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Integrating morphometric and molecular data to reassess the taxonomy of *Cyperus* L. in Egypt: A revised classification

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Abstract

The genus *Cyperus* L. (Cyperaceae) is one of the largest and most taxonomically complex genera within the sedge family, characterized by extensive morphological diversity and ecological significance. Despite its importance, the classification of *Cyperus* has been challenging due to convergent evolution, polyphyletic subgroups, and overlapping morphological traits. This study aims to reassess the taxonomy of *Cyperus* in Egypt by integrating morphometric and molecular approaches to provide a more robust and natural classification system. A total of 18 *Cyperus* species from Egypt were analyzed using 39 morphological characters (30 qualitative and 9 quantitative) and molecular data from five chloroplast markers (*rbc*L, matK, trnH-psbA, rpl32-trnL, and ndhF). Morphometric analyses, including hierarchical clustering and principal component analysis (PCA), revealed significant morphological variability among the taxa, with key vegetative and reproductive traits such as rhizome structure, culm characteristics, spikelet morphology, and achene traits proving critical for species differentiation. Pearson's correlation analysis identified rhizome scale, spikelet shape, and achene morphology as highly correlated with taxonomic distinctions. Phylogenetic analysis, combining morphological and molecular data, resolved the taxa into six main clades, strongly supporting the paraphyletic nature of the paraphyly of C_3 *Cyperus* and the monophyly of C_4 *Cyperus*. Notably, *Cyperus alternifolius* emerged as a distinct clade, while *Cyperus fuscus* and *Cyperus difformis* formed a well-supported cluster. The integration of molecular data with morphometric results provided a clearer resolution of species relationships, highlighting the limitations of morphology-based classifications and the importance of

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combining multiple data sources for taxonomic revisions. Based on the findings, we propose a revised sectional classification for *Cyperus* in Egypt, dividing the genus into three main complexes: *Papyrus*, *Cyperus*, and *Bobartia*, each encompassing several sections. This study demonstrated the efficacy of integrating morphometric and molecular data to resolve taxonomic complexities in *Cyperus*, offering a model for future taxonomic revisions in other taxonomically challenging plant groups. The results contribute to a deeper understanding of the evolutionary history and diversity of *Cyperus* in Egypt, providing a foundation for further research and conservation efforts

Keywords: chloroplast markers; Egyptian flora; molecular phylogenetics; morphometric analysis; species delimitation; taxonomic revision.

Introduction

The Cyperaceae family, commonly known as the sedge family, is one of the largest families of monocotyledons, comprising over 5,000 species distributed across approximately 90 genera (Goetghebeur, 1998; Simpson, 2019). Among these, the genus *Cyperus* L. stands out as one of the most species-rich and ecologically significant genera, with 949 accepted species globally (POWO, 2025). According to Goetghebeur (1998) the family includes over 5,000 species distributed across 109 genera, organized into four subfamilies and 14 tribes. However, the World Checklist of Cyperaceae (Simpson, 2019) recognizes 89 genera, while Plants of the World Online (POWO, 2025) lists 94 accepted genera. Approximately 10% of the species within the Cyperaceae family have documented uses worldwide (Simpson, 2019).

The tribe Cypereae (subfamily Cyperoideae) is the most species-rich within the Cyperaceae family, and it includes the genus *Cyperus*, which is the largest and most common genus in the family. *Cyperus* is particularly prominent in tropical regions (Armitage, 2020). The genus is not only ecologically important but also holds considerable economic and cultural value (Bayton, 2019). Species within this genus have diverse uses: some are grown as houseplants (e.g., *Cyperus alternifolius*), others are considered problematic weeds (e.g., *Cyperus rotundus*), and some are cultivated for their edible tubers (e.g., *Cyperus esculentus*). Historically, the stems of *Cyperus papyrus* were used to produce papyrus paper (Bayton, 2020). In Egypt, the Cyperaceae family comprises 12 genera, with the genus *Cyperus* classified under the subfamily Cyperoideae and tribe Cypereae. According to El-Habashy and Boulos (2005), 19 species and 21 taxa of *Cyperus* have been recorded in Egypt.

The genus *Cyperus* s.l. is taxonomically complex, with significant challenges in its circumscription and classification (Goetghebeur, 1998; Muasya *et al.*, 2002, 2009; Shalabi and Gazer, 2015). The classification of *Cyperus* species has been a subject of extensive debate among taxonomists. Early classifications laid the groundwork for understanding the genus by dividing it into several subgenera and sections based on morphological traits (Kunth, 1837; Nees von Esenbeck, 1842; Clarke, 1884, 1908; Kükenthal, 1936; Haines and Lye, 1983; El-Habashy, 1988).

Modern taxonomic developments, particularly those by Goetghebeur (1989, 1998) have proposed a simplified classification of *Cyperus* into two subgenera: *Cyperus* (characterized by Kranz anatomy and C_4 photosynthesis) and *Anosporum* (lacking Kranz anatomy and exhibiting C_3 photosynthesis). This division is based on anatomical and inflorescence characteristics. However, the taxonomic boundaries of *Cyperus* remain contentious, with some authors recognizing additional genera, such as *Kyllinga, Pycreus,* and *Torulinium*, as distinct entities (Goetghebeur, 1998).

Traditional morphological and anatomical characteristics have proven insufficient to resolve these taxonomic issues, largely due to convergent evolution and the polyphyletic nature of some subgroups (Verloove, 2014). Molecular phylogenetic studies, utilizing plastid DNA sequence data (e.g., *rbc*L, rps16 intron, trnL intron, and trnL-F spacer) have provided powerful tools for inferring evolutionary relationships and addressing these taxonomic challenges (Muasya *et al.*, 2002). Recent phylogenetic and molecular studies such as those by Bruhl (1995), Huygh *et al.* (2010), Reynders *et al.* (2011a), Larridon *et al.* (2011b, 2013, 2014, 2021) and (Reid *et al.*, 2017) have supported the recognition of only two subgenera within *Cyperus*. These studies have also led to the reclassification of several segregated genera (e.g., *Ascolepis, Kyllinga,* and *Pycreus*) into *Cyperus* s.l., reflecting a more inclusive approach to the genus.

Morphometric analysis has emerged as a robust methodology for examining taxonomic distinctions, population variability, and ecological adaptations. This approach has been employed to explore the interrelationships between *Cyperus squarrosus* and its allied species, with a particular focus on *C. granitophilus* populations (Lowe and Carter, 2023). The application of traditional and geometric morphometrics, often combined with multivariate statistical techniques such as hierarchical clustering and principal component analysis (PCA), is widespread in the field (Ellmouni, 2019; Mohamed *et al.*, 2024). The integration of molecular data with morphological evidence has proven pivotal in addressing taxonomic challenges, deciphering evolutionary relationships, and delineating species boundaries within *Cyperus* s.l., ultimately leading to a more robust and natural classification system (Muasya *et al.*, 2009; Larridon *et al.*, 2021; De Ryck *et al.*, 2023) .

Geometric morphometrics benefits from the versatility of the R programming language, which enables comprehensive statistical analysis and visualization of shape variations (*R Core Team R*, 2016). To address concerns in the morphometric field, researchers have employed multivariate statistical analysis (Bousbia *et al.*, 2021; Eltahan *et al.*, 2021). Traditionally, these analytical approaches focus on evaluating sets of angular measurements or spatial distances. However, contemporary advancements in theoretical frameworks, computational capabilities, and related disciplines have shifted morphometric methodologies toward the investigation of specific spatial points (Mitteroecker and Gunz, 2009).

This study aims to reassess the taxonomy of *Cyperus* in Egypt by integrating morphometric and molecular approaches. We analyzed 18 *Cyperus* taxa using 39 morphological characters and five chloroplast DNA markers to provide a more robust and natural classification system. By combining detailed morphological assessments with phylogenetic insights, we attempted to elucidate the evolutionary relationships and diversity of *Cyperus* in Egypt, ultimately proposing a revised sectional classification that reflects both morphological and molecular evidence. This integrated approach not only addresses the taxonomic challenges within *Cyperus* but also provides a model for future studies on other taxonomically complex plant groups.

Materials and Methods

Plant Material

This investigation focused on 18 *Cyperus* taxa occurring in Egypt, utilizing herbarium specimens housed at the Cairo University Herbarium (CAI). The remaining taxa were excluded from this study due to the unavailability of comparable molecular data. The taxonomic nomenclature and identification of the studied taxa were confirmed using two authoritative sources: the Taxonomic Name Resolution Service (TNRS) ((Boyle *et al.*, 2013) and Plants of the World Online (POWO, 2025). The results of this process are presented in Table (1).

Morphometric and phylogenetic analysis

This study incorporated a total of 39 morphological characters, comprising 30 qualitative and 9 quantitative traits, derived from the morphological features of the examined taxa. These characters were encoded into a multistate matrix (Supplementary Table 1a, b).

