

# Delimiting the genera of the Ficinia Clade (Cypereae, Cyperaceae) based on molecular phylogenetic data

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## ABSTRACT

Generic delimitations in the Ficinia Clade of tribe Cypereae are revisited. In particular, we aim to establish the placement of annual species currently included in *Isolepis* of which the phylogenetic position is uncertain. Phylogenetic inference is based on two nuclear markers (ETS, ITS) and five plastid markers (the genes *matK*, *ndhF*, *rbcL* and *rps16*, the *trnL* intron and *trnL-F* spacer) data, analyzed using model based methods. Topologies based on nuclear and plastid data show incongruence at the backbone. Therefore, the results are presented separately. The monophyly of the smaller genera (*Afroscirpoides*, *Dracoscirpoides*, *Erioscirpus*, *Hellmuthia*, *Scirpoides*) is confirmed. However, *Isolepis* is paraphyletic as *Ficinia* is retrieved as one of its clades. Furthermore, *Ficinia* is paraphyletic if *I. marginata* and allies are excluded. We take a pragmatic approach based on the nuclear topology, driven by a desire to minimize taxonomic changes, to recircumscribe *Ficinia* to include the annual *Isolepis* species characterized by cartilaginous glumes and formally include all the *Isolepis* species inferred outside the core *Isolepis* clade. Consequently, the circumscription of *Isolepis* is narrowed to encompass only those species retrieved as part of the core *Isolepis* clade. Five new combinations are made (*Ficinia neocapensis*, *Ficinia hemiuncialis*, *Ficinia incomtula*, *Ficinia leucoloma*, *Ficinia minuta*). We present nomenclatural summary at genus level, identification keys and diagnostic features.

**Subjects** Biodiversity, Evolutionary Studies, Plant Science

**Keywords** Taxonomy, Phylogenetics, Cyperaceae, Classification, Nomenclature, Cape Flora, *Isolepis*, *Ficinia*

## INTRODUCTION

The paradigm shift towards recognition of genera as monophyletic entities has necessitated changes in generic circumscription (*Humphreys & Linder, 2009*). Within Cyperaceae, a number of changes have been made within the last decade, for example the merger of segregate genera into the paraphyletic core in *Carex* L. (*Global Carex Group (GCG), 2015*) and *Cyperus* L. (*Larridon et al., 2011a, 2011b, 2013, 2014; Bauters et al., 2014*). A number of genera have been found to be polyphyletic, especially in the tribe Schoeneae, resolved by reclassification of entities and naming of a number of lineages as

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new genera (Elliott & Muasya, 2017; Larridon et al., 2018; Larridon, Verboom & Muasya, 2018; Barrett, Wilson & Bruhl, 2019). Each of the four Cyperaceae genera recognized by Linnaeus (1753) has been reclassified over the years, with Linnaeus' circumscription of *Scirpus* L. as encompassing species with bisexual flowers and spiral glume arrangement representing the most heterogeneous assemblage. Embryo morphology data (Van der Veken, 1965; Goetghebeur, 1986; Semmouri et al., 2019) have unequivocally demonstrated that lineages with distinct morphology were included in *Scirpus*. In his seminal treatment of the family, Goetghebeur (1998) placed the 24 taxa previously named *Scirpus* by Linnaeus (1753) in the tribes Cypereae, Fuireneae and Scirpeae, with *S. sylvaticus* L. being the only species described by Linnaeus recognized as a true *Scirpus* and two of the species recognized as members of *Isolepis* R.Br.

Within tribe Cypereae, the Ficinia Clade (sensu Muasya et al., 2009b) comprises taxa whose placement has been most contentious. Goetghebeur (1998) diagnosed tribe Cypereae to include species characterised by either a Cyperus or a Ficinia type embryo, where glumes are arranged distichously (*Cyperus* and allies) or spirally (*Isolepis*, *Ficinia* Schrad., *Scirpoides* Ség.). Lineages bearing perianth segments were added to the clade based on molecular phylogenetic data, moving *Hellmuthia* Steud. from Chysitricheae (Vrijdaghs et al., 2006; Muasya et al., 2009a, 2009b), *Erioscirpus* Palla from Scirpeae (Yano et al., 2012), and recognizing southern African taxa previously placed in *Scirpus* as a distinct genus *Dracoscirpoides* Muasya (Muasya et al., 2012). Furthermore, the delimitation of *Scirpoides* has been altered to exclude *Afroscirpoides* García-Madr. and Muasya (García-Madrid et al., 2015) and the addition of two species that were ambiguously placed (Browning & Gordon-Gray, 2011; Reid et al., 2017). These genera are annual to perennial herbs, have basal leaves which vary in blade development, have considerable variation in inflorescence and floral morphology, and are diagnosed by a combination of morphological features (see Table 2 in García-Madrid et al., 2015).

Generic delimitation between *Isolepis* and *Ficinia* is based on few morphological characters. *Isolepis* have a varied habit (annual to perennial) and are widespread, whereas *Ficinia* are perennial and predominantly occur within the Cape flora and in Africa (Goetghebeur, 1998; Muasya & Simpson, 2002). A further distinction is the presence of a gynophore in *Ficinia*, but several species having a gynophore and occurring outside Africa were previously excluded from the genus. For example, the New Zealand iconic sand dune taxon (*Desmoschoenus spiralis* (A.Rich.) Hook.f.) is embedded within core *Ficinia* (as *Ficinia spiralis* (A.Rich.) Muasya and De Lange; Muasya & De Lange, 2010), and the more widespread *Ficinia nodosa* (Rottb.) Goetgh., Muasya and D. A. Simpson was retained in *Isolepis* despite having a well developed gynophore (Muasya, Simpson & Goetghebeur, 2000). Furthermore, *Isolepis* may not be monophyletic as *Ficinia* is one of the three to four clades recovered in *Isolepis* (Muasya & De Lange, 2010; García-Madrid et al., 2015; Hinchliff & Roalson, 2013; Spalink et al., 2016; Semmouri et al., 2019). Challenges on distinguishing *Ficinia* from *Isolepis* have persisted over the last 200 years, as evident from at least one in six of the currently recognized *Ficinia* species having a validly published epithet in *Isolepis* (Govaerts et al., 2020).

We use an expanded molecular phylogenetic study to investigate the generic limits in the *Ficinia* Clade. We infer the phylogenetic relationships and placement of ambiguously placed *Isolepis* species, namely (1) *I. hemiuncialis* (C. B. Clarke) J. Raynal and *I. incomtula* Nees—which have been previously recovered as sister to the core *Isolepis*/*Ficinia* clade; (2) *I. marginata* (Thunb.) A. Dietr. and allies (*I. antarctica* (L.) Roem. and Schult., *I. capensis* Muasya, *I. leucoloma* (Nees) C. Archer, *I. minuta* (Turrill) J. Raynal)—previously recovered as sister to core clade of *Ficinia*. The aim is to establish whether the genera in the *Ficinia* Clade, particularly *Isolepis* and *Ficinia*, are monophyletic, and to evaluate what characters diagnose the inferred (sub)clades.

## MATERIALS AND METHODS

### Ethics statement

Part of the specimens studied were collected during field expeditions predominantly in Western Cape province of South Africa funded by grants from the National Research Foundation and with additional support from the University of Cape Town. Permit to collect these specimens were issued by the Cape Nature authorities (CN35-28-5831). The other specimens studied are available in publicly accessible herbaria (BOL, K; B. Thiers, continuously updated, <http://sweetgum.nybg.org/science/ih/>) and voucher details provided in [Tables S1](#) and [S2](#).

### Nomenclature and taxonomy

A nomenclatural study including the taxonomic history of the genus and its species, critical for the correct coining of the new names and the proper use of prior ones, was performed. The electronic version of this article in Portable Document Format will represent a published work according to the International Code of Nomenclature for algae, fungi and plants, and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. In addition, new names contained in this work which have been issued with identifiers by IPNI will eventually be made available to the Global Names Index. The IPNI LSIDs can be resolved and the associated information viewed through any standard web browser by appending the LSID contained in this publication to the prefix “<http://ipni.org/>”. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS.

