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Evolution of macro and micromorphology of *Eriocaulon* (Eriocaulaceae) and its relation with the aquatic environment

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Abstract: *Eriocaulon* L. is a pantropical genus comprising approximately 495 species. Previous taxonomic studies have proposed infrageneric classifications based on selected morphological characters; however, molecular phylogenetic analyses have shown that most of these classifications are paraphyletic. A recent multivariate analysis of anatomical data identified two major groups within the genus: one composed of amphibious species and the other of aquatic species. In this context, the present study aims to test the hypothesis that these groups correspond to distinct evolutionary clades by conducting a cladistic analysis of *Eriocaulon* based on morphological data. Our analysis included 65 species of *Eriocaulon* and seven outgroup species, using a dataset of 89 macro- and micromorphological characters. Parsimony analyses conducted in TNT recovered 24 equally parsimonious trees. In all analyses, *Eriocaulon* was resolved into two main clades. One clade comprises amphibious species from Africa and the Americas and shares plesiomorphic character states with *Mesanthemum* Körn., including palisade epidermal cells, stomatal chambers, and numerous vascular bundles in the leaf. The other clade, comprising aquatic species distributed across all continents, is characterized by derived character states, including a reduced number of vascular bundles, isodiametric epidermal cells, and the loss of stomatal chambers. These results suggest that the evolutionary history of *Eriocaulon* is closely tied to anatomical adaptations that facilitate colonization of aquatic environments.

Keywords: Poales, Pipeworts, Taxonomy, Anatomy, Aquatic habitat, Evolution

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Introduction

The genus *Eriocaulon* L. (Eriocaulaceae) comprises 495 accepted species with amphibious and aquatic habits (POWO, 2025). The genus exhibits pantropical distribution and has centers of diversity in Africa, South America, and the Indian subcontinent (Leach, 2017; Govaerts, 2006). It is a monophyletic group within the subfamily *Eriocauloideae* (Andrade *et al.*, 2010; Giulietti *et al.*, 2012) and is closely related to *Mesanthemum* Körn., an African genus with 16 species (Liang, 2019; POWO, 2025). Past taxonomic studies have predominantly focused on Asian species of *Eriocaulon* (Fyson, 1919-1923; Satake, 1940; Wei-Liang, 1991; Ansari & Balakrishnan, 1994; Zhang, 1999), generating extensive data on species morphology and resulting in infrageneric classifications based on arbitrary characters. However, these morphology-based studies have highlighted the challenges in classifying species within this genus due to a significant intraspecific variability and limited interspecific differences (Fyson, 1919-1923; Zhang, 1999). Zhang (1999) was the first to perform a phylogenetic analysis using morphological data, confirming the monophyly of the genus. More recently, Larridon *et al.* (2019) conducted the first molecular phylogenetic study on *Eriocaulon*. Their topology, based on four plastid and one nuclear marker, revealed two major clades: one comprising a few robust species from Asia and Australia, and the other including the remaining species. A subsequent molecular phylogeny based on Indian species (Darshetkar *et al.*, 2021) recovered three major clades. Most recently, Baleeiro *et al.* (2025) expanded Larridon's sampling by including all Australian species and identified five major clades, with Asian, African, and American taxa being sister to Australian species in each clade, suggesting multiple migration events. Although these phylogenies represent significant contributions to understanding the evolutionary relationships within *Eriocaulon,* they do not provide a global framework for the evolution of morphological characters across the genus. A recent study using Principal Component Analysis (PCA) indicated a correlation between life form and leaf anatomy in *Eriocaulon*, with amphibian and aquatic species exhibiting distinctive anatomical traits (Khoshnaw *et al.*, 2022). However, it remains unclear whether this correlation reflects underlying evolutionary processes. Morphology-based cladograms are crucial for evaluating evolutionary patterns and elucidating the origin and diversification of characters (Wheeler, 2008). Furthermore, accurate mapping of synapomorphies to clades is only possible when morphology is integrated into phylogenetic analysis, producing more robust results (Assis, 2009; Assis & Rieppel, 2011). In this study, we present a morphology-based cladistic analysis of *Eriocaulon* to test the hypothesis that amphibian and aquatic species represent distinct clades and to explore additional hypotheses related to character evolution.

Materials and Methods:

Morphological data: A thorough selection of morphological characters was conducted across a wide range of specimens from the following herbaria: BHCB, CESJ, HUFS, HUFU, INPA, OUPR, P, R, RB, SP, SPF, and UB herbaria (Thiers, continuously updated), online herbarium databases (K, P, RB), and specialized literature (Körnicke, 1863; Ruhland, 1903; Phillips, 1997; Ansari & Balakrishnan, 1994, 2009; Zhang, 1999). The seeds were examined using a Jeol JSM 6390 LV scanning electron microscope (SEM). The samples were placed on metal stubs previously coated with carbon tape and then subjected, for about three minutes, to gold–palladium sputtering in a Denton Vacuum Desk IV device. The terminology of seed ornamentation follows Barthlott (1981). The shape of secondary projections was defined according to the terminology of Radford (1986). The terms "T-" and "ribbon-" shaped used by Nair (1987), Giulietti *et al.* (1988), and Zhang (1999) were followed. The "J" shape is proposed here and named because of its resemblance to that letter of the alphabet. Anatomical preparation and observation were standardized as per Khoshnaw *et al.* (2022).

Terminal species: The analyses included 72 species, with the ingroup comprising 65 species (Appendix 1). Among these, 36 species are exclusive to the Americas, six to Africa, 14 to Asia, six to Oceania, one to both Europe and North America, and two species are widely distributed across multiple regions. Terminal taxa were selected to represent all the categories proposed by Körnicke (1863) and Zhang (1999), including the type species and others that exemplify morphological diversity (Appendix 2). The outgroup consisted of species belonging to the genus *Mesanthemum* (4 spp.), *Syngonanthus* Ruhland, *Comanthera* L.B. Sm., and *Paepalanthus* Mart. (Appendix 1). Some states of character were raised using specialized literature (Appendix 1).

Characters: 89 characters were selected, 66 referring to the external morphology of the vegetative and reproductive parts, and 23 related to the anatomy (Appendix 3). Among them, 87 were informative. The first two characters are continuous and were analysed as such (Goloboff, 2006); all others are discrete. The discrete characters were elaborated following the methodology proposed by Sereno (2007). Character states were unordered.