Phylogenetic analyses were conducted using a combined approach, integrating the binary matrix of morphological data with molecular information. The molecular component consisted of sequences from five chloroplast markers (*rbc*L, matK, trnH-psbA, rpl32-trnL, ndhF), which were obtained from the NCBI database (Supplementary Table 2).

Table 1 *Cyperus* taxa used for this study arranged in alphabetical order according to (El-Habashy and Boulos, 2005). Localities of voucher specimens are provided, and herbarium acronyms are given in parentheses.

No.	Taxa	Selected specimens
1	***C. alopecuroides*** Rottb.	El-Mansoura, 26/4/1983, El Habashy s.n. (CAI)
2	***C. alternifolius*** subsp. ***flabelliformis*** Kük.	Giza, Orman garden, 18/5/1983, El Habashy s.n. (CAI)
3	***C. articulatus*** L.	El-Mansoura, 26/4/1983, El Habashy s.n. (CAI)
4	***C. bulbosus*** Vahl.	Gebel Elba, 14/1-6/2/1933; Fahmy & Hassib s.n. (CAI)
5	***C. capitatus*** Vand.	Abu Mady 50 km. from El-Mansoura, 6/6/1983, El Habashy s.n. (CAI)
6	***C. conglomeratus*** Rottb.	Gamasa, 26/4/1983, El Habashy s.n. (CAI)
7	***C. compressus*** L.	Damietta, Ehrenberg s.n. (CAI)
8	***C. difformis*** L.	El-Mansoura, 20/6/1983, El Habashy (CAI)
9	***C. digitatus*** subsp. ***auricomus*** (Sieber ex Spreng.) Kük.	El-Mansoura, Batra 26/4/1983, El Habashy s.n. (CAI)
10	***C. esculentus*** L.	Rosetta, 26/4/1983, El Habashy s.n. (CAI)
11	***C. fuscus*** L.	Bahariya Oasis, 29/11/1978, Abd El-Ghani 1030 (CAI)
12	***C. imbricatus*** Retz.	Aswan, 15/5/1959. M Abdallah s.n. (CAI)
13	***C. laevigatus* L.** subsp. ***laevigatus***	El-Mansoura, 2/5/1983, El Habashy s.n. (CAI)
14	***C. laevigatus*** subsp. ***distachyos*** (All.) Ball.	El-Manzala, 15/5/1983, El Habashy s.n. (CAI)
15	***C. michelianus*** (L.) Delile subsp. ***pygmaeus*** (Rottb.) Asch. & Graebn.	Aswan, Nasser Lake, 25/2/1985, Aly 7467 s.n. (CAI)
16	***C. papyrus*** L.	Giza, Orman garden, 18/5/1983, El Habashy s.n. (CAI)
17	***C. rotundus*** L.	El-Mansoura, 24/4/1983, El Habashy s.n. (CAI)
18	***C. longus*** L. subsp. ***longus*** **(= *Cyperus rotundus*** L. var. ***fenzelianus*** (Steud.) Habashy	El-Mansoura, 24/3/1983, El Habashy s.n. (CAI)

Data processing and analysis

The cladogenesis of the genus was represented through a phylogenetic tree constructed via Bayesian analysis, utilizing the MrBayes 3.2 software (Ronquist *et al*., 2012). MrModel-test v.2.3 (Posada and Crandall, 1998) was employed to decide on the most applicable substitution model (SYM+G) based on the Akaike Information Criterion (AIC). The Markov chain Monte Carlo (MCMC) process was conducted for 3,000,000 generations, with tree sampling occurring every 1000 generations across 16 chains. Stationarity was achieved when the average standard deviation of the split frequencies remained below 0.01, leading to the subsequent exclusion of the initial 25% of the runs. Phylogenetic relationships within the examined genus were investigated by integrating data derived exclusively from five chloroplast barcode sequences with morphological characteristics.

Morphological data comprising 30 qualitative and nine quantitative characters were analyzed using R software and R-studio as the interface for R-software (*RStudio Team*, 2015; *R Core Team R*, 2016). The phylogenetic tree generated by MrBayes was used in conjunction with a to construct a phylogenetic correlation matrix (Paradis, 2014).

Principal Component Analysis (PCA) was applied to datasets, employing the "factoextra" and "ggplot2" packages to visualize the distance matrices utilized in PCA, resulting in the creation of species scatter diagrams Kassambara and Mundt (2017). Additionally, the "Corrplot" package facilitated the representation of correlation coefficients, depicting the relationships among variables and incorporating significant level stars (Soetewey, 2022).

Results

Morphological vegetative characters

Longevity: The taxa under study exhibited two life spans: annuals and perennials. Perennials were the most common, while the annual species included *Cyperus compressus, C. difformis, C. fuscus,* and *C. michelianus* subsp. *pygmaeus* (Fig. 1a).

Rhizome: Most of the examined taxa possessed rhizomes, except for four annual species: *C. compressus*, *C. difformis*, *C. fuscus*, and *C. michelianus* subsp. *pygmaeus*. Among the remaining taxa, variations were observed in rhizome characteristics, including state, scale color, and shape (Fig. 1b).

Root: The origin of roots was restricted to the bases of culms in *C. articulatus, C. bulbosus, C. esculentus, C. laevigatus, C. rotundus,* and *C. longus*, while in other taxa, roots emerged from the lower half of the horizontal rhizome. Root color was one of the most distinctive characteristics observed among the studied taxa (Fig. 1c).

Tuber: This feature was particularly specific to *C. esculentus, C. rotundus*, and *C. longus*, while it was absent in the other taxa (Fig. 1c).

Culm characteristics: The presence of basally bulbous traits was exclusive to *C. bulbosus, C. conglomeratus, C. esculentus,* and *C. rotundus*, while culm septa were distinguishing features in *C. articulatus* and *C. esculentus*. The culm cross-section varied among taxa, appearing in three forms: terete, trigonous, and triquetrous. Specifically, *C. articulatus, C. capitatus, C. conglomeratus, C. laevigatus,* and *C. papyrus* exhibited a terete cross-section, whereas *C. alopecuroides, C. alternifolius, C. bulbosus, C. compressus, C. difformis, C. imbricatus,* and *C. michelianus* subsp.*pygmaeus* displayed a trigonous form. In contrast, a triquetrous cross-section was observed in *C. digitatus, C. esculentus,* *C. fuscus, C. rotundus,* and *C. longus*. Culm nature varied among taxa, with character states including solitary, tufted, tufted to solitary, and solitary or branched patterns. Notably, *C. rotundus* and *C. longus* exhibited solitary culms, while *C. bulbosus* had either solitary or branched one. The remaining taxa showed a transition from tufted to solitary forms (Fig. 1d).

Leaf habit: Reduction in leaf sheaths was exclusively observed in *C. alternifolius, C. articulatus,* and *C. laevigatus,* whereas the other taxa possessed basal leaves. Ligule: This character was limited to *C. difformis, C. fuscus,* and *C. rotundus* among the studied taxa (Fig. 1e).

Morphological reproductive characters

Bract and Inflorescence: The characteristics of bract habit, insertion, and margin provided key descriptors for various taxa. Close bract insertion was noted in five taxa: *C. alternifolius, C. articulatus, C. michelianus* subsp. *pygmaeus, C. laevigatus* subsp. *laevigatus,* and *C. laevigatus* subsp. *distachyos,* while the other taxa exhibited separated bract insertion. The observed bract habit included spreading, erect, and erect patent, with margins categorized as serrate or entire. Notably, *C. alopecuroides, C. rotundus,* and *C. longus* were identified by their erect-patent and serrate bracts; *C. fuscus* also displayed an erect-patent habit but with an entire margin. Serrate and erect bracts were documented in *C. articulatus, C. difformis,* and *C. digitatus,* with entire and erect bracts being the most common. The spreading bract habit was exclusively observed in *C. michelianus* subsp. *pygmaeus, C. laevigatus* subsp. *laevigatus,* and *C. laevigatus* subsp. *distachyos* (Fig. 2a). The terminal position of the inflorescence was a common trait across all taxa, except for *C. laevigatus* subsp. *laevigatus* and *C. laevigatus* subsp. *distachyos,* which display a pseudo-lateral position. The inflorescence type varied between capitate and umbel-like forms. Notably, both capitate and umbel-like structures were observed in *C. fuscus* and *C. imbricatus*. The capitate form was characteristic of *C. capitatus, C. conglomeratus, C. compressus, C. michelianus* subsp. *pygmaeus, C. laevigatus* subsp. *laevigatus,* and *C. laevigatus* subsp. *distachyos*. In contrast, the remaining taxa exhibited umbel-like branched inflorescences (Fig. 2b).