### Molecular study

The *Ficinia* Clade, our focus group, includes the genera *Afroscirpoides* (one species), *Dracoscripoides* (three species), *Erioscirpus* (two species), *Ficinia* (81 species), *Hellmuthia* (one species), *Isolepis* (75 species) and *Scirpoides* (four species). A total of 166 ingroup accessions were sequenced ([Table S1](#)), representing: one species of *Afroscirpoides* (100%), three *Dracoscripoides* (100%), one *Erioscirpus* (50%), 64 (plus three undescribed) *Ficinia* (78%), one *Hellmuthia* (100%), 57 *Isolepis* (plus some infraspecific taxa) (76%) and three *Scirpoides* (75%). The outgroup taxa, selected based on [Semmour et al. \(2019\)](#) and [Larridon et al. \(2021\)](#), consists of 114 accession ([Table S2](#)) representing the six genera of

tribe Fuireneae and the genus *Cyperus*, the only genus of the Cyperus Clade of tribe Cyperaceae after *Androtrichum* was recently synonymised with *Cyperus* (Pereira-Silva et al., 2020). The DNA extraction protocol, primers, and material and methods for PCR amplification and sequencing follow Viljoen et al., 2013.

Sequences were assembled and edited in Geneious R8 (<http://www.geneious.com>, Kearse et al., 2012), aligned using MAFFT 7 (Katoh, Asimenos & Toh, 2009; Katoh & Standley, 2013) with “maxiterate” and “tree rebuilding number” set to 100 (long run), afterwards, alignments were checked manually in PhyDE 0.9971 (Müller et al., 2010).

We first inferred the gene trees for each of the regions separately to identify potential incongruence. As there were no instances of conflict at well-supported nodes between the two nuclear markers, and between the five chloroplast markers, the matrices of the regions were concatenated into a nuclear dataset (Data S1) including ETS and ITS, and in a chloroplast dataset (Data S2) including the genes *matK*, *ndhF*, *rbcL* and *rps16*, the *trnL* intron and *trnL-F* spacer for the downstream analyses. PartitionFinder 2.1.1 (Lanfear et al., 2012) was used to determine an appropriate data-partitioning scheme from potential partitions that were defined a priori (in this case, each marker was treated as a separate partition), as well as the best-fitting model of molecular evolution for each partition, using the Bayesian Information Criterion. For the nuclear dataset, PartitionFinder confirmed the a priori data-partitioning scheme, and the GTR+I+ $\Gamma$  (invgamma) model of sequence evolution was determined to be the best-fitting model for the two nrDNA markers. For the chloroplast dataset, PartitionFinder suggested partitioning the data in four partitions (*matK+rps16*, *ndhF*, *rbcL*, the *trnL* intron and *trnL-F* spacer) and the GTR+ $\Gamma$  (gamma) model of sequence evolution was determined to be the best-fitting model for all partitions except for *rbcL* for which the GTR+I+ $\Gamma$  (invgamma) model was suggested.

Maximum likelihood (ML) analyses of the optimally partitioned data were performed using RAxML 8.2.10 (Stamatakis, 2014). The search for an optimal ML tree was combined with a rapid bootstrap analysis of 1,000 replicates. Additionally, partitioned analyses were conducted using Bayesian Inference in MrBayes 3.2.6 (Ronquist et al., 2012). Rate heterogeneity, base frequencies, and substitution rates across partitions were unlinked. The analysis was allowed to run for 100 million generations across two independent runs with four chains each, sampling every 10,000 generations. Convergence, associated likelihood values, effective sample size values and burn-in values of the different runs were verified with Tracer 1.5 (Rambaut & Drummond, 2007). The first 25% of the trees from all runs were excluded as burn-in before making a majority-rule consensus of the posterior distribution trees using the “sumt” function. All phylogenetic analyses were run using the CIPRES portal (<http://www.phylo.org/>; Miller, Pfeiffer & Schwartz, 2011), and were executed for both full and reduced sampling alignments. Trees were drawn using TreeGraph2 (Stöver & Müller, 2010).

### Morphological study

Herbarium specimens of BOL, BR, GENT, K, NBG, PRE (B. Thiers, continuously updated, <http://sweetgum.nybg.org/science/ih/>) were studied morphologically using a Leica

(Leica Microsystems, Wetzlar, Germany) binocular microscope. Measurements were made with a ruler and digital calipers (e.g., leaf and culm length), or using a binocular microscope with graticule (e.g., spikelet and glume length). When examining width, this was done near the middle of the organ (e.g., middle of the nutlet).

## RESULTS

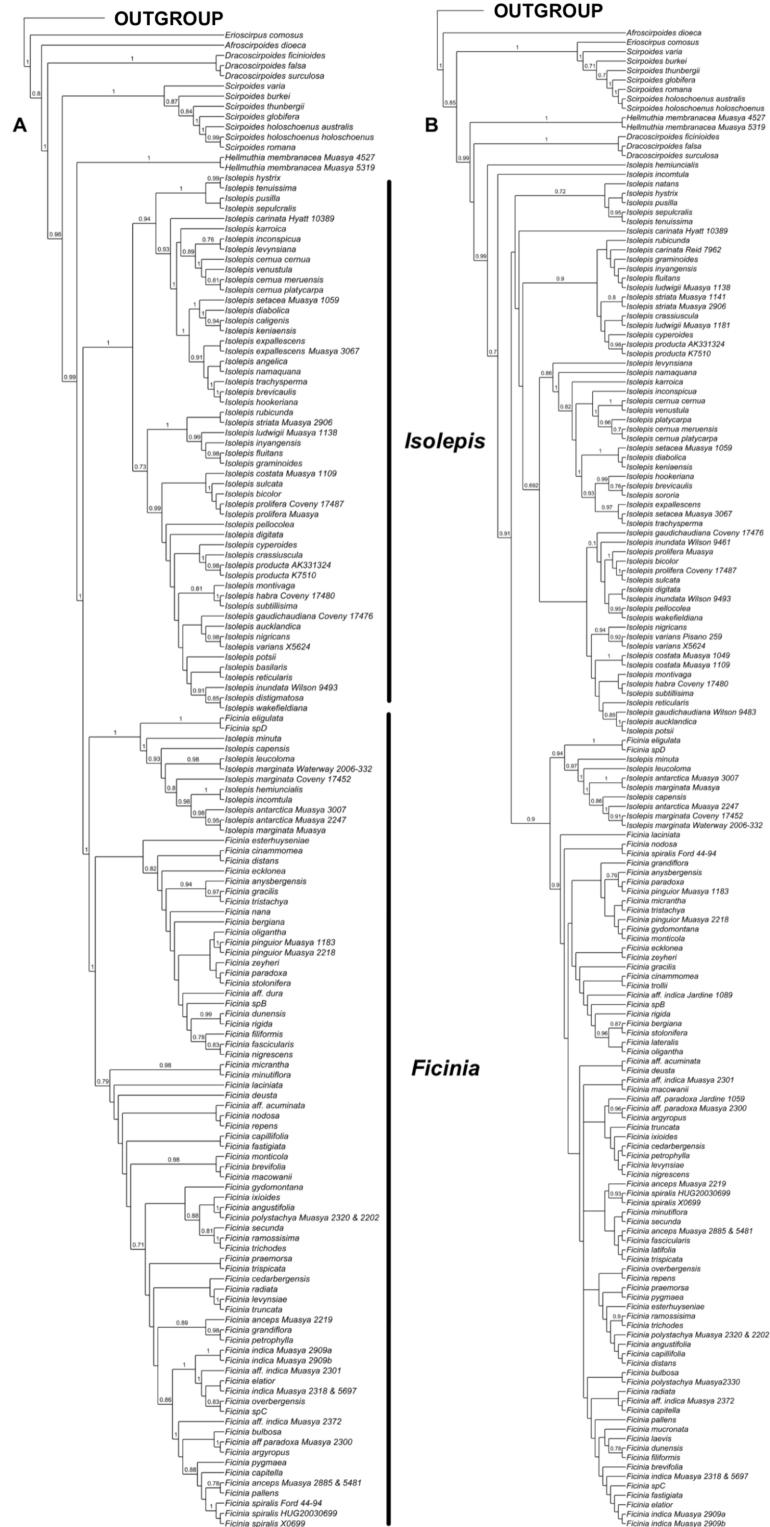
### Molecular study

Analyses of the individual markers show congruence within the nuclear and plastid markers, as well as congruence among the methods of analyses (Fig. S1). However, the nuclear (Fig. 1A) and plastid phylogenies (Fig. 1B) had conflicting backbone topologies and are therefore presented separately. Regardless, there is strong support in both data sets for the tribe Cypereae with the *Cyperus* and *Ficinia* clades as sister (Figs. S1–S4). In the plastid topology (Fig. 1B), *Afroscirpoides* diverged first, then strongly supported sister clades comprising (i) *Erioscirpus* sister to *Scirpoides*, and (ii) a clade comprising *Hellmuthia*, *Dracoscirpoides*, *Isolepis* and *Ficinia*. In the nuclear topology, there is a grade showing successive divergence starting with *Erioscirpus*, *Afroscirpoides*, *Dracoscirpoides*, *Scirpoides*, *Hellmuthia*, then *Isolepis* and *Ficinia*. In both analyses, there is strong support for the monophyly of the *Dracoscirpoides*, *Hellmuthia* and *Scirpoides*, but *Isolepis* is paraphyletic with *Ficinia* as one of the clades.