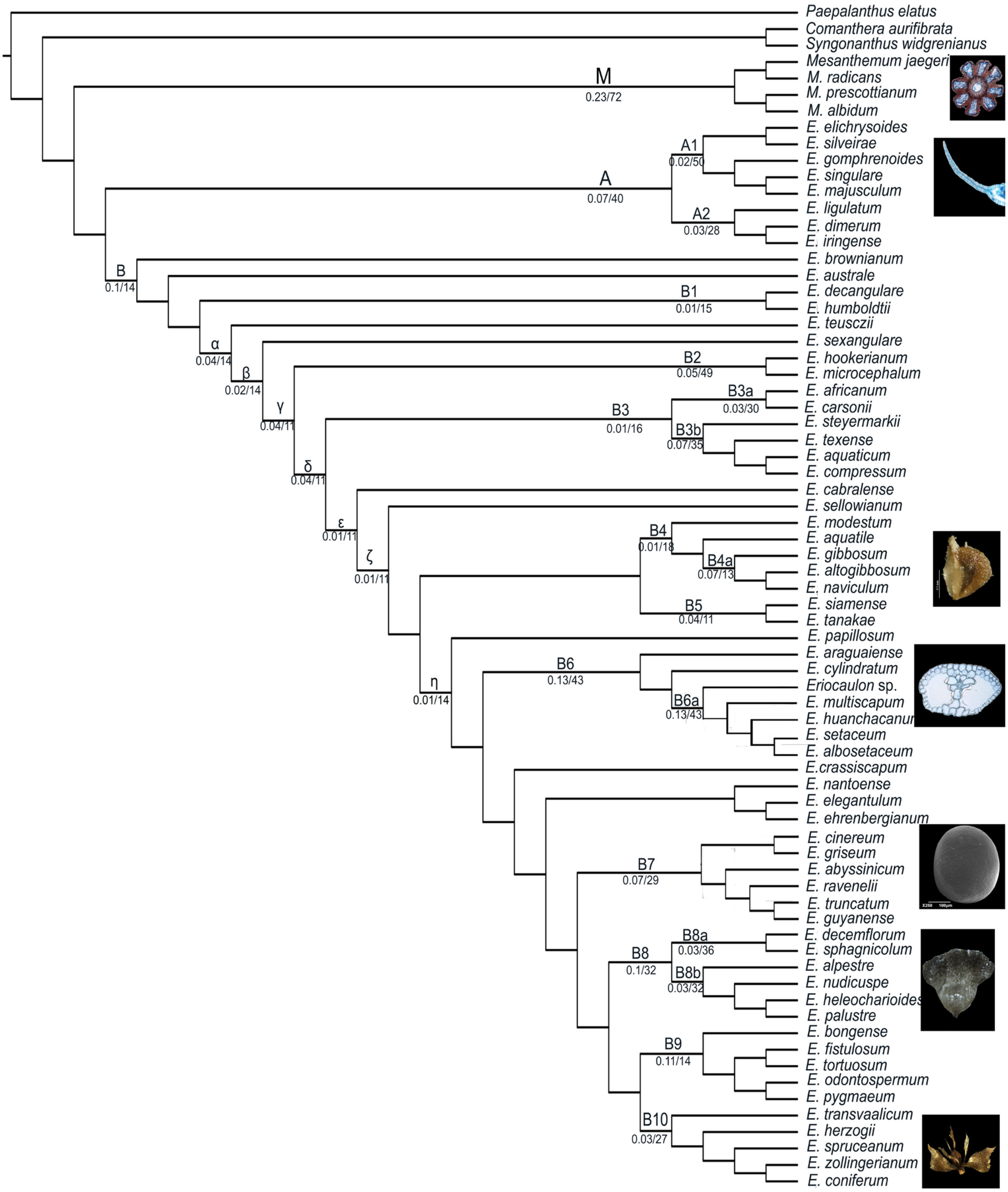

Fig. 1. Tree obtained from cladistic analysis of continuous and numerical morphological data set. Numbers indicate absolute/relative Bremer index. M indicates the Mesanthemum clade. The letters A and B indicate the main clades in *Eriocaulon*. Letters α-η indicate major clades inside B with synapomorphies linked to the conquest of the aquatic environment: α reduction of leaf vein number, leaf sinuous/terete in cross section. β annual life cycle, γ the stomatic chambers are absent, and the diaphragm is loosely aggregated, δ leaf with obtuse margin in cross section and hypodermis with circular cells, ε show floral bracts obtrullate and *palisade* epidermal cells, ζ adaxial sheath extension absent and *vascular bundle* is near of epidermis, η the leaf number becomes less than nine. A1-A2 small clades inside A. B1-B10 indicating small clades inside B. Photos - clade M scape in cross section of M. jaegeri showing radial symmetry with the ribs composed of diaphragm tissue and a lacuna in the medulla. Clade A leaf in cross-section of *E. ligulatum* showing the acute edge of the leaf. Clade B4 gibbous sepals of *E. gibbosum*. Clade B6 leaf in cross-section of *E. setaceum*, showing one nerve. Clade B7 seeds without secondary projections of *E. griseum*. Clade B8 sepal in the spathe of the pistillate flowers of *E. palustre*. Clade B10 winged sepals of pistillate flowers of *E. eurypeplon*.

Matrix: To create the data matrix of discrete characters, we used Nexus (Xu *et al.*, 2020). The matrix of continuous characters was elaborated in TNT, and subsequently, we combined the two matrices in the TNT program to perform the cladistic analysis (Goloboff & Catalano, 2016).

Searches: We performed searches with a numeric and mixed (continuous and numeric characters) matrix, with and without implied weighting. The following searches were performed: traditional search with 10000 replicates, retaining one tree per replicate, and using the new technology: sect search + tree fusion, drift + tree fusion, and ratchet + tree fusion. We used the algorithm to search for the best k values in g concavity (Goloboff *et al.*, 2008, 2018). The support values for the branches in the TNT were calculated using the Bremer index (1994), retaining trees with up to five additional steps beyond the number of steps in the most parsimonious trees, and collapsing branches with support equal to zero. Additionally, we utilize the combined Bremer support retaining trees up to five steps, with the fit difference set to one.

Trees: The searches provided twenty-four trees. We selected the only tree found in the traditional search, using the mixed matrix and K = 10 to analyze synapomorphies, and the only tree found in the traditional search using the numerical matrix with K = 10 to reconstruct characters. The Figtree program (Rambaut, 2010) was used to map the evolution of characters. The synapomorphies (*) and features that help to characterize the clades are summarized in the results.

Results

The tree of mixed matrix and traditional search (Fig. 1) yields CI 0.23, RI 0.6, and a fit of 24.58097. *Mesanthemum* is recovered as the sister group to *Eriocaulon*. *Mesanthemum* includes amphibious and aquatic species characterized by spathulate and petaloid floral bracts and pistillate flowers with membranous sepals. Seeds are spheroid, and the seed coat bears cells with anticlinal and periclinal walls of similar length, each bearing long pyramidal projections (Fig. 2a, b), which confer a fringed appearance. Scapes exhibit radial symmetry, with ribs composed of diaphragm tissue; between ribs occur sclerenchyma columns (Fig. 2c). The endodermis surrounds the external vascular bundles, and the medulla contains a lacuna (Fig. 2c). *Eriocaulon* is distinguished by staminate flowers with free petals (Fig. 2d), olive-colored anthers, ovoid seeds with secondary projections on anticlinal and periclinal walls (Fig. 2e), and scapes bearing sclerenchyma in the ribs (Fig. 2f).