Spikelet: Significant variation in spikelet morphology was observed across the *Cyperus* taxa examined. Spikelet shape ranged from lanceolate in *C. capitatus,* to lanceolate oblong in *C. fuscus,* and linear in *C. articulatus, C. bulbosus, C. papyrus,* and *C. rotundus*. Other shapes included linear-lanceolate (*C. longus*), linear-oblong (*C. compressus, C. difformis, C. digitatus, C. esculentus*), oblong-lanceolate (*C. conglomeratus, C. michelianus* subsp. *pygmaeus, C. laevigatus* subsp. *laevigatus, C. laevigatus* subsp. *distachyos*), and ovate-lanceolate (*C. alopecuroides*). *C. alternifolius* displayed a range from ovate to oblong-linear. The predominant spikelet arrangement was spicate, with notable exceptions: digitate in *C. difformis* and sub-digitate in *C. articulatus, C.*

compressus, C. rotundus, and *C. longus*. Rachilla wing presence was variable, with wingless rachillas identified in *C. alopecuroides, C. alternifolius, C. capitatus, C. conglomeratus, C. difformis, C. fuscus, C. laevigatus* subsp. *laevigatus, C. laevigatus* subsp. *distachyos,* and *C. michelianus* subsp. *pygmaeus,* while the other species exhibited winged rachillas (Fig. 2c).

Glume and keel: Glume morphology in the studied *Cyperus* taxa showed considerable diversity. Glume shape ranged from broadly ovate in *C. capitatus* to elliptical-ovate in *C. papyrus*. Lanceolate to ovate glumes were found in *C. alternifolius, C. compressus,* and *C. michelianus* subsp. *pygmaeus,* while *C. articulatus, C. conglomeratus, C. fuscus, C. imbricatus, C. laevigatus* subsp. *laevigatus,* and *C. laevigatus* subsp. *distachyos* had ovate glumes. *C. alopecuroides, C. esculentus, C. digitatus,* and *C. rotundus* exhibited ovate-elliptical glumes. *C. bulbo*sus displayed glumes ranging from oblong-ovate to lanceolate, and *C. longus* had oblong-lanceolate glumes. The apex morphology varied from acute to obtuse, and significant variability in glume coloration was also observed (Fig. 2d). The keel vein configuration varied among the taxa. *C. bulbosus, C. capitatus,* and *C. compressus* exhibited multiple veins, while *C. digitatus* possessed two parallel veins, and *C. michelianus* subsp. *pygmaeus* displayed one to three veins. The keel coloration encompassed various hues, including brown, green, dark green, and yellowish green (Fig. 2e).

Achene: The morphological diversity of achenes within *Cyperus* was remarkable, showcasing variation in shape, base structure, and coloration. Achene shapes ranged from broadly ellipsoid to obovoid, with species like *C. alternifolius* exhibiting broadly ellipsoid to slightly obovoid forms, while the two subspecies of *C. laevigatus* were consistently ellipsoid. Other taxa, such as *C. alopecuroides* and *C. difformis,* displayed ellipsoid to slightly obovoid shapes, whereas *C. michelianus* subsp. *pygmaeus, C. rotundus,* and *C. longus* featured ellipsoid-oblong forms. In contrast, *C. compressus* and *C. conglomeratus* have

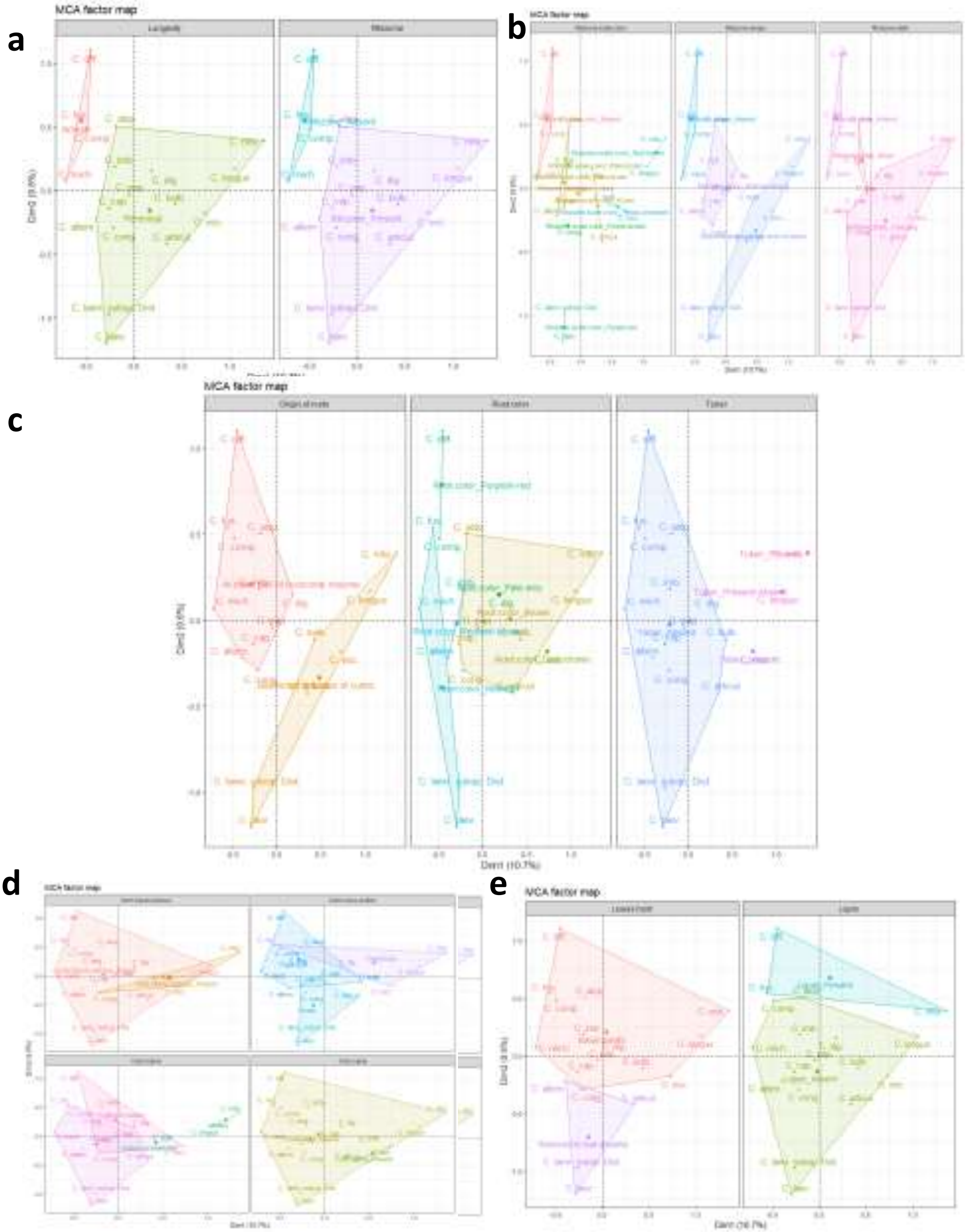


Fig. 1 MCA factor map ellipses from multiple correspondence analysis (MCA): **(a)** longevity and rhizome traits, **(b)** rhizome state, rhizome scale color, rhizome shape traits, **(c)** origin of roots, root color, and tuber, **(d)** culm traits (basely bulbous, cross-section, nature, and septa), and **(e)** leaf habit and ligule traits.