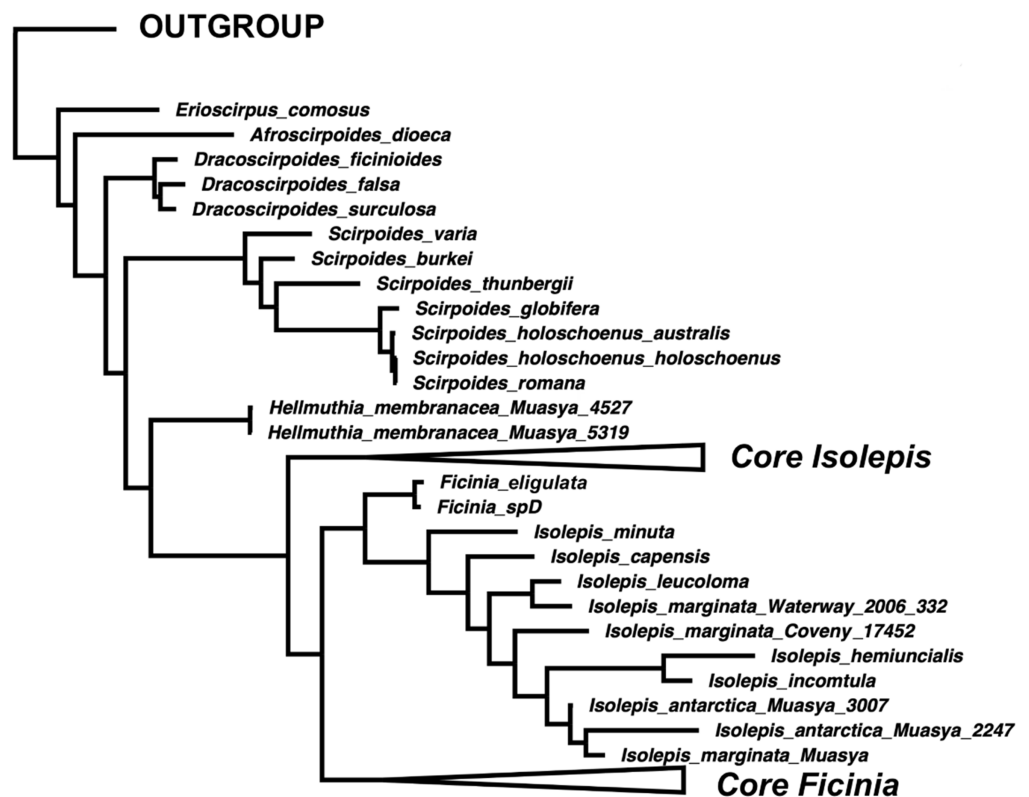
The position of *Isolepis hemiuncialis* and *I. incomtula* differed in the two analyses. These two species formed an early diverging grade leading to a polytomy among core *Isolepis* in the plastid topology (Fig. 1B), but were part of the *I. marginata* clade in the nuclear phylogeny (Figs. 1 and 2). On the other hand, *I. marginata* and allied species (*I. antarctica*, *I. capensis*, *I. leucoloma* and *I. minuta*) were consistently resolved as part of a clade including *Ficinia eligulata* and sister to the core *Ficinia* clade. The nuclear topology is better resolved, showing subclades in core *Isolepis* which coincide with current infrageneric groups, but these groups are not clearly discernable in the plastid topology. In addition, the nuclear ITS alignment shows a three nucleotide insertion (ATA; position 1890–1892, Data S1), unique to the core *Isolepis* clade and lacking in the outgroup as well other *Isolepis* (*I. hemiuncialis*, *I. incomtula*, *I. marginata* and allies) and *Ficinia*.

### Morphological study

Table 1 summarises the morphological diversity among genera in the ingroup. All *Ficinia* Clade taxa share the presence of *Cyperus* or a modified type (*Ficinia*) embryo. They are annuals or perennials; are mostly scapose, though multiple nodes are observed in *Ficinia* (e.g., *F. trichodes* (Schrad.) B. D. Jacks.); and have leaf blades well developed or reduced to a lobe, with or without ligule. The inflorescence is diverse (single terminal, for example, *I. ludwigii* (Steud.) Kunth, Fig. 3A; capitate, for example, *F. ecklonea* (Steud.) Nees, Fig. 3I; pseudolateral, for example, *Afroscirpoides*; to anthelate, for example, *S. burkei* (C. B. Clarke) Goetgh., Muasya and D. A. Simpson). Glume arrangement is predominantly spiral, with distichous arrangement in some species of *Isolepis* and *Ficinia* (e.g., *I. levynsiana* Muasya and D. A. Simpson, Fig. 3B; *F. distans* C. B. Clarke). The flowers



**Figure 1** The majority-rule consensus Bayesian Inference of the *Ficinia* Clade, showing posterior probabilities at nodes, based on MrBayes analyses. (A) Concatenated nuclear, (B) concatenated plastid DNA sequence data. [Full-size !\[\]\(1679558f37f6db0dd8360a2a7e913e90\_img.jpg\) DOI: 10.7717/peerj.10737/fig-1](https://doi.org/10.7717/peerj.10737/fig-1)



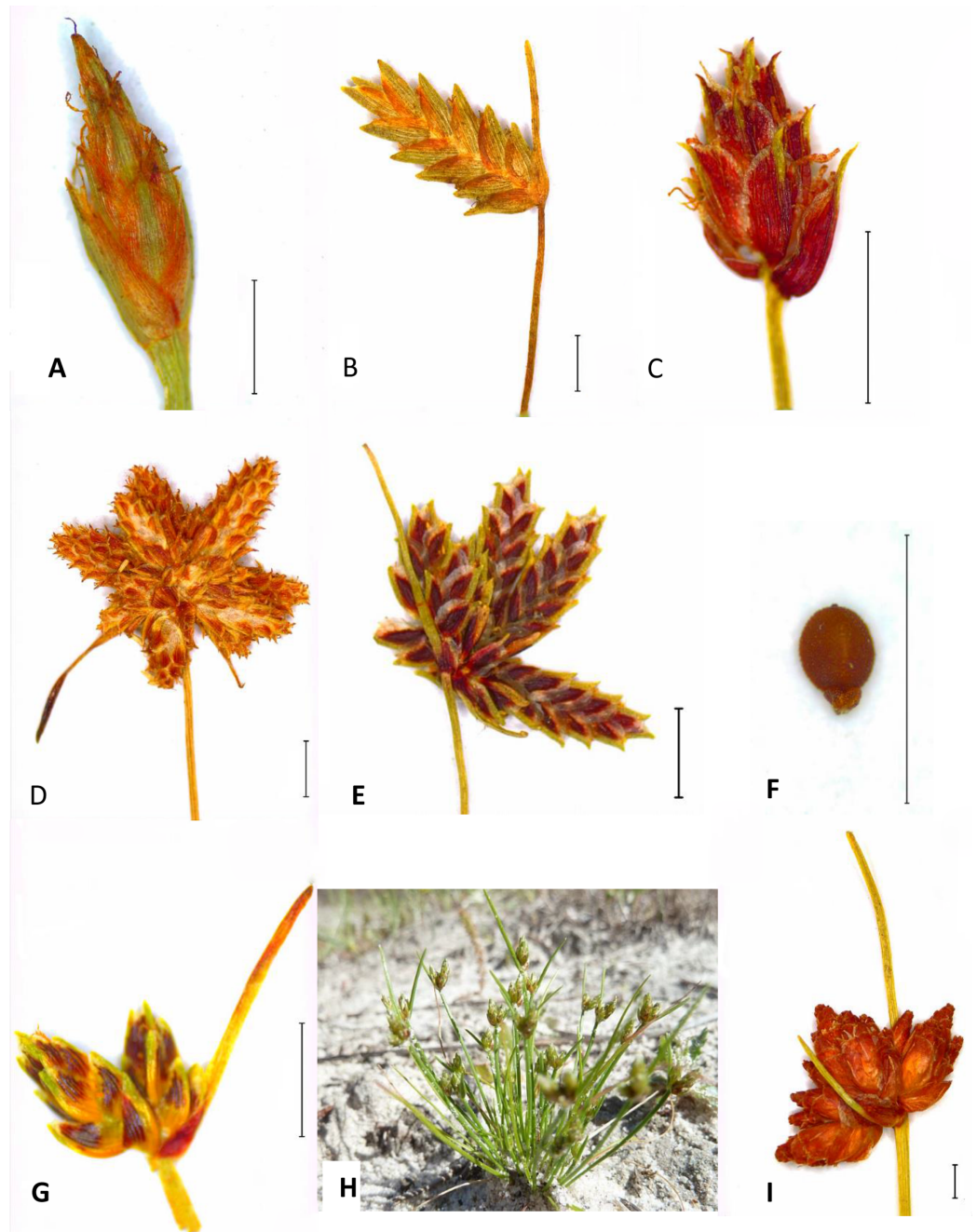
**Figure 2** A simplified majority-rule consensus Bayesian Inference of the ingroup based on the concatenated nuclear DNA sequence data. [Full-size !\[\]\(fd7fe780e8fd8eece60268c87d0c3e04\_img.jpg\) DOI: 10.7717/peerj.10737/fig-2](https://doi.org/10.7717/peerj.10737/fig-2)