In all searches, *Eriocaulon* is resolved into two main clades (Fig. 1). Clade A comprises robust, amphibious species from Africa (AF) and South America (SA) (Fig. 3a). These species exhibit a closed scape sheath with a truncate apex (Fig. 3b), and large, compact inflorescences (Fig. 3c). Seeds typically bear J-shaped projections adhered to the seed coat (Fig. 3d, e). Plesiomorphic character states shared by *Mesanthemum* and clade A include an amphibious, robust habit, a perennial life cycle, linear, chartaceous leaves with numerous veins (often more than one hundred), large, compact inflorescences, coriaceous, ovate, triangulate involucral bracts of cream color, staminate flowers with free sepals, and median petals equal in size to the lateral petals. Anatomical plesiomorphic character states of the leaf include a linear cross-sectional outline (Fig. 3f) with acute or acuminate margins (Fig. 3g), palisade cells on the adaxial epidermis, simple stomatic chambers (Fig. 3h), palisade cells in the hypodermal chlorenchyma, compact diaphragm tissue, vascular bundles positioned centrally in the mesophyll with the main larger than the accessory bundles, and sclerenchyma in the vascular bundle sheath extensions (Fig. 3i). Additionally, roots contain numerous metaxylem elements.

Derived character states are concentrated in clade B, which includes most *Eriocaulon* species from all the continents. They exhibit an aquatic habit, with emergent (Fig. 4a), rheophyte (Fig. 4b), or submerged (Fig. 4c) life forms; *E. brownianum* (AS) is the only amphibian species within this clade. Most species are slender and annual, bearing lanceolate, membranous leaves with few veins (fewer than sixty). The scape sheaths terminate in a laciniate apex, and inflorescences are small and lax. Involucral bracts are membranous, obovate, and dark olive, while floral bracts are obovate (Fig. 4d). Staminate flowers generally have fused sepals, and median petal is longer than the lateral petals in most species of clade B. Derived anatomical states of the leaf include a sinuous or terete cross-sectional outline, isodiametric cells on the adaxial epidermis, loss of stomatic chambers, circular cells in the hypodermal chlorenchyma, a lax arrangement of diaphragm tissue, and vascular bundles positioned near the adaxial surface, with the main bundle equal in size to the accessory bundles and lacking sclerenchyma in the vascular bundle sheath extensions. The root typically contains a single metaxylem element.

Eriocaulon brownianum Mart. (AS), *E. teusczii* Engl. & Ruhland ex Ruhland (AF), *E. decangulare* L. (SA), *E. humboldtii* Kunth (SA), and *E. cabralense* Silveira (AS) are robust species similar in a general way to the members of clade A, including leaf anatomical

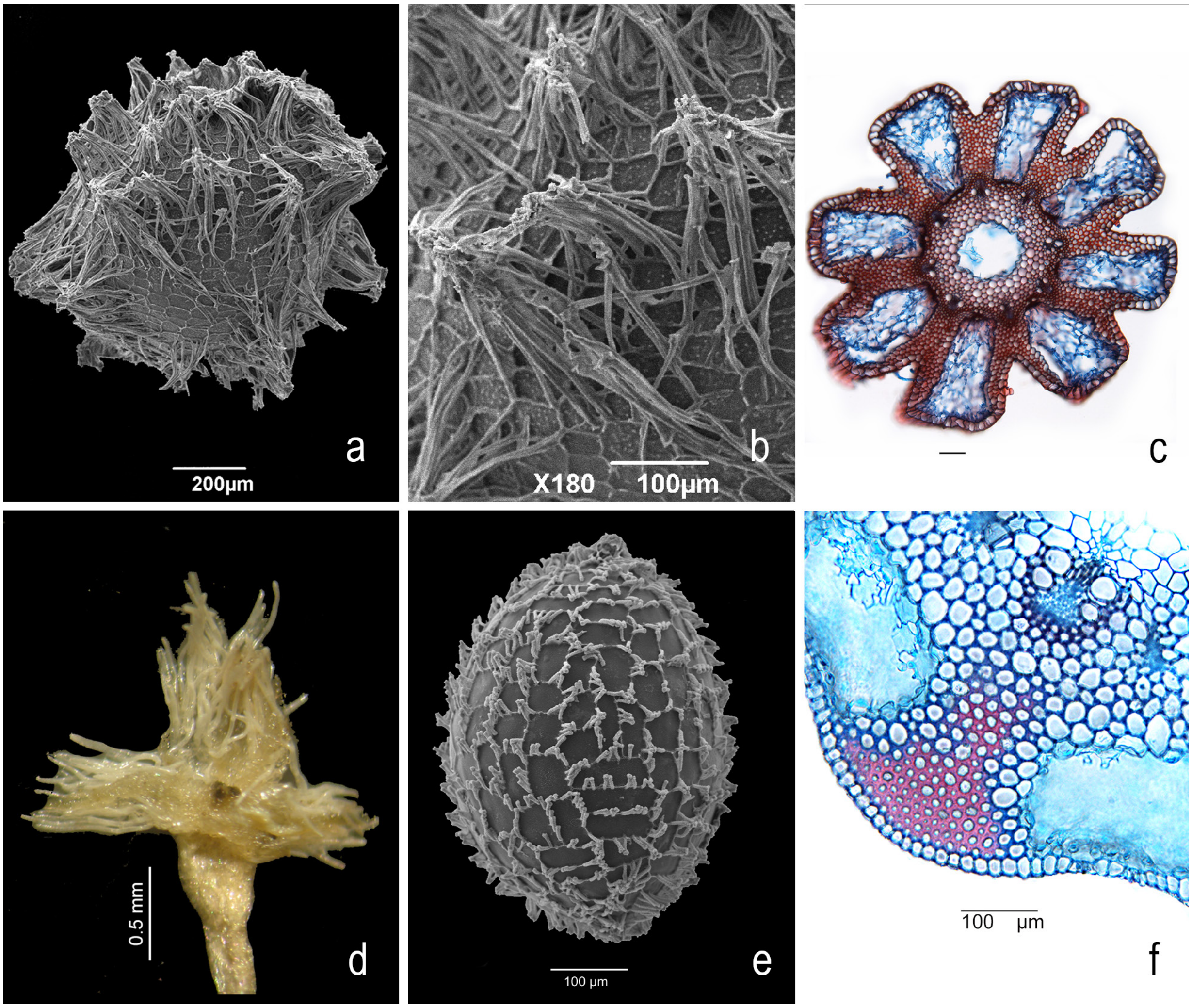

Fig. 2. *Mesanthemum* and *Eriocaulon* synapomorphies. **a-c.** *Mesanthemum jaegeri* **a**. the seed in general view with fringed appearance; **b.** detail of the seed showing pyramidal secondary projections; **c**. Scape showing radial symmetry with the ribs composed of diaphragm tissue, alternating with sclerenchyma columns and lacunae in the central cylinder; **d-f.** *Eriocaulon*; **d.** staminate flowers with free petals of *E. aquatile*; **e**. seeds ovoid with secondary projection in anticlinal and periclinal walls of *E. ravenelii*; **f.** detail of the scape showing the endodermis surrounding the external vascular bundles of *E. ligulatum*.