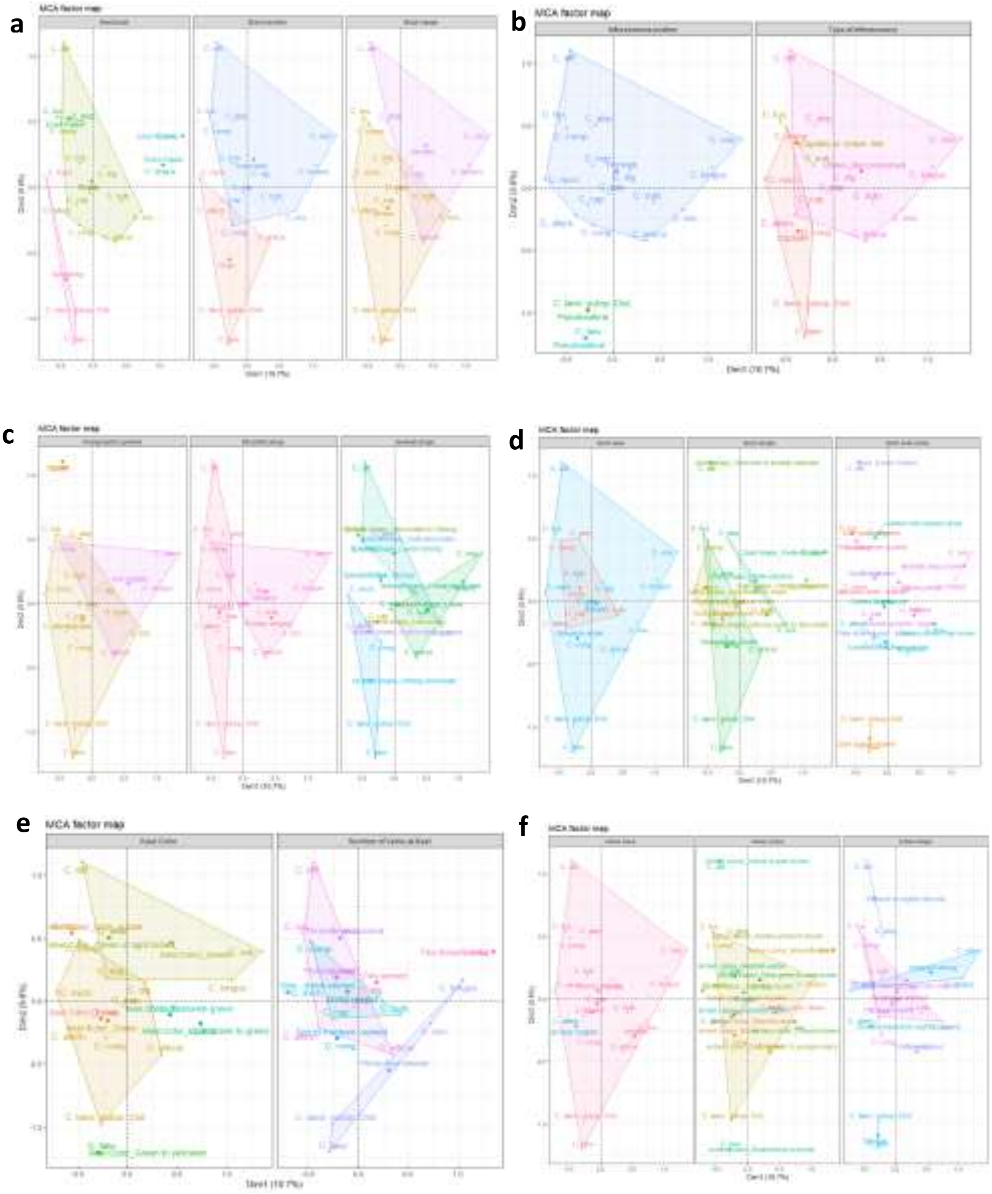


Fig. 2 MCA Factor map ellipses from the multiple correspondence analysis (MCA): **(a)** Bract traits (habit, insertion, and margin), **(b)** Inflorescence (type and position), **(c)** Spikelet (shape, arrangement, and Rachilla), **(d)** Glume traits (apex, color, and shape), **(e)** Keel (color and number of vein), **(f)** Achene traits (base, color and shape).

Obovoid achenes, and species like *C. bulbosus* and *C. esculentus* showed a range from obovoid to ellipsoid. Base structures also vary, with *C. papyrus* having a sessile base, *C. alternifolius* a broadly stipitate base, and *C. articulatus* and *C. esculentus* stipitate bases, while most other taxa possess short stipitate bases. Additionally, achene coloration varies significantly across species (Fig. 2f).

Pearson's correlations

Pearson's correlation analysis was performed to evaluate significant relationships and correlations among morphological traits (Fig. 3). The correlogram highlighted key characters that contributed to the differentiation between the examined taxa. The descriptors most strongly correlated with taxonomic differentiation included rhizome scale, root color, spikelet shape, number of flowers per spikelet, glume characteristics, glume side color, number of veins on the keel, keel color, achene shape, achene color, and achene length. In contrast, the remaining descriptors showed no significant correlation with the taxa under study. Positive correlations were observed among longevity, rhizome characteristics (scale, shape, and state), while these traits exhibited a negative correlation with root color. Reproductive descriptors displayed fluctuations, ranging from moderate positive to negative correlations.

Morphometric analysis

The morphometric analysis utilized multistate data comprising 30 qualitative and nine quantitative descriptors for the 18 taxa under investigation. The "factoextra" package in R was employed to perform hierarchical clustering and visualize the results as a dendrogram. This analysis identified five clusters derived from two main clusters. The first cluster (a), positioned at the bottom, included *C. conglomeratus, C. bulbosus,* and *C. capitatus* in subcluster a1, along with *C. articulatus, C. esculentus, C. rotundus,* and *C. longus* in subcluster a2. The second cluster (b) comprised three additional subclusters: subcluster 1b, which consisted of *C. laevigatus* and *C. laevigatus* subsp. *distachyos*; subcluster 2b, containing *C. compressus, C. difformis, C. fuscus,* and *C. michelianus* subsp. *pygmaeus*; and subcluster 3b, which included *C. papyrus, C. digitatus, C. imbricatus, C. alopecuroides,* and *C. alternifolius* (Fig. 4).

The principal component analysis (PCA) of 18 *Cyperus* taxa (Fig. 5), based on 39 qualitative and quantitative morphometric features, revealed a cumulative variance of 17% in the first dimension (Dim. 1) and 14.4% in the second dimension (Dim. 2). The first dimension (Dim. 1) primarily differentiates the taxa based on the variable's rhizome scale, glume width, culm basely bulbous, origin of roots, keel color, tuber, bract insertion, glume length, achene base, and spikelet width (Table 2).

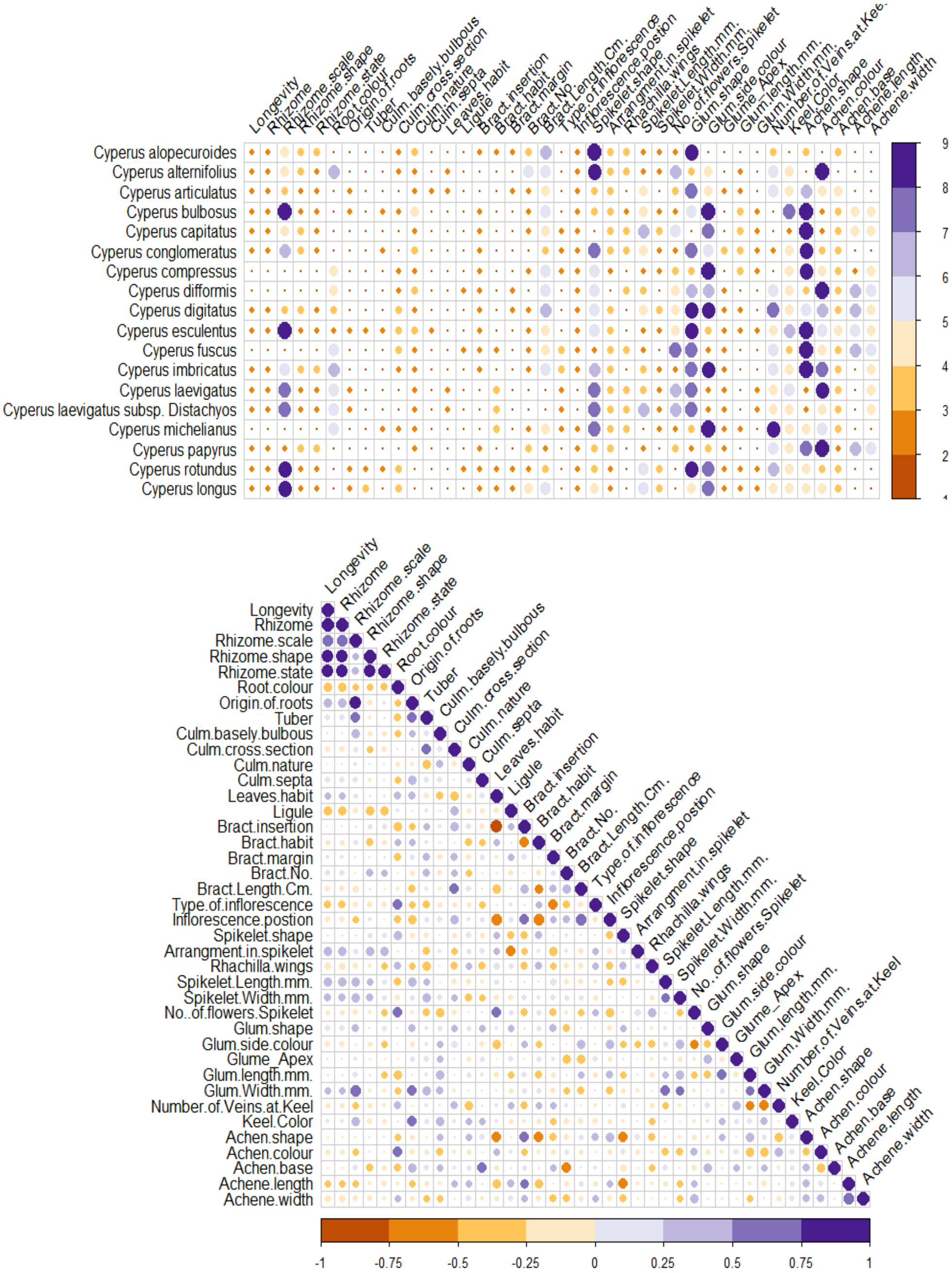


Fig. 3 Pearson's correlation analysis based on the correlation coefficients of morphological descriptors for positive and negative correlation variables, showed the most important character affected on the separation between the examined taxa

