exclude them from *Saccharum*. As such, *Saccharum sensu stricto* includes only those species within genus *Saccharum* itself. Though these species should all be included within the Saccharinae subtribe.

From Figure 2, as well as *Saccharum sensu stricto* and the n=15 clade, the Saccharinae should also include *Miscanthus* and *Sarga* (which also includes *Cleistachne* and *Asthenochloa*).

There is a clade that is sister to the core Saccharinae formed from *Sorghas-*

trum, *Ischaemum*, *Spodiopogon*, *Eulalia*, *Polytrias*, *Microstegium vimineum*, *Kerriochloa* and *Selima*. As this is proximal to the core Saccharinae (as compared with the Core Andropogoneae) by one argument this grouping should also be included within the Saccharinae subtribe. All other genera can be excluded as being either sister to the Core Andropogoneae or distal to them.

The 'Saccharum complex', as a potentially interbreeding group of species must be restricted to *Miscanthus*, *Miscanthidium*, *Pseudosorghum*, *Narenga*, *Erianthus s.s.*, *Narenga*, trans-Himalayan species and *Saccharum*. In effect, the Saccharum complex hypothesis has been overturned and it has no validity, at least in terms of these species being involved in the direct evolution of *Saccharum*. However, the core species within the re-defined 'Saccharum complex' (which now correspond to the core species of the Saccharinae subtribe) may still be of interest to sugarcane breeders. It should also be noted that whilst hybridization and reticulation (network evolution) is common in the Andropogoneae as a whole, we find no evidence for reticulate evolution in the genera *Saccharum*, *Miscanthus* and *Miscanthidium*, though it has occurred in *Narenga* and in the *Erianthus* species from the Americas and the trans-Himalayas.

Materials and Methods

Natural Language Processing:

A proprietary natural language processing algorithm (Lloyd Evans and Joshi 2020) was employed to search for, index and mine text corpora (abstracts, full length papers, pre-prints, books, PhD thesis and on-line materials) for keyword combinations of genera and species plus the keywords phylogenetics, phylogenomics, phylogeny, taxonomy, relationships in all combinations. The subset of identified publications were read manually and meaningful data were extracted. Phylogenies identified in the publications (if not available on-line or in a database) were manually converted to Newick format.

ITS-based Phylogeny

GenBank was searched with keywords to identify ITS sequences \approx 500bp corresponding to 'Core' Andropogoneae, *Sorghum*, *Sarga*, *Saccharum*, *Miscanthus* and those species identified as lying between *Miscanthus* and *Saccharum*. *Tripidium* (*Erianthus* sect *Ripidium*) was employed as an outgroup. Longer sequences of 900bp (Snyman et al. 2018; Lloyd Evans and Joshi 2020) were employed as a backbone. The alignment was optimized as described previously (Martin et al. 2017) and a Maximum-Likelihood phylogeny was generated with IQ-Tree (Nguyen et al. 2015). Branch supports were derived as SH-aLRT single branch tests and non-parametric bootstrap with IQ-Tree as well as Bayesian Inference with Mr Bayes (Huelsenbeck, and Ronquist 2001). Phylogenetic trees were drawn with FigTree (<http://tree.bio.ed.ac.uk/software/figtree/>) and finished with Inkscape (<https://inkscape.org/>). Species names and voucher accessions along with NCBI accessions for the sequences employed in the phylogeny are given in Supplementary Table 1.

Community Based Phylogeny

The phylogeny of Lloyd Evans et al. (2019) was employed as the backbone for the community tree. Additional phylogenies were integrated with the phangorn R framework (Schliep et al. 2016). Where possible, branch lengths of the backbone tree were retained and branch lengths of appended subtrees were scaled based on conserved common nodes. Individual nodes derived from academic literature were appended to the finished phylogeny using Archaeopteryx (Han & Zmasek 2009).

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