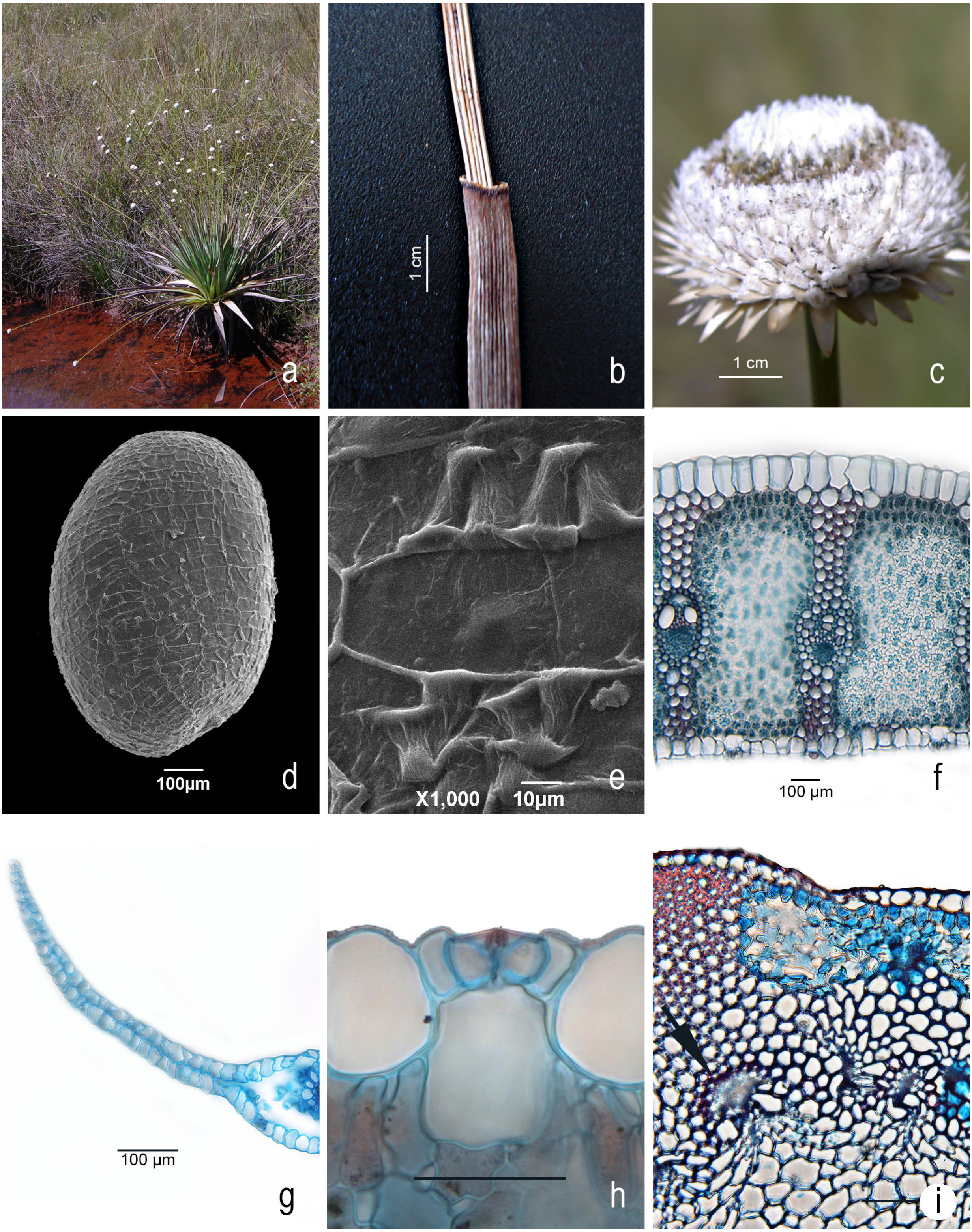

Fig. 3. The clade A. **a-c.** *Eriocaulon elychrysoides*, **a**. amphibious and robust habit; **b.** Closed leaf sheath with truncate apex; **c.** compact inflorescence; **d-e.** *E. singulare*; **d.** general view of the seed; **e.** detail showing J seed projections; **f.** linear leaf in cross section of *E. elychrysoides*; **g**. acuminate leaf margins in cross-section of *E. ligulatum*; **h.** detail showing stomatic chamber of *E. majusculum*; **i.** detail showing peryclice only on main vascular bundle of *E. ligulatum*.

features. However, in these species, the number of veins starts to drop, indicating a gradual transition to an aquatic condition, and the root typically contains a single metaxylem element.

The clade α (alpha) (Fig. 1) shows a reduction of leaf vein number to twelve or less, the involucral bracts are chartaceous, obovate, the floral bracts are cream with olive apex (Fig. 4d), the seeds have a rough lumen (Fig. 4e), and the leaf cross-section presents a sinuous terete outline (Fig. 4f). The clade β (beta) (Fig. 1) are annual with lanceolate leaf, lax inflorescence and external involucral bracts obovate. In the clade γ (gamma) (Fig. 1), stomatal chambers are absent, and the diaphragm is loosely aggregated. The clade δ (delta) (Fig. 1) exhibits leaves with obtuse margins in cross section and hypodermis with circular cells (Fig. 4f). The clade ε (epsilon) (Fig. 1) shows floral bracts obtrullate and isodiametric epidermal cells. The clade ζ (zeta) (Fig. 1) has species without adaxial sheath extension with vascular bundles near the epidermis (Fig. 4f). In the clade η (eta) (Fig. 1) the leaf number becomes less than nine, staminate flowers have concave sepals, seeds present a rough lumen, hypodermis in abaxial surface is absent, and the pericycle outlining only main vascular. Most of features are adaptations to aquatic life.