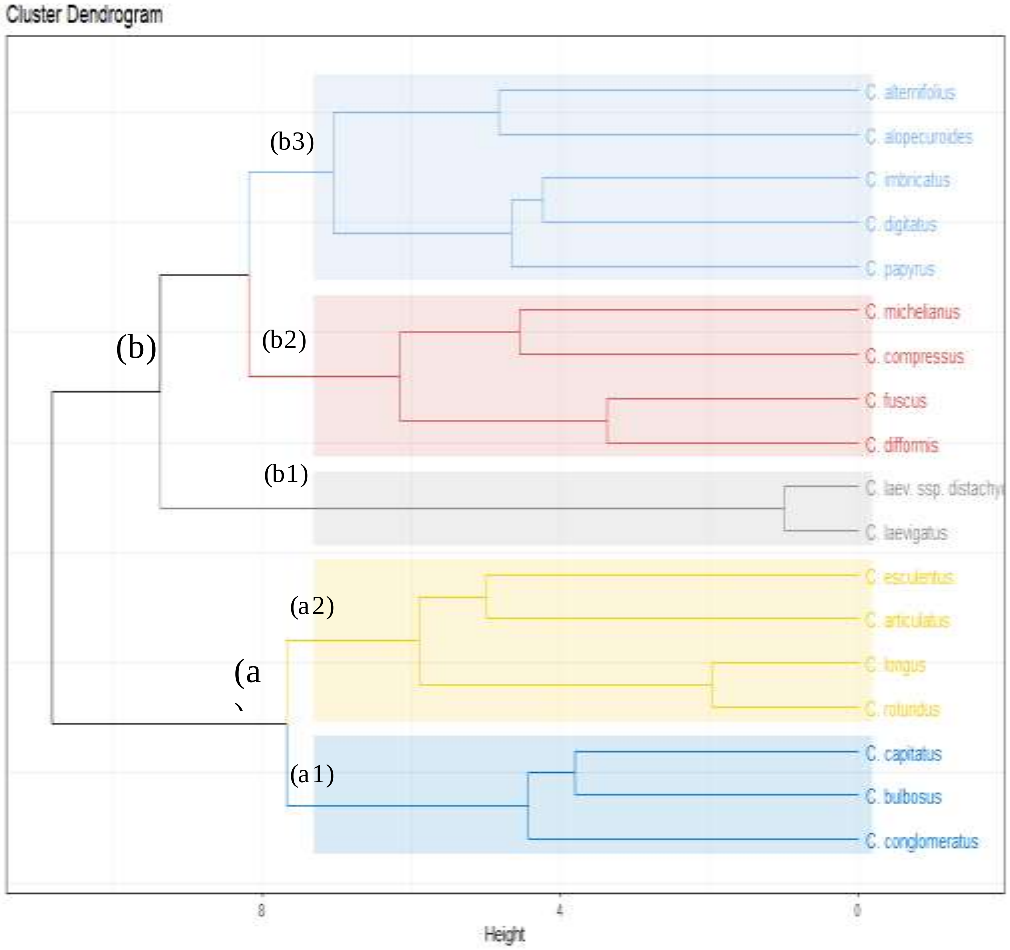


Fig. 4 Hierarchical clustering dendrogram based on multistate data for taxa under study

Taxa with high scores for these variables, including *C. conglomeratus, C. capitatus, C. articulatus, C. esculentus, C. bulbosus, C. rotundus,* and *C. longus*, were located in the positive direction of Dim. 1. Conversely, taxa with low scores for these variables, such as *C. laevigatus* subsp. *laevigatus, C. laevigatus* subsp. *distachyos, C. alternifolius, C. alopecuroides, C. imbricatus, C. papyrus, C. difformis, C. fuscus,* and *C. michelianus* subsp. *pygmaeus*, were in the negative direction of Dim 1. The second dimension (Dim. 2) primarily differentiates the taxa based on the variables leaves habit, rhizome, longevity, origin of roots, bract habit, ligule, achene length, bract insertion, and inflorescence position (Table 2).

The PCA biplot (Fig. 5) showed that the 18 taxa were clustered into five groups. The first group, located in the lower right quadrant of the biplot and along the positive end of Dim 1, included *C. conglomeratus*, *C. capitatus*, *C. articulatus*, *C. esculentus*, *C. rotundus*, and *C. longus*. The second group, located in the upper left quadrant of the biplot occupying the positive end of Dim 2, included *C. laevigatus* subsp. *laevigatus* and *C. laevigatus* subsp. *distachyos*. The third group, located in the lower left quadrant of the biplot, included *C. compressus*, *C. difformis*, *C. fuscus*, and *C. michelianus* subsp. *pygmaeus*. The fourth group, located in the bottom left quadrant of the biplot, occupied a median position in the diagram, including *C. papyrus*, *C. digitatus*, and *C. imbricatus*. The fifth group, including *C. alternifolius*, was in the upper left quadrant of the biplot occupying the negative end of Dim. 1, close to the second group.

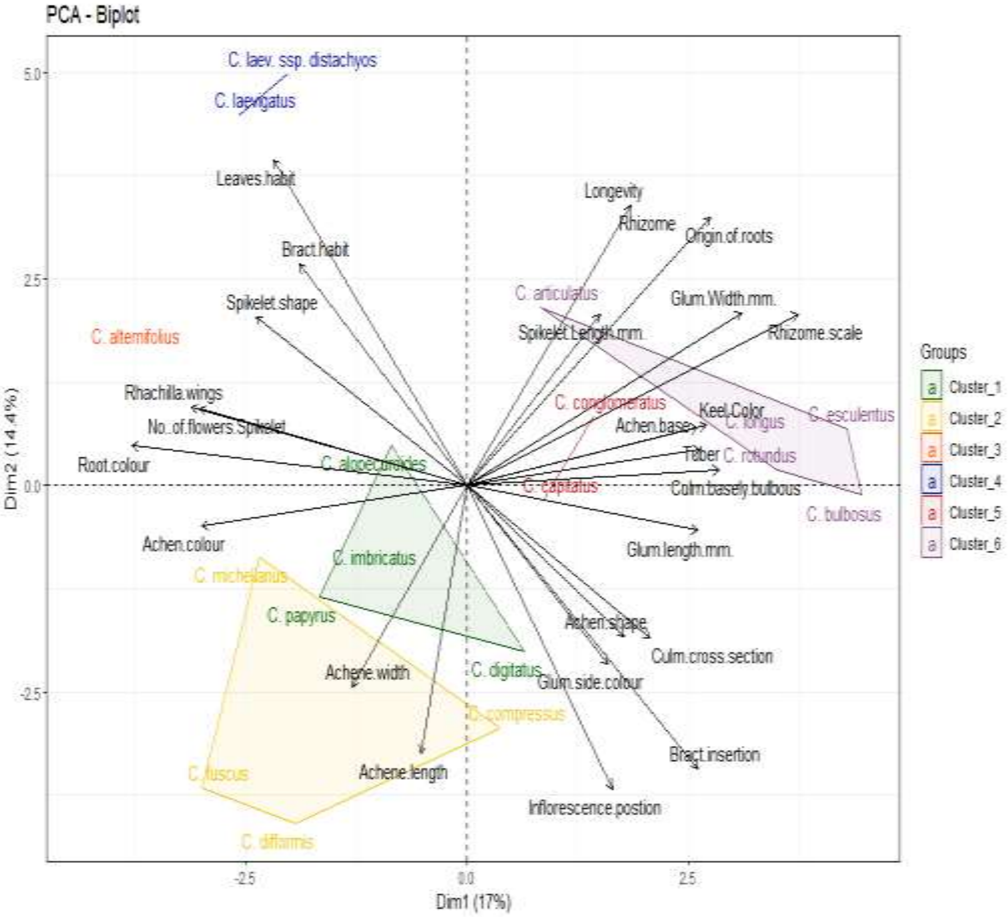


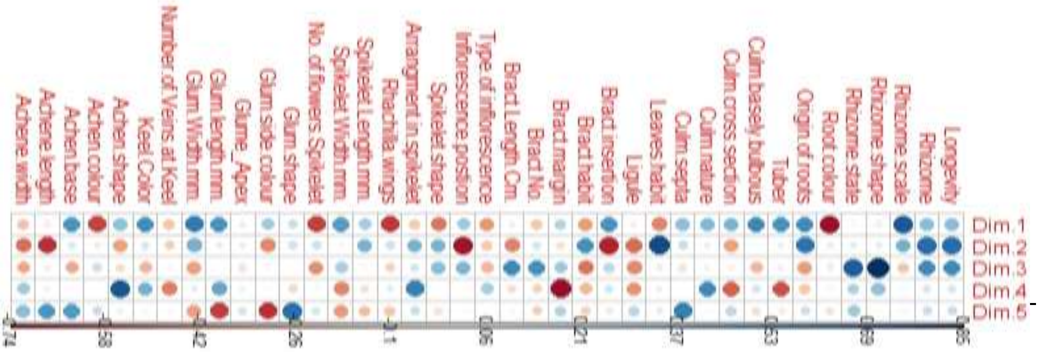
Fig. 5 Principal Component Analysis (PCA) of 18 *Cyperus* taxa using 39 qualitative and quantitative morphometric features, focusing on the association between different variables along the first two components. The length of the

variable arrow indicates the importance of distinct factors, with longer arrows contributing the most to the cluster discrimination

Table 2. Principal component analysis (PCA) was performed with the major characteristics related to the ordination of Dim. 1 and Dim. 2, including their eigenvalues and variance. Including figure-to-Pearson’s correlation for the significant character in the five dimensions, the blue circles indicate positive correlation, and the red circles indicate negative correlation. Significant correlations: *** = 0.001, ** = 0.01.