are bisexual and occurring in most florets, but dioecy is observed in *Afroscirpoides*. While majority of taxa lack perianth, these occur in *Erioscirpus* (large and plumose as seen in *Eriophorum* L.), *Dracoscirpoides* (bristles) and *Hellmuthia* (scales). Nutlets are trigonous to oval in cross section, with the base extended to form a gynophore in the majority of *Ficinia*.

Species in the *Isolepis* and *Ficinia* clades vary in subtle morphological and ecological features (Table 1; Fig. 3). *Isolepis hemiuncialis* and *I. incomtula* are annual species, whose gross morphology and ecology is similar to annual species in the core *Isolepis* clade and *I. marginata* (and allies). *Ficinia* is unique in its ecology, frequently growing as perennial in dry habitats and unlike perennial *Isolepis* species that are restricted to wetlands. An additional feature, the presence of a gynophore is unique to *Ficinia*, eventhough several species (e.g., *F. filiformis* (Lam.) Schrad., *F. trollii* (Kük.) Muasya and D. A. Simpson) lack this feature and vestigial gynophore occasionally occur in *Isolepis marginata*. Glume texture is chartaceous in *Isolepis* (including *I. hemiuncialis* and *I. incomtula*), whereas it is cartilaginous in *Ficinia* (including *I. marginata* and allies).

## DISCUSSION

This study has inferred the phylogeny of the Ficinia Clade using a large species sample (78% of species) and Sanger sequencing of nuclear and plastid markers. The patterns observed are similar to previous studies (*Muasya et al., 2009a, 2009b*;



**Figure 3** Morphological diversity in the Ficinia Clade. (A) *I. ludwigii* (Schlechter 1821 BOL); (B) *I. levynsiana* (Muasya 2274 BOL); (C) *I. hemiuncialis* (Muasya et al. 6040 BOL); (D) *I. incomtula* (BOL6370); (E) *I. leucoloma* (Levyns 7618 BOL); (F–G) *I. marginata* (Verboom 1241 BOL); (G) *I. marginata* (in situ); (I) *F. ecklonea* (Muasya and Stirton 3215 BOL). Images of the inflorescences were made using a Leica S9i and habit photograph (H) made by Muthama A. Muasya.

Full-size  DOI: [10.7717/peerj.10737/fig-3](https://doi.org/10.7717/peerj.10737/fig-3)

*Muasya & De Lange, 2010; Hinchliff & Roalson, 2013; Spalink et al., 2016; Semmouri et al., 2019*), confirming the monophyly of the smaller genera but recovering *Ficinia* to be nested in *Isolepis*. The backbone differs between the plastid and nuclear topology, especially



**Table 1** Comparison of genera in the *Ficinia* clade, reflecting the revised classification.

	<i>Erioscirpus</i> Palla	<i>Afroscirpoides</i> García-Madr. & Muasya	<i>Dracoscirpoides</i> Muasya	<i>Scirpoides</i> Ség.	<i>Hellmuthia</i> Steud.	<i>Isolepis</i> R.Br.	<i>Ficinia</i> Schrad.
Life form	Perennial	Perennial	Perennial	Perennial	Perennial	Annual and perennial	Perennial, few annual
Leaf blade	Well developed	Poorly developed (<5 mm long)	Well developed	Mostly poorly developed	Mostly poorly developed	Mostly well developed	Mostly well developed
Inflorescence type	Anthelate	Capitate, pseudolateral	Capitate, pseudolateral	Capitate, anthelate, pseudolateral	Capitate	Capitate, terminal	Capitate, spike, pseudolateral
Glume arrangement	Spiral	Spiral	Spiral	Spiral	Spiral	Spiral, few distichous	Spiral, few distichous
Perianth type in fertile flowers	>6 Bristles, cotton-like	Absent	6 (7) Bristles, scabrid	Absent	3 Scales in lower flowers	Absent	Absent (single case recorded)
Gynophore	Absent	Absent	Absent	Absent	Absent	Absent	Mostly present
Embryo type	<i>Cyperus</i>	<i>Cyperus</i>	<i>Cyperus</i>	<i>Cyperus</i>	<i>Cyperus</i>	<i>Cyperus</i> and <i>Ficinia</i>	<i>Ficinia</i>
Number of species	2	1	3	4	1	70	~90
Distribution	Asia	Southern Africa	Southern Africa	Southern Africa, Eurasia, Americas	Southern Africa (Cape)	Southern and Tropical Africa, Australasia, Europe, Americas,	Southern and Tropical Africa, Australasia, circumpolar

relating to the position of *Dracoscirpoides* which is positioned between *Afroscirpoides* and *Scirpoides* (nuclear, Fig. 1A) or between *Hellmuthia* and the *Isolepis/Ficinia* clade (plastid, Fig. 1B). Similarly, these varied topologies have been observed in previous studies (*García-Madrid et al., 2015*). As the majority of the deeper nodes in the *Ficinia* Clade are highly supported (PP above 0.95, Figs. 1A and 1B), we suspect that the observed pattern is caused by evolutionary phenomena such as reticulate evolution (*Pelser et al., 2010*).

The phylogenetic position of *Isolepis hemiuncialis* and *I. incomtula* is unstable, shifting based on the markers analyzed. These taxa form a lineage (or grade) separate from the core *Isolepis* and *Ficinia* clades based on plastid data in this and previous studies (*García-Madrid et al., 2015; Spalink et al., 2016*), and a similar pattern was observed in a combined plastid and nuclear analysis (*rps16* and ITS; *Muasya & De Lange, 2010*). In addition, the nuclear markers differ in their placement of these samples, with ITS having a pattern similar to plastid markers (similarly observed in Figs. S1 and S2 of *García-Madrid et al. (2015)*), but ETS placing these species as part of clade with *I. marginata* (similarly observed in Figs. S3 and S4 of *García-Madrid et al. (2015)*). In the combined nuclear matrix, these two species are part of the *I. marginata* clade. In contrast, *I. marginata* (and allied species) have been consistently observed to be forming a clade sister to core *Ficinia* in separate and combined analyses, and these species are in same clade with *F. eligulata* Gordon-Gray ex Muasya from the Drakensberg Mountain.

A unique three base-pair insertion in ITS2 further supports the uniqueness of the core *Isolepis*. This insertion is missing in *I. hemiuncialis*, *I. incomtula* as well as the species in the *I. marginata* clade, and can therefore be used as a synapomorphy for the core *Isolepis* clade. Similar use of indels, located at the 5.8S gene of the nuclear ribosomal DNA, as synapomorphies has been suggested for the Cyperaceae ([Yano et al., 2012](#)) and Cyperaceae ([Starr et al., 2007](#)).