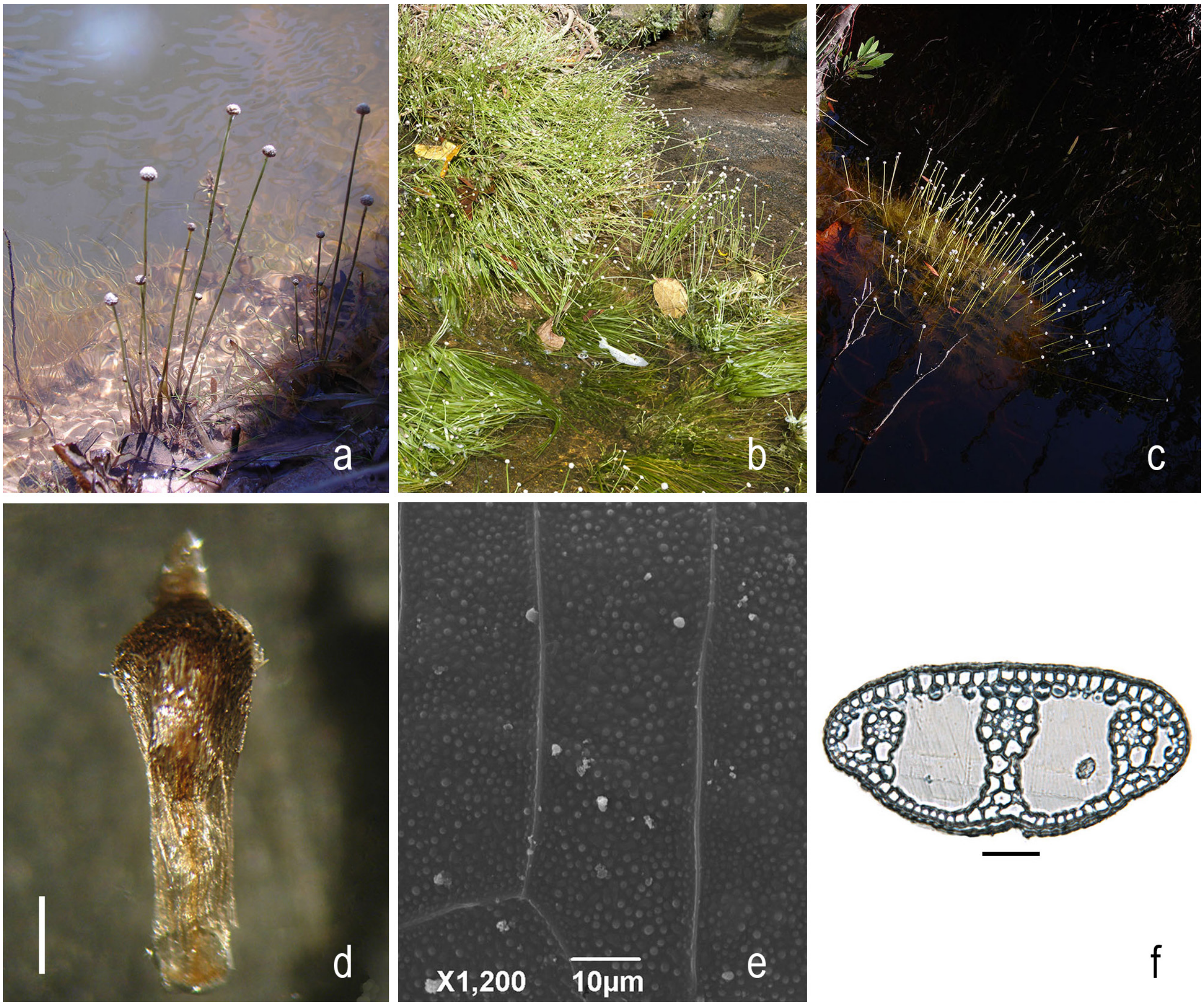

Fig. 4. The clade B. **a.** emergent species *Eriocaulon altogibbosum*; **b.** rheophytic species *E. spruceanum*, **c.** submerged species *E. setaceum* L.; **d.** obovate floral bracts cream with apex olive of *E. modestum*; **e.** detail of seed showing rough lumen of *E. abyssinicum* in α clade; **f.** leaf in cross section of *E. aquatile* showing a terete outline (α), isodiametric epidermal cells (ε), absence of stomatic chambers (γ), hypodermis with circular cells (δ), loosely aggregated diaphragm (γ), and vascular bundles near the epidermis (ζ).

The clade B3 (Fig. 1) shares membranous leaves, and all floral parts are membranous except the involucral bracts. There are two clades, B3a with *Eriocaulon africanum* Hochst. (AF) and *E. carsonii* F.Muell. (AU), that show small and compact inflorescences, and the clade B3b with North American species, *E. steyermarkii* Moldenke (SA) and *E. aquaticum* (Hill) Druce (EU), shows dimerous flowers.

The clade B4 (Fig. 1), which is exclusively composed of South American species, shares the presence of equal petals in the staminate flowers and seeds without secondary projections, with a smooth lumen (Fig. 5a, b). In this clade, *E. modestum* Kunth and *E. aquatile* Körn. (Fig. 5c) are submerged species, forming a sister clade of B4a. The clade B4a encompasses emergent species with 10-12-nerved leaves, gibbous sepals in the pistillate flowers (Fig. 5d), and the staminate flowers with concave sepals. The clade B5 (Fig. 1) is composed of *Eriocaulon siamense* Moldenke and *E. tanakae* Ruhland, both from Asia. These species share the presence of scape sheath longer than the leaf, and the median petal much longer than laterals in both staminate and pistillate flowers, similar to those found in the allied species *E. modestum* (Fig. 5e). The seeds show T-shape secondary projections located only in periclinal walls (Fig. 5f), an uncommon feature in *Eriocaulon*.