Dim. 1	**Correlation**	**Dim. 2**	**Correlation**
Rhizome scale	0.719***	Leaves habit	0.757***
Glume width (mm)	0.596***	Rhizome	0.651***
Culm basely bulbous	0.547**	Longevity	0.651***
Origin of roots	0.529**	Origin of roots	0.623***
Keel color	0.52**	Bract habit	0.514**
Tuber	0.505**	Ligule	-0.475**
Bract insertion	0.502**	Achene length	-0.624***
Glume length (mm)	0.501**	Bract insertion	-0.657***
Achene base	0.5**	Inflorescence position	-0.705***
Spikelet width (mm)	0.474**		
Achene color	-0.574**		
No. of flowers spikelet	-0.579**		
Rhachilla wings	-0.597**		
Root color	-0.725**		

	Dim. 1	Dim. 2	Dim. 3	Dim. 4
Eigenvalue	6.62	5.63	4.41	3.91
Variance %	16.97	14.42	11.30	10.03
Cumulative variance %	16.97	31.40	42.70	52.74



Morphometric and molecular combined data

The integration of molecular data (generated from five markers deposited at NCBI) and morphological data (comprising 39 multistate descriptors) provided a distinct resolution of the taxa under study (Fig. 6). The outgroup *Scirpoides holoschoenus* was distinctly isolated with a bootstrap value of 100. This was followed by five clusters, including three clusters and two single branches. The first cluster grouped *C. fuscus* and *C. difformis* with a bootstrap value of 100. Next, a single branch of *C. alternifolius* was separated with a bootstrap value of 89. Subsequently, a cluster containing *C. bulbosus* and *C. capitatus* was formed with a bootstrap value of 50, followed by a single branch of *C. conglomeratus*. The remaining taxa were grouped into a large cluster, which was further divided into three subclusters. The first subcluster, at the bottom, grouped *C. esculentus* and *C. compressus* with a bootstrap value of 100. The second subcluster, separated with a bootstrap value of 83, consisted of a clade containing *C. laevigatus* and another clade comprising *C. articulatus, C. rotundus,* and *C. longus*. The final subcluster, separated with a bootstrap value of 78, included a clade of *C. digitatus* and *C. michelianus* subsp. *pygmaeus*, and another clade containing *C. papyrus*, *C. imbricatus,* and *C. alopecuroides* with a bootstrap value of 83.

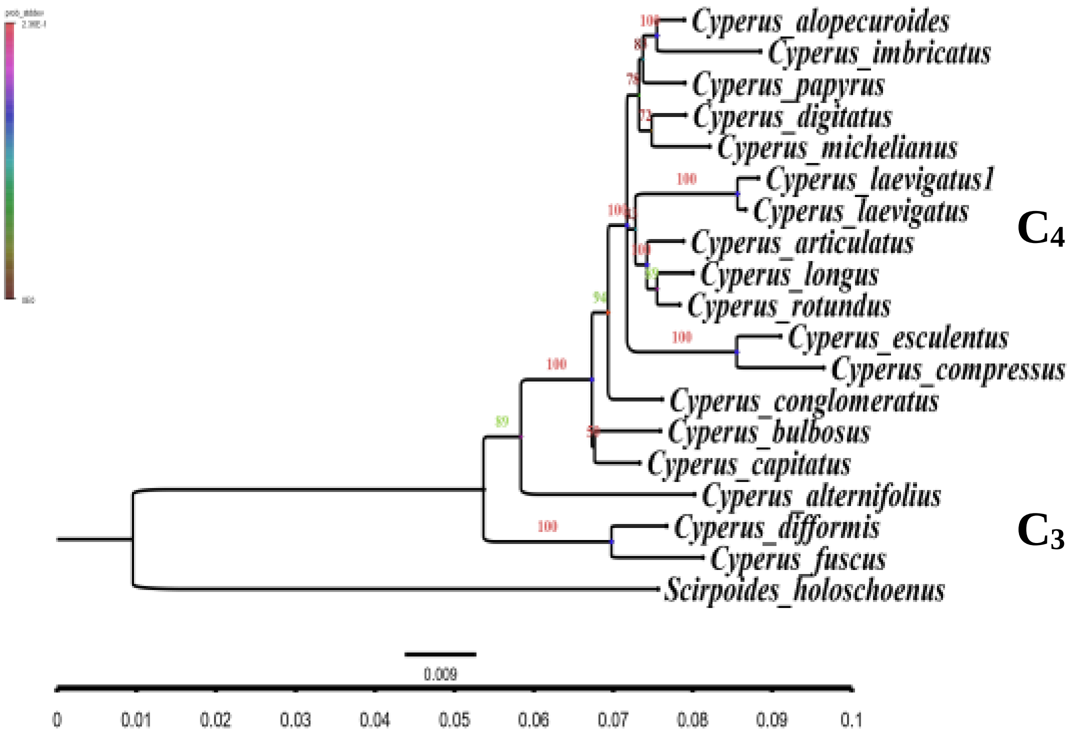


Fig. 6 Phylogenetic tree based on combined molecular and morphological data from the taxa studied

Discussion

The genus *Cyperus* is renowned for its taxonomic complexity, a consequence of its extensive morphological diversity and the challenges posed by convergent evolution and polyphyletic subgroups (Goetghebeur, 1998; Muasya *et al.*, 2002). In this study, we utilized an integrated approach combining morphometric analyses of 39 morphological characters with molecular data from five chloroplast markers to reassess the taxonomy of 18 *Cyperus* taxa in Egypt. Our findings elucidate the morphological variability and phylogenetic relationships within the genus, offering insights into its classification and suggesting potential sectional divisions.

Morphological variability and taxonomic significance

Our morphological analysis revealed considerable variability among the 18 *Cyperus* taxa, encompassing both vegetative and reproductive traits. Vegetative characters, such as longevity (annual vs. perennial), rhizome presence and structure, culm characteristics (e.g., basally bulbous, cross-section shape), and leaf habit, proved critical in distinguishing between taxa. For instance, the absence of rhizomes in annual species (*C. compressus, C. difformis, C. fuscus,* and *C. michelianus* subsp. *pygmaeus*) contrasted with their presence in perennials, while unique traits like reduced leaf sheaths in *C. alternifolius* and *C. articulatus* further highlighted species-specific differences (El-Habashy and Boulos, 2005).

Reproductive characters, including bract insertion, inflorescence position, spikelet shape, glume morphology, and achene structure, also exhibited significant variation. Pearson's correlation analysis identified key descriptors—such as rhizome scale, spikelet shape, glume morphology, and achene traits—as highly correlated with taxonomic distinctions. These findings corroborate earlier studies emphasizing the diagnostic value of reproductive structures in *Cyperus* taxonomy (Haines and Lye, 1983; Hefler and Longhi-Wagner, 2008; Shalabi and Gazer, 2015). However, our study extends this by demonstrating the complementary role of vegetative characters, which have been underutilized in traditional classifications.

The observed morphological correlations underscore the importance of selecting independent characters for taxonomic studies, as interdependent traits may obscure evolutionary relationships (Nasar *et al.*, 2024). Our integrated approach mitigates this by combining morphology with molecular data, providing a more robust framework for classification.

Morphometric clustering and Principal Component Analysis

Morphometric analyses, including hierarchical clustering and principal component analysis (PCA), grouped the 18 taxa into five distinct clusters based on morphological similarities. Cluster (a) comprises species like *C.*

conglomeratus, C. bulbosus, and *C. capitatus* (subcluster a1), sharing basally bulbous culms and specific rhizome traits, and *C. articulatus, C. esculentus, C. rotundus,* and *C. longus* (subcluster a2), united by traits like tuber presence and triquetrous culms. Cluster (b) included three subclusters, grouping species such as *C. laevigatus* subspecies (subcluster b1) based on pseudo-lateral inflorescences, and *C. compressus, C. difformis, C. fuscus,* and *C. michelianus* subsp. *pygmaeus* (subcluster b2) by their annual habit and spikelet characteristics **(**Fig. 4).

The PCA biplot, explaining 31.40% of the variance in the first two dimensions, reinforced these groupings. For example, *C. alternifolius* was distinctly separated due to its reduced leaf sheaths and close bract insertion, while *C. laevigatus* subsp. *laevigatus* and subsp. *distachyos* clustered together, reflecting their shared inflorescence and achene traits. These morphometric clusters provide a phenotypic basis for taxonomic delineation but require phylogenetic validation to distinguish evolutionary lineages from convergent adaptations (Muasya *et al.*, 2009; Gaafar *et al.*, 2021).