A number of the genera in the ingroup can be distinguished unambiguously based on one or few characters ([Table 1](#)). The presence and type perianth segments, even though perhaps arising independently, are unique in *Dracoscirpoides* (scabrid bristles; [Muasya et al., 2012](#)), *Erioscirpus* (cotton-like bristles; [Yano et al., 2012](#)) and in *Hellmuthia* (scale-like; [Vrijdaghs et al., 2006](#)). Among the taxa lacking perianth segments, *Afroscirpoides* and *Scirpoides* have densely tufted culms which have reduced leaf blades (>5 mm, but some *Scirpoides* have well developed leaf blades), with the former having dioecious individuals whereas the later has bisexual florets. *Ficinia* is most similar in gross morphology and ecology to *Afroscirpoides* and *Scirpoides*, diagnosed by the presence of a cupular disk (gynophore; [Vrijdaghs et al., 2005](#)) at the base of the nutlets (except in several species where the trait is lost; [Muasya et al., 2014](#)). *Isolepis* is most similar to *Ficinia*, sharing presence of bisexual florets and glumes with well defined parallel veins, but differing in *Isolepis* lacking the gynophore. The glume texture appears to offer additional separation, being chartaceous to hyaline (herbaceous; [Muasya & Simpson, 2002](#)) in *Isolepis* but cartilaginous (or coriaceous) in *Ficinia*.

Generic boundaries within *Isolepis* and *Ficinia* have been noted as problematic. *Eleogiton*, still recognized as distinct in some floras (e.g., Germany, [Kadereit et al., 2016](#)) based on possessing multiple internodes and peduncle termination in a single terminal spikelet, is confirmed to be a clade in *Isolepis* (subgenus *Fluitantes*; [Muasya et al., 2001](#); [Muasya & Simpson, 2002](#)). In *Ficinia*, *Sickmania* Nees has been previously recognized based on a capitate inflorescence with multiple leaf-like bracts (*F. radiata*) whereas *Desmoschoenus* has primary bracts adnate to axis and covering congested spikelets ([Goetghebeur, 1998](#)). The phylogenetic inference showing *I. marginata* and other annual species that lack a gynophore being closer to *Ficinia* further blurs the generic boundaries.

Cyperaceae has experienced shifting generic classification in the last two decades. The paradigm shift to recognize monophyletic genera ([Humphreys & Linder, 2009](#)) accompanied by the use of DNA sequence data have enabled disentangling phylogenetic relatedness of taxa obscured by extreme morphological modification. Several highly diversified lineages appear to have been split into genera based on one of few characters, at times such characters arising independently. This phenomenon was epitomized *Cyperus*, now recognized as a single genus ([Larridon et al., 2011a, 2011b, 2013, 2014](#); [Bauters et al., 2014](#)), where 13 segregate genera were diagnosed based on morphology of reproductive structures (spikelet size and organization, nutlet orientation, style branching; [Muasya et al., 2009b](#)). This study supports a further refinement within the Cyperaceae, recognizing the core *Isolepis* and an enlarged *Ficinia* at generic level.

We speculate that the *Ficinia* clade evolved in southern Africa, given that majority of lineages and species occur in the region. Diversification in *Isolepis* and *Ficinia* has occurred

since the Miocene (Besnard *et al.*, 2009), perhaps ecologically driven by aridification associated with onset of the Mediterranean climate (Linder & Verboom, 2015), where emerging traits include annual life form, colonization of permanently wet habitats, sprouting regeneration driven by the frequent fires in sclerophyllous habitats, and ant dispersal of seeds (gynophore in *Ficinia*; Bond & Slingsby, 1983). Within southern Africa, the *Ficinia* Clade members are predominantly occurring in the Greater Cape Flora and exhibit the typical diversification pattern whereby lineages in the Fynbos are older than those in the Succulent Karoo biome (Verboom *et al.*, 2009). Dispersal out of the Cape appears to be predominantly to other similar habitats, especially in Mediterranean Eurasia (*Erioscirpus*, *Isolepis*, *Scirpoides*), within temperate zones of high mountains in tropical Africa (*Dracoscirpoides*, *Ficinia*, *Isolepis*, *Scirpoides*) and austral temperate areas (*Ficinia*, *Isolepis*). Dispersal to Australasia in *Isolepis* has been accompanied by hybridization in *Isolepis* (Ito *et al.*, 2016).

## TAXONOMIC TREATMENT

The current generic classification is supported for the smaller genera (*Afroscirpoides*, *Dracoscirpoides*, *Erioscirpus*, *Hellmuthia*, *Scirpoides*). However, *Isolepis* is paraphyletic as *Ficinia* is one of its clades as well as *Ficinia* is paraphyletic if *I. marginata* and allies are excluded. We acknowledge the conflicting topology between the nuclear and plastid phylogenies, particularly regarding the position of *I. hemiuncialis* and *I. incomtula*, opting to follow the nuclear phylogeny. We take a pragmatic approach, to recognize clades that will minimize nomenclatural changes, by adopting a classification framework based on the nuclear phylogeny (Fig. 2). We therefore recognize an expanded concept of *Ficinia*, to include annual species with mostly cartilaginous glumes and lacking a gynophore (occasionally a gynophore is observed among Australian *I. marginata*, see Fig. 3F). As a consequence, *Isolepis* is now considered in a narrower concept which encompasses the core *Isolepis* and excludes the seven annual species placed within the *Ficinia* clade (*I. antactica*, *I. capensis*, *I. hemiuncialis*, *I. incomtula*, *I. leucoloma*, *I. marginata* and *I. minuta*). Subclades within *Isolepis* can be recognized as infrageneric groups, recognizing four subgenera where three are similar to classification by Muasya & Simpson (2002) but elevating sect. *Proliferae* to subgeneric rank. In *Ficinia*, previous infrageneric groups (Clarke, 1897; Pfeiffer, 1921) are not supported, but the two clades each with subclades could form basis for future infrageneric classification. Formal taxonomic changes are made here, but we note the need of a comprehensive taxonomic revision of *Ficinia*.

### Key to the species of *Ficinia* clade genera

- 1 Plants perennial or annual; perianth segments absent.....4
- 1 Plants perennial; perianth segments present.....2
- 2 Perianth segment cotton-like, restricted to Asia..... 1. *Erioscirpus*
- 2 Perianth segment bristle or scale-like; restricted to southern Africa .....3
- 3 Slender plants, culm < 4 mm diameter; perianth bristle-like; in Drakensberg and surrounding areas ..... 2. *Dracoscirpoides*
- 3 Robust plant, culm > 5 mm diameter; perianth scale-like; in Cape area.....3. *Hellmuthia*

- 4 Perennial habit; inflorescence in globose clusters of over 10 spikelets; nutlet lacking a gynophore; embryo Cyperus-type.....5.
- 4 Perennial or annual habit; inflorescence in clusters mostly of under 10 spikelets; nutlet with or without a gynophore; embryo Cyperus- or Ficinia-type .....6.
- 5 Plants leafless; inflorescence pseudolateral, dioecious ..... 4. *Afroscirpoides*.
- 5 Plants leafless or well developed blades; inflorescence with bisexual flowers, pseudolateral to anthelate..... 5. *Scirpoides*.
- 6 Glumes chartaceous, nutlet lacking gynophore..... 6. *Isolepis*.
- 6 Glumes cartilaginous, nutlet mostly bearing gynophore .....7. *Ficinia*

1. *Erioscirpus* Palla, Bot. Zeitung (Berlin) 54: 151 (1896). Type species – *Erioscirpus comosus* (Wall.) Palla, designated here.

Two species of perennial hemicyptophytes, diagnosed on presence of cotton-like perianth. Taxonomic revision as part of regional flora, for example, Flora of Pakistan (<http://www.tropicos.org/Project/Pakistan>).

Distributed in Asia, from Iran to China, occurring in shallow soil and rocky crevices, at 700–2,300 m.

2. *Dracoscirpoides* Muasya, S. African J. Bot. 78: 108 (2012). Type species—*Dracoscirpoides falsa* (C.B.Clarke) Muasya.

Three species of perennial hemicyptophytes or rhizomatous geophytes, taxonomy revised in *Muasya et al. (2012)*.

Restricted to southern Africa, occurring in montane grasslands.