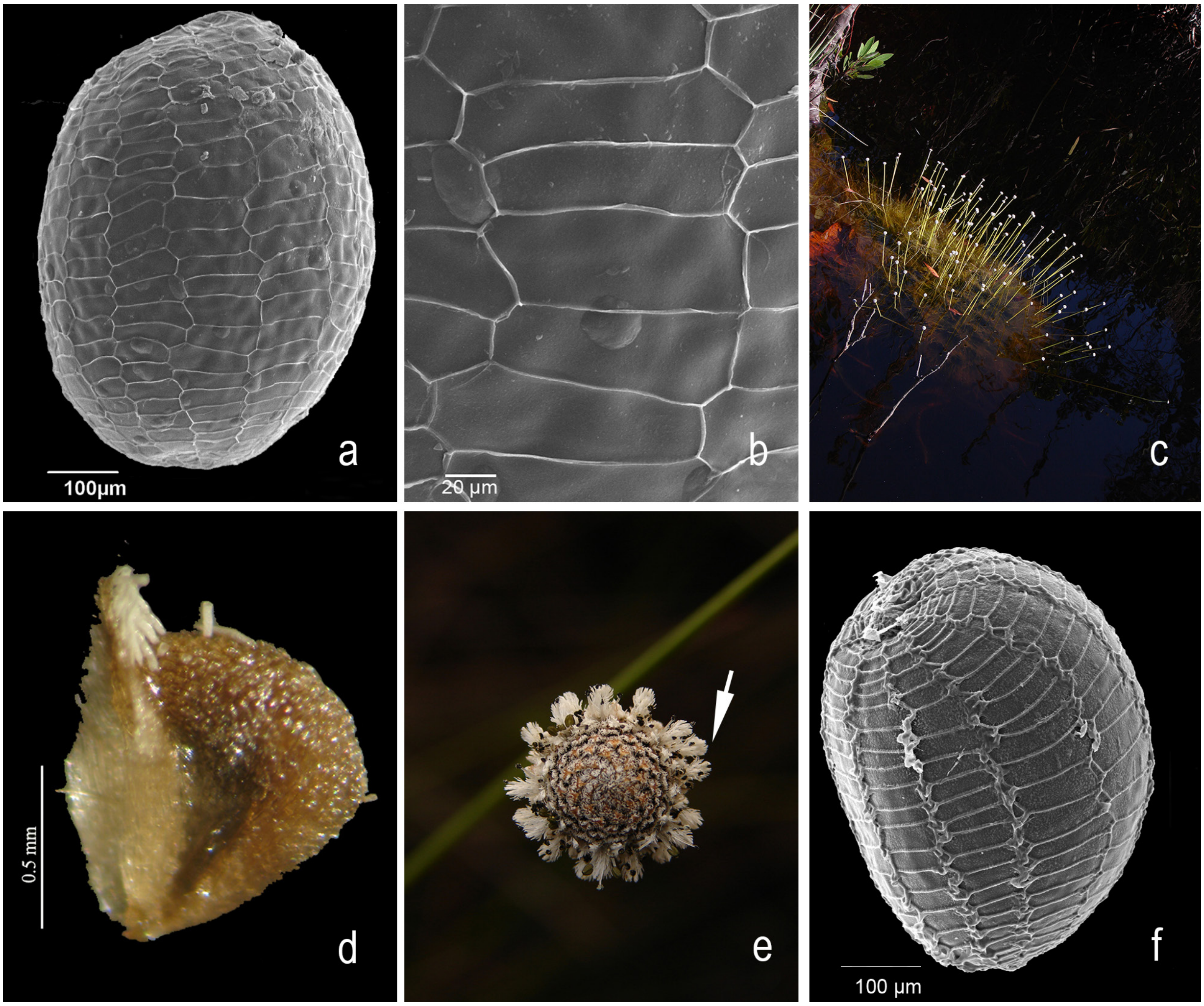

Fig. 5. Clade B4 and B5. Clade B4. **a-c.** *Eriocaulon aquatile*. **a.** seed without secondary projections; **b.** detail showing smooth lumen; **c.** submerged life form; **d.** *E. gibbosum* with gibbous sepals in the pistillate flowers; **e.** *E. modestum* inflorescence, arrow showing staminate median petal much longer than laterals; **f.** *E. siamense* seeds with T-shaped secondary projections located in periclinal walls.

The clade B6 (Fig. 1) encompasses only species from South America and the broadly distributed *E. setaceum* L. They show one-nerved leaves with spiral arrangement and narrowly linear blade (Fig. 6a). Two species, *E. araguaiense* A.L.R.Oliveira & C.P.Bove and *E. cylindratum* A.L.R.Oliveira & C.P.Bove, are emergent and raise as sisters of a smaller clade B6a with only submerged species. The clade B6a is joined by the dark olive, membranous floral bracts (Fig. 6b), membranous sepals of staminate and pistillate flowers, and seeds with ribbon jar shape projections (Fig. 6c-d). It exhibits the highest degree of adaptation to aquatic life, with perennial species featuring one-nerved, submerged leaves that do not support long periods of dryness.

The clade B7 (Fig. 1) encompasses AS, AF, SA, and NA species and the broadly distributed *E. cinereum* R.Br. The species of B7 are very small with a spreading habit, leaves with four to seven veins, and generally grey inflorescences (Fig. 6e). The floral bracts are longer than the flowers, the sepals of the staminate flowers are membranous, and the seeds have no secondary projections (Fig. 6f).

The clade B8 (Fig. 1) has species from Asia and *E. palustre* Salzm. ex Steud. from South America. These species exhibit a scape sheath that is shorter than the leaves, totally fused sepals in the pistillate flowers, and seeds with T-shaped projections. There are two smaller clades inside it. The clade B8a encompasses *E. decemflorum* Maxim. (AS)

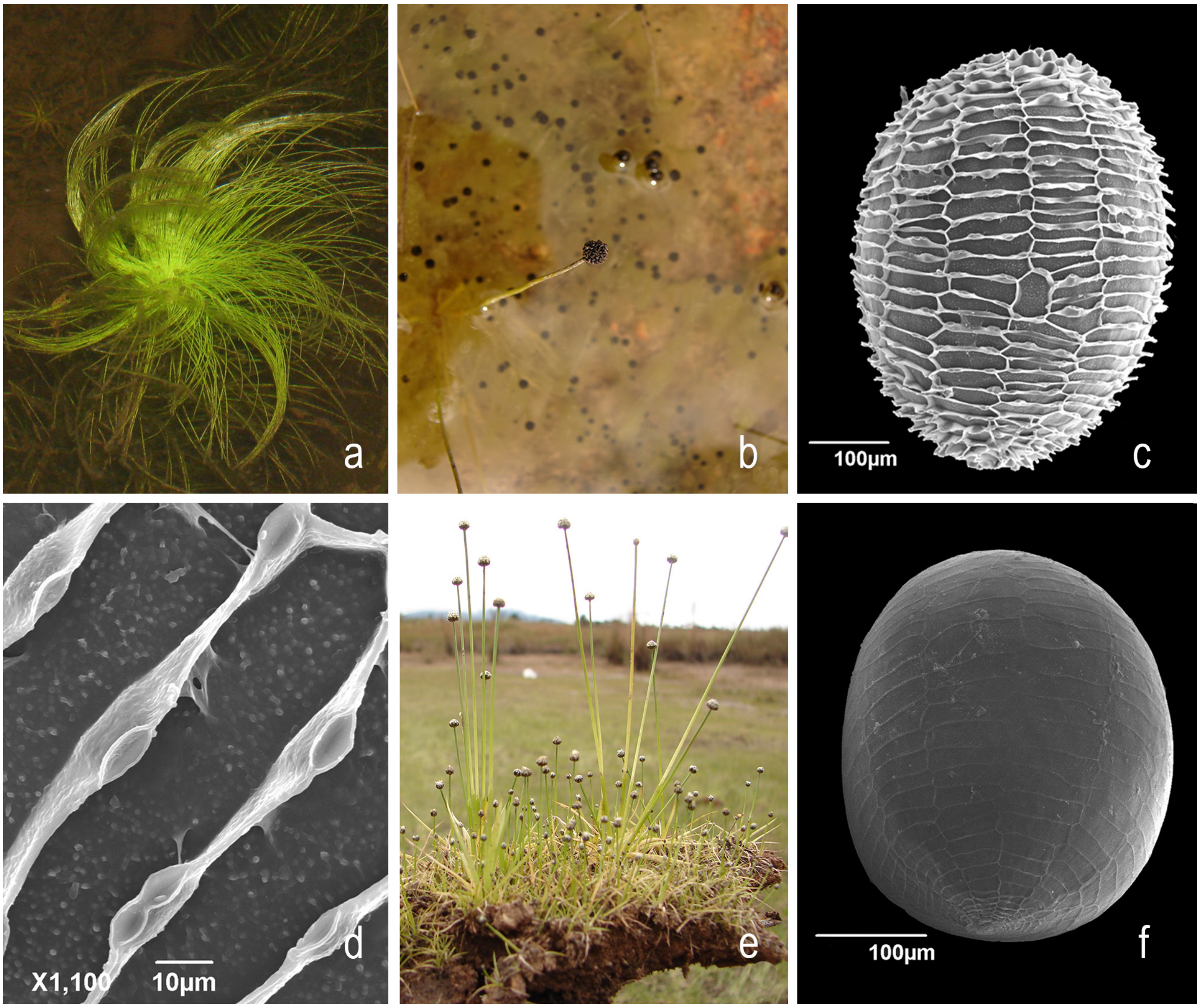

Fig. 6. The clade B6 and B7. **a-b.** *Eriocaulon setaceum*; **a.** submerged life form, with narrowly linear blade, one-nerved and spirally arranged, **b.** dark olive floral bracts, **c-d.** *E. albosetaceum* seeds with jar-shaped projections; **d.** detail showing the shape of projections like a jar; **e-f.** *E. cinereum*; **e.** small and spread habit with gray inflorescences; **f.** seeds without secondary projections.

and *E. sphagnicolum* Ohwi (AS), characterized by dimerous flowers with four stamens and involucral bracts closing the inflorescence. The clade B8b comprises species with floral bracts that are longer than the flowers and lack tertiary projections. The clade B9 (Fig. 1) encompasses emergent species from Australia only, characterized by chartaceous leaves, floral bracts longer than the flowers, and the absence of glands in the petals. The instability of floral number and linear sepals in the pistillate flowers is also a common feature of Australian species, being rare in species from other continents. The clade B10 (Fig. 1) comprises AF, AS, and SA emergent species, except *E. spruceanum* Körn., which is a rheophyte. This clade shows sepals of pistillate flowers winged and median petals of pistillate flowers longer than lateral ones.