Phylogenetic insights from combined data

The phylogenetic tree, constructed from combined morphological and molecular data, offered a resolved classification with six main clades (excluding the outgroup *Scirpoides holoschoenus*) and strongly supported the paraphyletic of C_3 *Cyperus* that is basal to a monophyletic C_4 clade. It is notable that the clustering of *C. fuscus* and *C. difformis* (bootstrap value 100), supported by their shared annual habit and spikelet morphology, while *Cyperus alternifolius* emerged as a distinct clade (bootstrap value 89), consistent with its unique morphological features.

Among New World *Cyperus* species, *C. laevigatus* stands out as one of just two members of the subgenus *Juncellus* (sensu Kükenthal 1936). Its distinctive characteristics set it apart from all other New World *Cyperus* species: the presence of two stigmas and a highly compressed, disc-like achene. Notably, this achene is positioned with its face directed towards the rachilla., according to (Larridon *et al.*, 2013) *Cyperus laevigatus* recognised as Core *Pycreus* clade that appear as a paraphyletic entity including several *Cyperus* spp. *Cyperus esculentus* and *C. compressus* (bootstrap value 100), despite morphological differences, suggesting a close evolutionary relationship. This finding is also supported by (Reid *et al.*, 2014;Reid *et al.*, 2017), consistent with our results, while *C. rotundus* and *C. longus* grouped together, supporting their close affinity but with sufficient divergence to warrant separate species status.

These phylogenetic relationships both aligned with and further refined the morphometric clusters. For instance, the separation of *C. conglomeratus* from *C. bulbosus* and *C. capitatus* in the molecular tree (bootstrap value 50) suggests finer distinctions than morphology alone indicates. The integration of chloroplast markers (*rbc*L, matK, trnH-psbA, rpl32-trnL, ndhF) with morphological data enhances resolution, addressing limitations of morphology-based classifications prone to convergent evolution (Muasya *et al.*, 2002; Larridon *et al.*, 2014; Reid *et al.*, 2017).

In contrast to the classification proposed by NCBI Taxonomy (Schoch *et al.*, 2020), our analysis yielded divergent results for the taxa under examination. While NCBI Taxonomy categorized most of the studied taxa as *Cyperus* subgenus *Cyperus,* C_4 *Cyperus incertae sedis* (no rank), we observed discrepancies in this classification. Notably, NCBI Taxonomy placed *Cyperus laevigatus* within *Cyperus* subgen. *Cyperus* (*Pycreus* clade) and assigned *Cyperus fuscus* to Clade C_3 *Cyperus, Cyperus* section *Fusci,* which only partially aligns with our findings.

Implications for taxonomy and sectional classification

Our integrated approach lays the groundwork for revising the sectional classification of *Cyperus* in Egypt. Morphometric and phylogenetic analyses confirmed that the taxa *C. alternifolius, C. fuscus,* and *C. difformis* belong to the C_3 *Cyperus* clade, specifically within the subgenus *Anosporum*. This clade is divided into two sections (Larridon *et al.*, 2011 b): (1) *Cyperus* section *fusci*, comprising *C. fuscus* and *C. difformis*, which share an annual growth habit, and lanceolate spikelets, and (2) *Cyperus* section *alternifolii* (previously section *Vfiginati* Boeck (sensu Kükenthal, 1936), which includes *C. alternifolius,* characterized by reduced leaf sheaths and closely inserted bracts.

The Core *Pycreus* clade, corresponding to *Cyperus* subgenus *Juncellus* (*Cyperus* section *Juncellus* Griseb.), includes *C. laevigatus* and its subspecies: *laevigatus* and *distachyos,* noted for their pseudo-lateral inflorescences and ellipsoid achenes. The subgenus *Cyperus* (C_4 *Cyperus*) consists of members from eleven sections identified by Kükenthal (1936), while El-Habashy (1988) acknowledged two subgenera and eight sections.-Additionally, Reynders *et al.* (2011a) and Larridon *et al.* (2013, 2014) recognized ten sections, as detailed in the supplementary Table (3).

To address the existing confusion, we propose the *Papyrus* complex, which includes five sections: *C. alopecuroides, C. imbricatus, C. papyrus, C. digitatus,* and *C. michelianus* subsp. *pygmaeus* (Reynders *et al.*, 2011a; Larridon *et al.*, 2013, 2014). We also suggest the *Cyperus* complex, encompassing four sections: *C. esculentus, C. compressus, C. articulatus, C. rotundus,* and *C. longus,* which may require further subdivision based on phylogenetic subclades. Lastly, the *Bobartia* complex consists of three sections: *C. conglomeratus, C. capitatus,* and *C. bulbosus,* all sharing bulbous culms and specific rhizome characteristics.

Limitations and Future Directions

Despite its strengths, our study has limitations. The use of herbarium specimens may introduce preservation biases, potentially affecting morphological measurements. The reliance on chloroplast markers, while informative, captures only maternal lineages, necessitating the inclusion of nuclear markers in future studies to provide a more comprehensive genetic perspective. Expanding the taxon sampling to encompass additional *Cyperus* species from the broader *Cyperus s.l.* clade would further refine phylogenetic relationships and validate our sectional proposals (Larridon *et al.*, 2021).

Conclusions

This study demonstrates the efficacy of integrating morphometric and molecular analyses to resolve taxonomic complexities in the genus *Cyperus*. By combining detailed morphological assessments with phylogenetic insights, we have elucidated the diversity and relationships among Egyptian *Cyperus* taxa, proposing a revised sectional classification. These findings enhance our understanding of the genus's evolutionary history and provide a model for future taxonomic revisions in taxonomically challenging plant groups.

Author contributions

All authors consented to participate, read, and approve the final manuscript for publication.

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Supplementary Table 1a. Description of studied taxa based on 30 qualitative morphological characters, character states and their codes for the data analyses.

Code	Morphological characters	Character states and taxonomic codes	Code	Morphological characters	Character states and taxonomic codes
1	Longevity	Annual (1), Perennial (2)	**16**	Bract habit	Erect (1), Erect-Patent (2), Spreading (3)
2	Rhizome	Absent (1), Present (2)	**17**	Bract margin	Entire (1), Serrate (2)
3	Rhizome scale color	Absent (1), Black (2), Brown (3), Dark- brown (4), Pale-brown (5), Purple- brown (6), Purple-red (7), Red-brown (8), Yellow-brownish (9)	**18**	Type of inflorescence	Umbel-like branched (1), Capitate (2), Capitate or Umbel-like (3)
4	Rhizome shape	Absent (1), in the form of stolon (2), Massive woody (3)	**19**	Inflorescence position	Pseudo lateral (1), Terminal (2)
5	Rhizome state	Absent (1), Creeping (2), short (3)	**20**	Spikelet shape	Lanceolate (1), Lanceolate to Oblong (2), Linear (3), Linear-lanceolate (4), Linear-oblong (5), Oblong (6), Oblong-lanceolate (7), Ovate to oblong-linear (8), Ovate-lanceolate (9)
6	Root color	Brown (1), Dark brown (2), Pale wiry (3), Purplish red (4), Reddish (5), Reddish brown (6)	**21**	Arrangement in spikelet	Digitate (1), Sub-digitate (2), Spictate (3)
7	Origin of roots	At lower half of horizontal rhizome (1), Restricted to bases of culms (2)	**22**	Rhachilla wings	Winged (1), Broadly winged (2), Wingless (3)
8	Tuber	Absent (1), Present (2), Present /Absent (3)	**23**	Glume shape	Broadly ovate (1), Elliptical-ovate (2), Lanceolate to ovate (3), Oblong-lanceolate (4), Oblong-ovate to lanceolate (5), Orbicular to broadly obovate (6), Ovate (7), Ovate-elliptical (8)

Contd. Supplementary Table 1a Description of studied taxa based on 30 qualitative morphological characters, character states and their codes for the data analyses.