3. *Hellmuthia* Steud., Syn. Pl. Glumac. 2: 90 (1855). Type species—*Hellmuthia membranacea* (Thunb.) R. W. Haines and Lye.

Monotypic, hemicyptophytes or rhizomatous geophytes, diagnosed by presence of scale-like perianth. Taxonomic studies in local flora (*Archer & Muasya, 2012*).

Restricted to South Africa, occurring coastal areas in calcareous sandy soils in the Cape Flora.

4. *Afroscirpoides* García-Madr. & Muasya, Taxon 64: 698 (2015). Type species—*Afroscirpoides dioeca* (Kunth) García-Madr.

Monotypic, densely tufted hemicyptophytes or rhizomatous geophytes, diagnosed by dioecious flowers borne in dense globose inflorescences whose bract terminates in a sharp-pointed tip.

Restricted to southern Africa, occurring in seepages and streambeds in brackish habitats.

5. *Scirpoides* Ség., Pl. Veron. 3: 73 (1754). Type species—*Scirpoides holoschoenus* (L.) Soják, designated here.

Four species recognized in *Govaerts et al. (2020)*, but two additional species segregated from the widespread *S. holoschoenus* by *García-Madrid et al. (2015)*.

Widespread in Mediterranean habitat in Mexico, Canary Is. through northern Africa and Eurasia to W. Himalaya, South Africa.

6. *Isolepis* R.Br., Prodr. Fl. Nov. Holland.: 221 (1810). Type species—*Isolepis setacea* (L.) R.Br.

About 70 species recognized here, after moving seven species to *Ficinia*. Nearly a third of species are therophytes, rest are hemicytrophites or rhizomatous geophytes. Most recent and comprehensive taxonomic revision in [Muasya & Simpson \(2002\)](#).

Nearly cosmopolitan distribution, with highest species densities in austral temperate southern Africa and Australasia.

7. *Ficinia* Schrad., Commentat. Soc. Regiae Sci. Gott. Recent. 7: 143 (1832). Type species—*Ficinia gracilis* Schrad.

About 90 species are recognized here, including the annual species transferred from *Isolepis*. Majority of species are perennial hemicytrophites or rhizomatous geophytes, adapted to survive frequent fires in the Fynbos biomes, but also few annual and pyrophytic short-lived perennials. The most comprehensive taxonomic study of *Ficinia* was part of the Flora Capensis ([Clarke, 1897](#)) and recent synopsis of the Cape Flora ([Archer & Muasya, 2012](#)). Ongoing studies reveal existence of undescribed species and the *Ficinia* is among the highest priority Cyperaceae for taxonomic revision in southern Africa.

Predominantly occurring in southern Africa in the Cape Flora and extending into montane areas of tropical Africa. Two species occur in Australasia, among which *F. nodosa* is nearly circumpolar.

### Species transferred from *Isolepis* to *Ficinia* in this study:

The annual *Isolepis* species forming a clade sister to *F. eligulata* ([Fig. 2](#)) are here transferred into *Ficinia*.

*Ficinia neocapensis* Muasya, **nom. nov.**

*Isolepis capensis* Muasya, Kew Bull. 57: 305 (2002). (basionym)

*Ficinia hemiuncialis* (C. B. Clarke) Muasya, **comb. nov.**

*Scirpus hemiuncialis* C. B. Clarke in É. A. J. De Wildeman, Pl. Nov. Horti Then. 1: 23 (1904). (basionym)

*Isolepis hemiuncialis* (C. B. Clarke) J. Raynal, Adansonia, n.s., 17: 55 (1977).

*Ficinia incomtula* (Nees) Muasya, **comb. nov.**

*Isolepis incomtula* Nees, Linnaea 10: 154 (1835). (basionym)

*Ficinia leucoloma* (Nees) Muasya, **comb. nov.**

*Cyperus leucoloma* Nees, Linnaea 10: 133 (1835). (basionym)

*Isolepis leucoloma* (Nees) C. Archer, Bothalia 28: 42 (1998).

*Ficinia marginata* (Thunb.) Fourc., Trans. Roy. Soc. South Africa 21: 76 (1932).

*Scirpus marginatus* Thunb., Prodr. Pl. Cap.: 17 (1794). (basionym).

*Isolepis marginata* (Thunb.) A. Dietr., Sp. Pl. 2: 110 (1833).

There appears to be continuity in the number of spikelets per inflorescence, with materials at extreme ends recognized as *I. marginata* versus *I. antarctica*. We retain the two

taxa as a single species, *Ficinia marginata*, and refrain from making a new combination pending a detailed taxonomic study of the complex.

*Ficinia minuta* (Turrill) Muasya, **comb. nov.**

*Scirpus minutus* Turrill, Bull. Misc. Inform. Kew 1925: 69 (1925). (basionym)

*Isolepis minuta* (Turrill) J. Raynal, Adansonia, n.s., 17: 56 (1977)

## CONCLUSIONS

This study aimed to establish the phylogenetic position of contentious annual species currently placed in *Isolepis* and to test the monophyly of the genera. All the other smaller genera in the *Ficinia* clade (*Afroscirpoides*, *Dracoscirpoides*, *Erioscirpus*, *Hellmuthia* and *Scirpoides*) are monophyletic. There is unambiguous placement of *I. marginata* and allies (*I. antarctica*, *I. capensis*, *I. leucoloma* and *I. minuta*) as a clade within *Ficinia* and not part of the core *Isolepis* clade. Inclusion of *I. hemiuncialis* and *I. incomtula* into a clade including *I. marginata* is supported by the nuclear phylogeny, but these taxa are placed in a grade outside the core *Isolepis* clade. We propose the reclassification of these *Isolepis* species, resolved outside the core *Isolepis*, as species within *Ficinia*. The proposed classification will add taxa lacking the gynophore, the currently used diagnostic character for *Ficinia*, with the core *Isolepis* diagnosed by a combination of morphology (e.g., chartaceous glumes, no gynophore) and a unique indel in ITS.

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### Author Contributions

- A. Muthama Muasya conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.

- Isabel Larridon analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.

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Voucher information of all material used in the molecular study, including GenBank accession numbers, are available in the [Supplemental Files](#).

### Data Availability

The following information was supplied regarding data availability:

Alignment of the concatenated nuclear/plastid DNA sequence data are available in the [Supplemental Files](#).

### New Species Registration

The following information was supplied regarding the registration of a newly described species:

*Ficinia neocapensis* Muasya, nom. nov.: 77213741-1

*Ficinia hemiuncialis* (C. B. Clarke) Muasya, comb. nov.: 77213737-1

*Ficinia incomtula* (Nees) Muasya, comb. nov.: 77213738-1

*Ficinia leucoloma* (Nees) Muasya, comb. nov.: 77213739-1

*Ficinia minuta* (Turrill) Muasya, comb. nov.: 77213740-1.

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## REFERENCES

- Archer C, Muasya AM. 2012.** *Strelitzia* 29: Cyperaceae. In: Manning J, Goldblatt P, eds. *Plants of the Greater Cape Floristic Region 1: The Core Cape Flora*. Pretoria: South Africa National Biodiversity Institute, 84–96.
- Barrett RL, Wilson KL, Bruhl JJ. 2019.** *Anthelepis*, a new genus for four mainly tropical species of Cyperaceae from Australia, New Caledonia and South-East Asia. *Australian Systematic Botany* 32:269–289.
- Bauters K, Larridon I, Reynders M, Asselman P, Vrijdaghs A, Muasya AM, Simpson DA, Goetghebeur P. 2014.** A new classification for *Lipocarpha* and *Volkiella* as infrageneric taxa of *Cyperus* s.l. (Cypereae, Cyperoideae, Cyperaceae): insights from species tree reconstruction supplemented with morphological and floral developmental data. *Phytotaxa* 166(1):1–32  
DOI 10.11646/phytotaxa.166.1.1.