Morphological evolution of characters

Leaves (Fig. 7a) are linear (25-40:1) in *Mesanthemum* and clade A, but show a broad blade and numerous veins (generally more than one hundred). In clade B, emergent species such as *E. teusczii*, *E. humboldtii,* and *E. decangulare* also exhibit linear blades, characterized by fewer veins. Additionally, clade β species exhibit lanceolate blades (1-20:1), except in clade B6, which features species with narrowly linear blades (50-200:1) and a single vein. The spathe, which involves the scape, is most often open at a lateral slit in *Eriocaulon* and *Mesanthemum*. In clade A, species show a closed spathe with a truncate apex (Fig. 3B), which is a derived state of character occurring in this clade. The apex of the scape sheath is acute in *Mesanthemum*, and laciniate in most species of the clade B.

Most of the time, external involucral bracts are cream colored, ovate, and coriaceous in *Mesanthemum* and *Eriocaulon* until the clade α, when they become chartaceous and obovate. The color of the floral bracts is creamy-white in *Mesanthemum* and most of the species in clade A. In clade B, they become creamy-white at the base with olive apex in most species and olive in clade B6 and B7. The median petal of the staminate

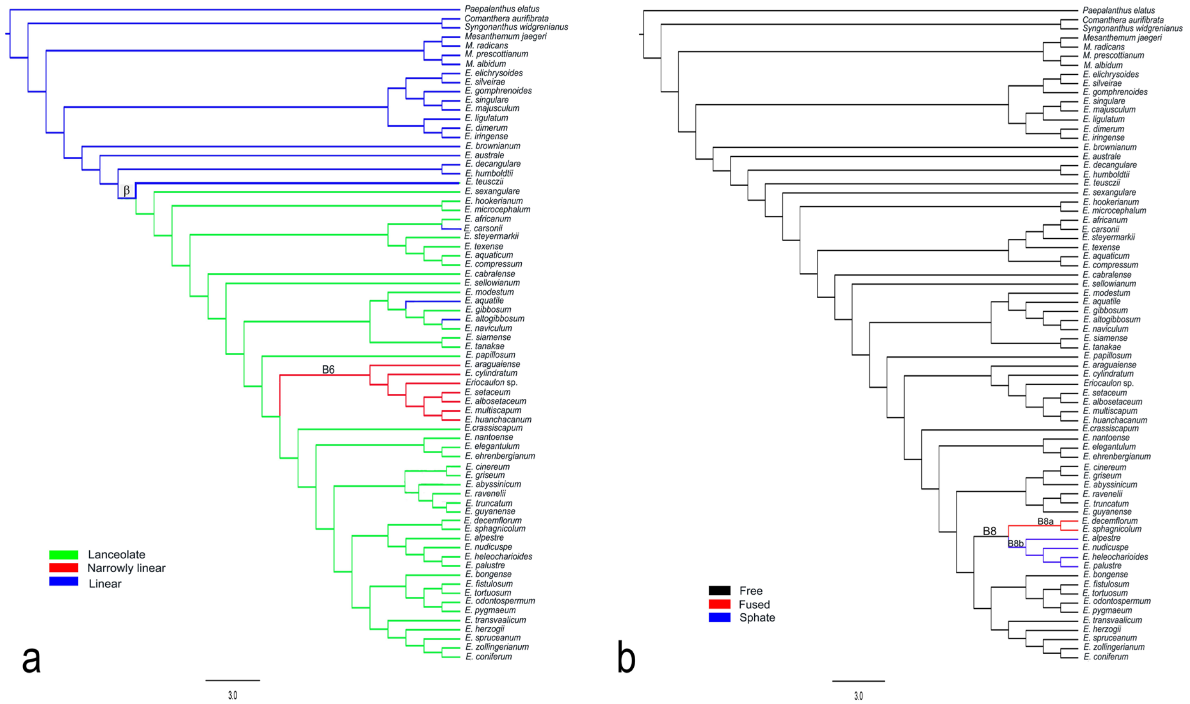

Fig. 7. Morphological character evolution in *Eriocaulon*: **a.** Leaf shape; **b.** Sepals of pistillate flowers fusion.

flower, most of the time, has the same shape and size as the lateral ones in the clade A, whereas in the clade B, the median petal becomes a little longer. Sometimes, it can be 1 mm or longer than the lateral ones, being apparent in the inflorescences, as in the clade B5, in *E. sexangulare* L., and in *E. modestum* Kunth (Fig. 5E), indicating independent evolution. Sepals of the staminate flowers are free or partially fused in *Mesanthemum*, and free in the clade A. In clade B, the sepals can be partially or totally fused, but it is possible to see the fusion line. The sepals are totally fused, forming a unique structure that occurs in staminate flowers of species of clades B8, B9, and B10. The sepals of pistillate flowers are free in *Mesanthemum* and *Eriocaulon*, except in clade B8, whose species have partially fused sepals; especially in clade B8b, the sepals are totally fused (Fig. 7b).

Trimerous flowers are present in most species, whereas dimerous flowers evolved independently in *Eriocaulon magnificum* and three times in the clade B (clade B3b, B7, and B8a). In the clade B9 with Australian species, the floral parts vary from one to three in the same species, indicating a recent evolution.

The shape of the seed in *Mesanthemum* is spheroid (1:1) with cells of the seed coat with anticlinal and periclinal walls of the same size (Fig. 2a-b). In *Eriocaulon*, the seed is ovoid (1.5:1-2:1) (Fig. 2E). In most of the *Eriocaulon* species, the cells of the seed coat are elongated in anticlinal walls. In clades with submerged species B6 and B4, the seeds become widely ovoid (1.2:1-1.4:1). The seed coat projections in *Eriocaulon* are highly variable and evolved in many directions (Fig. 8). *Mesanthemum* and *Eriocaulon cabralense* Silveira show narrowly pyramidal projections (Fig. 2 a-b). The species of clade A exhibit J-shaped projections (Fig. 3e). The post-shape projection is common and has evolved multiple times in *Eriocaulon* (Fig. 8a), being the type of projection found in clade B9 and B10. *Eriocaulon araguaiense* A.L.R.Oliveira & C.P.Bove and *E. cylindratum* A.L.R.Oliveira & C.P.Bove shows a belt shape larger than longer projection (Fig. 8b) whereas the clade B1 and some *Eriocaulon* (eg. *E. sellowianum* Kunth) shows a belt shape longer projection (Fig. 8c). Ribbon-shaped projections occur in *E. microcephalum* Cham. & Schltdl. (Fig. 8d), and double belt shape longer than larger projections is an autapomorphy of *E. papillosum* Körn. (Fig. 8e). The absence of secondary projections is a synapomorphy of the clade B4a with species of gibbous sepals and of the clade B7 (Fig. 5a-b, 6f). The one-nerved leaf, submerged species of clade B6, exhibits ribbon-jar shape projections (Fig. 6c-d). The T-shaped projections (Fig. 8F) occur in species of the clade B8b with totally fused sepals of pistillate flowers, but also in species of other clades such as B3b and B5. In this context, we believe that seed coat characters are useful in conjunction with other features to delimit small clades in *Eriocaulon.* The seeds of the clade A present the J-shaped secondary projections, whereas in the clade B, the secondary projections have different shapes or are absent. The high diversification of the seed and the absence of correlation with external groups indicate a specialized character in *Eriocaulon.* On the other hand, anatomical features identified as synapomorphies in the main groups likely facilitated adaptation to aquatic environments. For example, in *Mesanthemum* and clade A, the leaves exhibit a linear outline (Fig. 3f) with palisade epidermal cells. In contrast, in clade B, the leaves become terete, with the epidermal cells shifting to a isodiametric shape (Fig. 3d). Additionally, the simple stomatal chambers present in clade A and *Mesanthemum* are absent in clade B.