Code	Morphological characters	Character states and taxonomic codes	Code	Morphological characters	Character states and taxonomic codes
9	Culm basely bulbous	Absent (1), Present (2)	**24**	Glume side color	Golden with reddish strips (1), Dark purple Hyaline (2), Golden yellow-Pale brown (3), Greenish yellow-pale brown (4), Pale stramineous - brown (5), Red purple Hyaline (6), Reddish deep brown (7), Reddish-golden (8), Reddish-purplish hyaline (9), Straw-golden (10), Yellow (11), Yellowish brown hyaline (12), Yellowish white hyaline (13)
10	Culm cross-section	Terete (1), Trigonous (2), Triquetrous (3)	**25**	Glume Apex	Acute (1), Obtuse (2), Obtuse to acute (3)
11	Culm nature	Solitary (1), Tufted (2), Tufted to solitary (3), solitary or branched (4)	**26**	Number of Veins at Keel	Many-veined (1), Ten-fourteen-veined (2), Three-seven-veined (3), Three-five-veined (4), Three-veined (5), Two-three-veined (6), Two-veined (7), One-three-veined (8)
12	Culm septa	Absent (1), Present (2)	**27**	Keeling	Green or light brown (1), Brown (2), Dark purple (3), Green (4), Green to yellowish (5), Light brown to green (6), Yellowish-green (7)
13	Leaves habit	Basal leaves (1), Reduced to leaf sheaths (2)	**28**	Achene shape	Broadly ellipsoid to slightly obovoid (1), Ellipsoid (2), Ellipsoid to slightly obovoid (3), Ellipsoid-oblong (4), Oblong to narrowly ellipsoid (5), Oblong-ellipsoid (6), Oblong-triangular (7), Obovoid (8), Obovoid to ellipsoid (9)
14	Ligule	Absent (1), Present (2)	**29**	Achene color	Golden-yellow to brown (1), Black (2), Blackish-brown (3), Brown (4), Brown or black (5), Dark-brown (6), Dark-brown to purplish-black (7), Golden to brown (8), Grayish-brown (9), Olive-green to dark brown (10), Reddish-yellow (11), Stramineous to brown (12), Yellow to pale brown (13), Yellowish-brown (14)
15	Bract insertion	Close (1), Separated (2)	**30**	Achene base	Broadly stipitate (1), Sessile (2), Shortly stipitate (3), Stipitate (4)

Supplementary Table 1b. Description of studied taxa based on 9 quantitative morphological characters, character states, and their codes for the data analyses.

Code	Morphological characters	Character states and taxonomic codes	Code	Morphological characters	Character states and taxonomic codes
1	Bract no.	2-5 (1), 3-9 (2), 4-10 (3), 5-16 (4), 10-25 (5)	**6**	Glum length(mm)	≥2 (1), <2 (2), ≤3 (3)
2	Bract Length (cm)	2-4 (1), 3-6 (2), 5-30 (3), 10-20 (4), 15-50 (5), 60-70 (6)	**7**	Glum Width(mm)	≥1.5 (1), <1.5 (2)
3	Spikelet Length(mm)	2.5-5 (1), 3-12 (2), 4-23 (3), 5-45 (4), 8-6 (5), 10-50 (6)	**8**	Achene length (mm)	0.75-1.5 (1), 1.2-1.6 (2), 1.5-1.7 (3), 1.6-2.8 (4), 1.8-2 (5), 2.9-10 (6)
4	Spikelet Width (mm)	≥1.5 (1), ≤2 (2) ≤3 (3)	**9**	Achene width (mm)	0.3-0.7 (1), 0.5-0.8 (2), 0.6-0.9 (3), 0.8 – 1.8 (4), 1.9 – 4 (5).
5	No. of flowers/Spikelet	11-22 (1), 13-27 (2), 15-30 (3), 16-18 (4), 19-20 (5), 20-21 (6), 25-30 (7)			

Supplementary Table 2. List of the examined species of *Cyperus*, and the NBCI code of the *rbc*L, matK, trnH-psbA, rpl32-trnL, and ndhF sequences.

Molecular marker / Taxa	***rbc*L**	**matK**	**trnH-psbA**	**rpl32-trnL**	**ndhF**
Cyperus alopecuroides	MF668590_1	KX369424.1	KX405724.1	HE993687.1	KX405845.1
Cyperus alternifolius	AM999802.1	DQ401373.1	HQ705818.1	FM160528.1	HQ181110.1
Cyperus articulatus	KJ773422.1	KX369427.1	KX405726.1	KX405622.1	---------------
Cyperus bulbosus	----------------	---------------	HE993900.1	MN901104.1	---------------
Cyperus capitatus	AM999803.1	---------------	HE993901.1	HE993690.1	---------------
Cyperus conglomeratus	MF694699.1	---------------	MN885629.1	MN901102.1	---------------
Cyperus compressus	OL434796.1	KX369435.1	KX405735.1	KX405629.1	---------------
Cyperus difformis	HM849935.1	KX369441.1	KX405741.1	KX405633.1	KX405857.1
Cyperus digitatus	JQ591222.1	KX369442.1	HG963567.1	KX405635.1	KX405858.1
Cyperus esculentus	MG227263.1	KJ772700.1	KX405753.1	KX405647.1	KX405870.1
Cyperus fuscus	AM999806.1	KX369463.1	KX405761.1	KX405657.1	FM160532.1
Cyperus imbricatus	----------------	KX369471.1	KX405769.1	KX405664.1	KX405887.1
Cyperus laevigatus	MK529931.1	MK521640.1	HE993910.1	HE993701.1	---------------
Cyperus laevigatus	Y13017.1	--------------	HE993909.1	HE993700.1	---------------
Cyperus michelianus	NC_061334.1	NC_061334.1	---------------	NC_061334.1	NC_061334.1
Cyperus papyrus	KY627528.1	KX036931.1	OR523176.1	HQ705892.1	AY465642.1
Cyperus rotundus	MZ750368.1	MN492681.1	OR523180.1	MN901105.1	KX405926.1
Cyperus longus	AM999810.1	HM850855.1	HE993912.1	HE993702.1	FM160536.1

Supplementary Table 3. The sectional classification of *Cyperus* taxa under study in Egypt, proposed by Kükenthal (1936), El-Habashy (1988), and Larridon et al. (2013b, 2014) and NCBI Taxonomy (Schoch et al. 2020) (https://www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi?mode=Undef&id=4610&lvl=3&lin=f&keep=1&srchmode=1&unlock).

Classification	**Kükenthal (1935-36)**			**El-Habashy (1988) Unpublished work**		**Larridon et al. (2011a), Larridon et al. (2013), Verloove (2014)**		**NCBI Taxonomy Schoch et al. (2020)**		
Taxa	**Subgenus**	**Pars**	**Section**	**Subgenus**	**Section**	**Subgenus**	**Section**	**Clade**	**Subgenus or Section.**	**unrank**
C. laevigatus L.	Juncellus		*Laevigati* Kükenth.	*Juncellus*	*Laevigati*	subg. *Cyperus*	*Juncellus* Griseb.	Pycreus clade		
C. alopecuroides Rottb.	Eucyperus	Choristachys	*Exaltati* Kunth.	*Juncellus*	*Alopecuroidei*		*Alopecuroidei* Nees	C4 *Cyperus*	*C.* subgen. *Cyperus*	C4 Cyperus incertae sedis
C. imbricatus Retz.			*Exaltati* Kunth.	*Cyperus*	*Exaltati*		Not listed			
C. papyrus L.			*Papyrus* (Willd.) C. B. Clarke.	*Cyperus*	*Papyrus*		*Papyrus* (Willd.) C. B. Clarke.			
C. digitatus L.			*Fastigiati* Kükenth.	*Cyperus*	*Exaltati*		*Pygmaei* Cherm. ex Y.L. Chang,			
C. michelianus (L.) Link		Pycnostachys	*Dichostylis* (P. Beauv.) Baillon.	*Cyperus*	*Dichostylis*		*Dichostylis* sensu Kükenthal (1936)			

C. articulatus L.		Choristachys	*Brevifoliati* C. B. Garke.	*Cyperus*	*Brevifoliati*		Not listed			
C. rotundus L.			*Rotundi* C. B. Clarke.	*Cyperus*	*Cyperus*		Rotundi C.B.Clarke			
C. longus L.			*Rotundi* C. B. Clarke.	*Cyperus*	*Cyperus*		Rotundi C.B.Clarke			
C. esculentus L.			*Esculenti* Kükenth.	*Cyperus*	*Cyperus*		*Cyperus*			
C. compressus L.			*Compressi* KuntK.	*Cyperus*	*Compressi*		*Compressi* Nees			
C. bulbosus Vahl			*Tunicati* G. B. Glarke.	*Cyperus*	*Cyperus*		*Bulbosi* C.B. Clarke			
C. conglomeratus *Rottb*.		Pycnostachys	*Bobartia* (L.) C. B. Clarke.	*Juncellus*	*Bobartia*		*Bobartia* (L.) C.B. Clarke			
C. capitatus (Poir.) Vand.			*Bobartia* (L.) C.B. Clarke.	*Juncellus*	*Bobartia*		*Galilea* (Parl.) T.V. Egorova			
C. alternifolius L.	Eucyperus		*Vfiginati* Boeck.	*Cyperus*	*Alternifoliate*	subg. *Anosporum*	*Alternifolii* (Kunth) C.B. Clarke.		*C.* subgen. *Cyperus*	
C. difformis L.			*Fusci* Kunth.	*Cyperus*	*Fusci*		*Fusci* (Kunth) C.B. Clarke.			
C. fuscus L.			*Fusci* Kunth.	*Cyperus*	*Fusci*		*Fusci* (Kunth) C.B. Clarke.	C3 *Cyperus*	sect. *Fusci*	