- Besnard G, Muasya AM, Russier F, Roalson EH, Salamin N, Christin PA. 2009. Phylogenomics of C4 photosynthesis in sedges (Cyperaceae): multiple appearances and genetic convergence. *Molecular Biology and Evolution* 26(8):1909–1919 DOI 10.1093/molbev/msp103.
- Bond WJ, Slingsby P. 1983. Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. *South African Journal of Science* 79:231–233.
- Browning JBM, Gordon-Gray KD. 2011. Studies in Cyperaceae in South Africa 43: *Scirpoides varius* Browning—a new name for *Scirpus varius* Boeck. ex. C.B. Clarke. *South African Journal of Botany* 77(2):506–508 DOI 10.1016/j.sajb.2010.10.010.
- Clarke. 1897. *Ficinia*. In: Thiselton-Dyer WT, ed. *Flora capensis: being a systematic description of the plants of the Cape Colony, Caffraria, & Port Natal*. London: Lovell Reeve & Co., Ltd.
- Elliott TL, Muasya AM. 2017. Taxonomic realignment in the southern African *Tetraria* (Cyperaceae, tribe Schoeneae; Schoenus clade). *South African Journal of Botany* 112:354–360 DOI 10.1016/j.sajb.2017.06.011.
- García-Madrid AS, Muasya AM, Álvarez I, Cantó P, Molina JA. 2015. Towards resolving phylogenetic relationships in the *Ficinia* clade and description of the new genus *Afroscirpoides* (Cyperaceae: Cypereae). *Taxon* 64(4):688–702 DOI 10.12705/644.2.
- Global Carex Group (GCG). 2015. Making *Carex* monophyletic (Cyperaceae, tribe Cariceae): a new broader circumscription. *Botanical Journal of the Linnean Society* 179:1–42.
- Goetghebeur P. 1986. Genera Cyperacearum—Een bijdrage tot de kennis van de morfologie, systematiek en fylogeneze van de Cyperaceae-genera. Unpublished D Phil. thesis, Ghent University, Belgium.
- Goetghebeur P. 1998. Cyperaceae. In: Kubitzki K, ed. *The Families and Genera of Vascular Plants* 4. Berlin: Springer, 141–190.
- Govaerts R, Jiménez-Mejías P, Koopman J, Simpson DA, Goetghebeur P, Wilson KL, Egorova T, Bruhl JJ. 2020. World checklist of selected plant families—Cyperaceae: the board of trustees of the royal botanic gardens, Kew. Available at <http://www.kew.org/wcsp/monocots/> (accessed 6 January 2020).
- Hinchliff CE, Roalson EH. 2013. Using supermatrices for phylogenetic inquiry: an example using the sedges. *Systematic Biology* 62(2):205–219 DOI 10.1093/sysbio/sys088.
- Humphreys AM, Linder HP. 2009. Concept versus data in delimitation of plant genera. *Taxon* 58(4):1054–1074 DOI 10.1002/tax.584002.
- Ito Y, Viljoen JA, Tanaka N, Yano O, Muasya AM. 2016. Phylogeny of *Isolepis* (Cyperaceae) revisited: non-monophyletic nature of *I. fluitans* sensu lato and resurrection of *I. lenticularis*. *Plant Systematics and Evolution* 302(2):231–238 DOI 10.1007/s00606-015-1253-7.
- Kadereit JW, Albach DC, Ehrendorfer F, Galbany-Casals M, Garcia-Jacas N, Gehrke B, Kadereit G, Kilian N, Klein JT, Koch MA, Kropf M, Oberprieler C, Pirie MD, Ritz CM, Röser M, Spalik K, Susanna A, Weigend M, Welk E, Wesche K, Zhang LB, Dillenberger MS. 2016. Which changes are needed to render all genera of the German flora monophyletic? *Willdenowia* 46(1):39–91 DOI 10.3372/wi.46.46105.
- Katoh K, Asimenos G, Toh H. 2009. Multiple alignment of DNA sequences with MAFFT. *Methods in Molecular Biology* 537:39–64 DOI 10.1007/978-1-59745-251-9\_3.
- Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30(4):772–780 DOI 10.1093/molbev/mst010.
- Kearse M, Moir R, Wilson A, Stones-Haves S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A. 2012. Geneious



- basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* **28**(12):1647–1649 DOI [10.1093/bioinformatics/bts199](https://doi.org/10.1093/bioinformatics/bts199).
- Lanfear R, Calcott B, Ho SYW, Guindon S. 2012.** Partitionfinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* **29**(6):1695–1701 DOI [10.1093/molbev/mss020](https://doi.org/10.1093/molbev/mss020).
- Larridon I, Bauters K, Reynders M, Huygh W, Goetghebeur P. 2014.** Taxonomic changes in *C<sub>4</sub> Cyperus* (Cypereae, Cyperoideae, Cyperaceae): combining the sedge genera *Ascolepis*, *Kyllinga* and *Pycneus* into *Cyperus* s.l. *Phytotaxa* **166**(1):33–48 DOI [10.11646/phytotaxa.166.1.2](https://doi.org/10.11646/phytotaxa.166.1.2).
- Larridon I, Bauters K, Reynders M, Huygh W, Muasya AM, Simpson DA, Goetghebeur P. 2013.** Towards a new classification of the giant paraphyletic genus *Cyperus* (Cyperaceae): phylogenetic relationships and generic delimitation in *C<sub>4</sub> Cyperus*. *Botanical Journal of the Linnean Society* **172**(1):106–126 DOI [10.1111/boj.12020](https://doi.org/10.1111/boj.12020).
- Larridon I, Reynders M, Huygh W, Bauters K, Van de Putte K, Muasya AM, Boeckx P, Simpson DA, Vrijdaghs A, Goetghebeur P. 2011a.** Affinities in *C<sub>3</sub> Cyperus* lineages (Cyperaceae) revealed using molecular phylogenetic data and carbon isotope analysis. *Botanical Journal of the Linnean Society* **167**(1):19–46 DOI [10.1111/j.1095-8339.2011.01160.x](https://doi.org/10.1111/j.1095-8339.2011.01160.x).
- Larridon I, Reynders M, Huygh W, Bauters K, Vrijdaghs A, Leroux O, Muasya AM, Simpson DA, Goetghebeur P. 2011b.** Taxonomic changes in *C<sub>3</sub> Cyperus* (Cyperaceae) supported by molecular phylogenetic data, morphology, embryology, ontogeny and anatomy. *Plant Ecology and Evolution* **144**(3):327–356 DOI [10.5091/plecevo.2011.653](https://doi.org/10.5091/plecevo.2011.653).
- Larridon I, Semmouri I, Bauters K, Viljoen JA, Prychid CJ, Muasya AM, Bruhl JJ, Wilson KA, Goetghebeur P. 2018.** Molecular phylogenetics of the genus *Costularia* (Schoeneae, Cyperaceae) reveals multiple distinct evolutionary lineages. *Molecular Phylogenetics and Evolution* **126**:196–209 DOI [10.1016/j.ympev.2018.04.016](https://doi.org/10.1016/j.ympev.2018.04.016).
- Larridon I, Verboom GA, Muasya AM. 2018.** Revised delimitation of the genus *Tetraria*, nom. cons. prop. (Cyperaceae, tribe Schoeneae, Tricostularia clade). *South African Journal of Botany* **118**:18–22 DOI [10.1016/j.sajb.2018.06.007](https://doi.org/10.1016/j.sajb.2018.06.007).
- Larridon I, Spalink D, Jiménez-Mejías P, Márquez-Corro JI, Martin-Bravo S, Muasya AM, Escudero M. 2021.** The evolutionary history of sedges in Madagascar. *Journal of Biogeography* DOI [10.1111/jbi.14048](https://doi.org/10.1111/jbi.14048).
- Linder HP, Verboom GA. 2015.** The evolution of regional species richness: the history of the southern African flora. *Annual Review of Ecology, Evolution, and Systematics* **46**(1):393–412 DOI [10.1146/annurev-ecolsys-112414-054322](https://doi.org/10.1146/annurev-ecolsys-112414-054322).
- Linnaeus C. 1753.** *Species Plantarum: exhibentes Plantas Rite Cognitas, Ad Genera Relatas, Cum Differentiis Specificis, Nominibus Trivialibus, Synonymis Selectis, Locis Natalibus, Secundum Systema Sexuale Digestas*. Sweden: Berolini, G.C. Nauck.
- Miller MA, Pfeiffer W, Schwartz T. 2011.** The CIPRES science gateway: a community resource for phylogenetic analyses. In: *Proceedings of the 2011 TeraGrid Conference: Extreme Digital Discovery: 41*, New York. ACM.
- Muasya AM, De Lange P. 2010.** *Ficinia spiralis* (Cyperaceae) a new genus and combination for *Desmoschoenus spiralis*. *New Zealand Journal of Botany* **48**(1):31–39 DOI [10.1080/00288251003660703](https://doi.org/10.1080/00288251003660703).
- Muasya AM, Reynders M, Goetghebeur P, Simpson DA, Vrijdaghs A. 2012.** *Dracoscirpoides* (Cyperaceae)—a new genus from Southern Africa, its taxonomy and floral ontogeny. *South African Journal of Botany* **78**:104–115 DOI [10.1016/j.sajb.2011.05.011](https://doi.org/10.1016/j.sajb.2011.05.011).
- Muasya AM, Simpson DA. 2002.** A monograph of the genus *Isolepis* R.Br. (Cyperaceae). *Kew Bulletin* **57**(2):257–362 DOI [10.2307/4111111](https://doi.org/10.2307/4111111).

- Muasya AM, Simpson DA, Chase MW, Culham A. 2001.** A phylogeny of *Isolepis* (Cyperaceae) inferred using plastid *rbcL* and *trnL-F* sequence data. *Systematic Botany* **26**:342–353.
- Muasya AM, Simpson DA, Goetghebeur P. 2000.** New combinations in *Trichophorum*, *Scirpoides* and *Ficinia* (Cyperaceae). *Novon* **10**(2):132–133 DOI [10.2307/3393013](https://doi.org/10.2307/3393013).
- Muasya AM, Simpson DA, Verboom GA, Goetghebeur P, Naczi RFC, Chase MW, Smets E. 2009a.** Phylogeny of Cyperaceae based on DNA sequence data: current progress and future prospects. *Botanical Review* **75**(1):2–21 DOI [10.1007/s12229-008-9019-3](https://doi.org/10.1007/s12229-008-9019-3).
- Muasya AM, Viljoen JA, Dlodlu MN, Demissew S. 2014.** Phylogenetic position of *Cyperus clandestinus* (Cypereae, Cyperaceae) clarified by morphological and molecular evidence. *Nordic Journal of Botany* **32**(1):106–114 DOI [10.1111/j.1756-1051.2012.01700.x](https://doi.org/10.1111/j.1756-1051.2012.01700.x).
- Muasya AM, Vrijdaghs A, Simpson DA, Chase MW, Goetghebeur P, Smets E. 2009b.** What is a genus in Cypereae: phylogeny, character homology assessment and generic circumscription in cypereae. *Botanical Review* **75**(1):52–66 DOI [10.1007/s12229-008-9018-4](https://doi.org/10.1007/s12229-008-9018-4).
- Müller J, Müller K, Neinhuis C, Quandt D. 2010.** PhyDEPhylogenetic data editor, version 0.9971. Available at <http://www.phyde.de/> (accessed 10 January 2016).
- Pelser PB, Kennedy AH, Tepe EJ, Shidler JB, Nordenstam B, Kadereit JW, Watson LE. 2010.** Patterns and causes of incongruence between plastid and nuclear Senecioneae (Asteraceae) phylogenies. *American Journal of Botany* **97**(5):856–873 DOI [10.3732/ajb.0900287](https://doi.org/10.3732/ajb.0900287).
- Pereira-Silva L, Trevisan R, Rodrigues AC, Larridon I. 2020.** Combining the small South American genus *Androtrichum* in *Cyperus* (Cyperaceae). *Plant Ecology and Evolution* **153**(3):446–454 DOI [10.5091/plecevo.2020.1746](https://doi.org/10.5091/plecevo.2020.1746).
- Pfeiffer H. 1921.** *Revision der Gattung Ficinia Schrad.* Bremen: Druck und Verlag E. Gerst, 1–62.
- Rambaut A, Drummond AJ. 2007.** *Tracer, a MCMC trace analysis tool.* Edinburgh: Institute of Evolutionary Biology, University of Edinburgh.
- Reid CS, Doyle VP, Carter JR, Vargas-Rodriguez Y, Urbatsch LE. 2017.** Molecular systematics of targeted flat sedges (*Cyperus*, Cyperaceae) of the Americas. *Plant Ecology and Evolution* **150**(3):343–357 DOI [10.5091/plecevo.2017.1262](https://doi.org/10.5091/plecevo.2017.1262).
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012.** MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**(3):539–542 DOI [10.1093/sysbio/sys029](https://doi.org/10.1093/sysbio/sys029).
- Semmouri I, Bauters K, Léveillé-Bourret E, Starr JR, Goetghebeur P, Larridon I. 2019.** The phylogeny and systematics of Cyperaceae, the evolution and importance of embryo morphology. *Botanical Review* **85**(1):1–39 DOI [10.1007/s12229-018-9202-0](https://doi.org/10.1007/s12229-018-9202-0).
- Spalink D, Drew BT, Pace MC, Zaborsky JG, Starr JR, Cameron KM, Givnish TJ, Sytsma KJ. 2016.** Biogeography of the cosmopolitan sedges (Cyperaceae) and the area-richness correlation in plants. *Journal of Biogeography* **43**(10):1893–1904 DOI [10.1111/jbi.12802](https://doi.org/10.1111/jbi.12802).
- Stamatakis A. 2014.** RAXML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**(9):1312–1313 DOI [10.1093/bioinformatics/btu033](https://doi.org/10.1093/bioinformatics/btu033).
- Starr JR, Gravel G, Bruneau A, Muasya AM. 2007.** Phylogenetic implications of a unique 5.8S nrDNA insertion in Cyperaceae. *Aliso* **23**:84–98 DOI [10.5642/aliso.20072301.10](https://doi.org/10.5642/aliso.20072301.10).
- Stöver BC, Müller KF. 2010.** TreeGraph 2: combining and visualizing evidence from different phylogenetic analyses. *BMC Bioinformatics* **11**(1):7 DOI [10.1186/1471-2105-11-7](https://doi.org/10.1186/1471-2105-11-7).
- Van der Veken P. 1965.** Contribution à l'embryographie systématique des Cyperaceae-Cyperoideae. *Bulletin du Jardin Botanique de l'État à Bruxelles* **35**(3):285–354 DOI [10.2307/3667185](https://doi.org/10.2307/3667185).

- Verboom GA, Archibald JK, Bakker FT, Bellstedt DU, Conrad F, Dreyer LL, Forest F, Galley C, Goldblatt P, Henning JF, Mummenhoff K, Linder HP, Muasya AM, Oberlander KC, Savolainen V, Snijman DA, van der Niet T, Nowell TL. 2009.** Origin and diversification of the Greater Cape flora: ancient species repository, hot-bed of recent radiation, or both? *Molecular Phylogenetics & Evolution* **51**(1):44–53 DOI [10.1016/j.ympev.2008.01.037](https://doi.org/10.1016/j.ympev.2008.01.037).
- Viljoen J-A, Muasya AM, Barrett RL, Bruhl JJ, Gibbs AK, Slingsby JA, Wilson KL, Verboom GA. 2013.** Radiation and repeated transoceanic dispersal of Schoeneae (Cyperaceae) through the southern hemisphere. *American Journal of Botany* **100**(12):2494–2508 DOI [10.3732/ajb.1300105](https://doi.org/10.3732/ajb.1300105).
- Vrijdaghs A, Goetghebeur P, Muasya AM, Caris P, Smets E. 2005.** Floral ontogeny in *Ficinia* Schrad. and *Isolepis* R.Br. (Cyperaceae), with focus on the nature and origin of the gynophore. *Annals of Botany* **96**(7):1247–1262 DOI [10.1093/aob/mci276](https://doi.org/10.1093/aob/mci276).
- Vrijdaghs A, Goetghebeur P, Smets E, Muasya AM. 2006.** The floral scales in *Hellmuthia* (Cyperaceae, Cyperoideae) and *Paramapania* (Cyperaceae, Mapanioideae): an ontogenetic study. *Annals of Botany* **98**(3):619–630 DOI [10.1093/aob/mcl138](https://doi.org/10.1093/aob/mcl138).
- Yano O, Ikeda H, Watson MF, Rajbhandari KR, Jin XF, Hoshino T, Muasya AM, Ohba H. 2012.** Phylogenetic position of the Himalayan genus *Erioscirpus* (Cyperaceae) inferred from DNA sequence data. *Botanical Journal of the Linnean Society* **170**(1):1–11 DOI [10.1111/j.1095-8339.2012.01255.x](https://doi.org/10.1111/j.1095-8339.2012.01255.x).