The hypodermal chlorenchyma, which is composed of palisade cells in clade A and *Mesanthemum*, becomes circular in clade B. Furthermore, the main adaxial vascular bundles in clade A and *Mesanthemum* possess adaxial sheath extensions, whereas in most species of clade B, these extensions are absent. In the roots, *Mesanthemum* and in clade A contain multiple metaxylem elements, but in clade B, this number decreases to one.

Discussion

Phylogenetic studies on *Eriocaulon* have traditionally used Asian species as the majority of the accessions, with studies employing either morphological (Zhang, 1999) or molecular datasets (Larridon *et al.*, 2019; Darshetkar *et al.*, 2021). Larridon *et al.* (2019) recognized two main groups in *Eriocaulon*: A small group containing robust species from Asia, including *E. sexangulare* L. and *E. australe* R.Br. (AU), extending to Australia. The other clade encompasses all remaining species.

In our analysis, robust species similar to those used by Larridon (2019), including *E. sexangulare* and *E. australe*, are identified as the basal species of clade B, raised alone within this clade. Interestingly, clade A, which appears as a sister to clade B, was not previously observed in phylogenies, likely due to the absence of amphibian species from Africa and the Americas.

Sectional Groupings and Morphological Convergence

Robust Asian species with pilose involucral bracts have been placed in *Eriocaulon* sections such as sect. *Hirsutae* Fyson or sections II, III, and V (Ansari & Balakrishnan, 1994). Our analysis places these robust species in clade B, but they do not form a monophyletic group, indicating morphological convergence, rather than common ancestry.

Eriocaulon sect. *Disepala* (Satake) Zhang is characterized by the reduction of size or number of

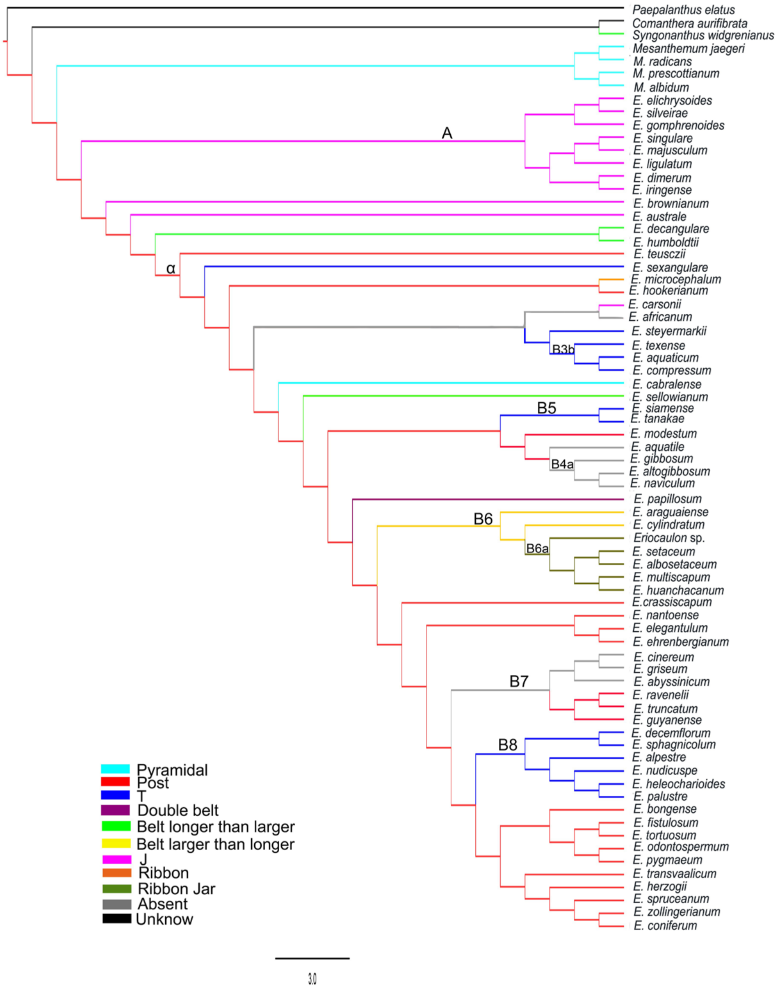

Fig. 8. Morphological character evolution in *Eriocaulon*: Seed projections shape.

the sepals of pistillate flowers (e.g., *E. echinulatum* Mart., *E. truncatum* Buch.-Ham. ex Mart., *E. thwaitesii* Körn., *E. zollingerianum* Körn.). The same occurs with *Eriocaulon* subg. *Astole* Körn. with *Eriocaulon guyanense* Körn., *E. koernickei* Britten, and *E. stramineum* Körn. that present dimerous flowers and white anthers. Our analysis encompasses a few species with dimerous flowers, but according to our results, this character evolved at least three times in *Eriocaulon*.

Our study, along with previous phylogenies, suggests that many existing taxonomic categories within *Eriocaulon* are artificial, relying on arbitrary morphological traits. For example, species with keeled sepals, which were traditionally placed in sections like *Heterochiton* Ruhland and *Cristato-Sepalae* Fyson, appear scattered across different clades in our analysis, corroborating previous phylogenies (Darshetkar *et al.* 2021; Larridon *et al.* 2019).

The presence of pistillate flowers with totally fused sepals is used to define monotypic taxonomic categories in many classifications. *Eriocaulon* subg. *Spathopeplus* Korn. with *E. palustre*, *Eriocaulon* sect. *Connato-Sepalae* Fyson and Section I of Ansari & Balakrishnan (1994) with *E. alpestre* Hook. f. & Thomson ex Körn. *Eriocaulon* sect. *Nicosia* Zhang and *Eriocaulon* sect. *Macropoda* (Satake) Zhang with *E. nudicuspe* Maxim. and *E. heleocharioides* Satake, respectively. According to Zhang's (1999) cladistic analysis, *E.*

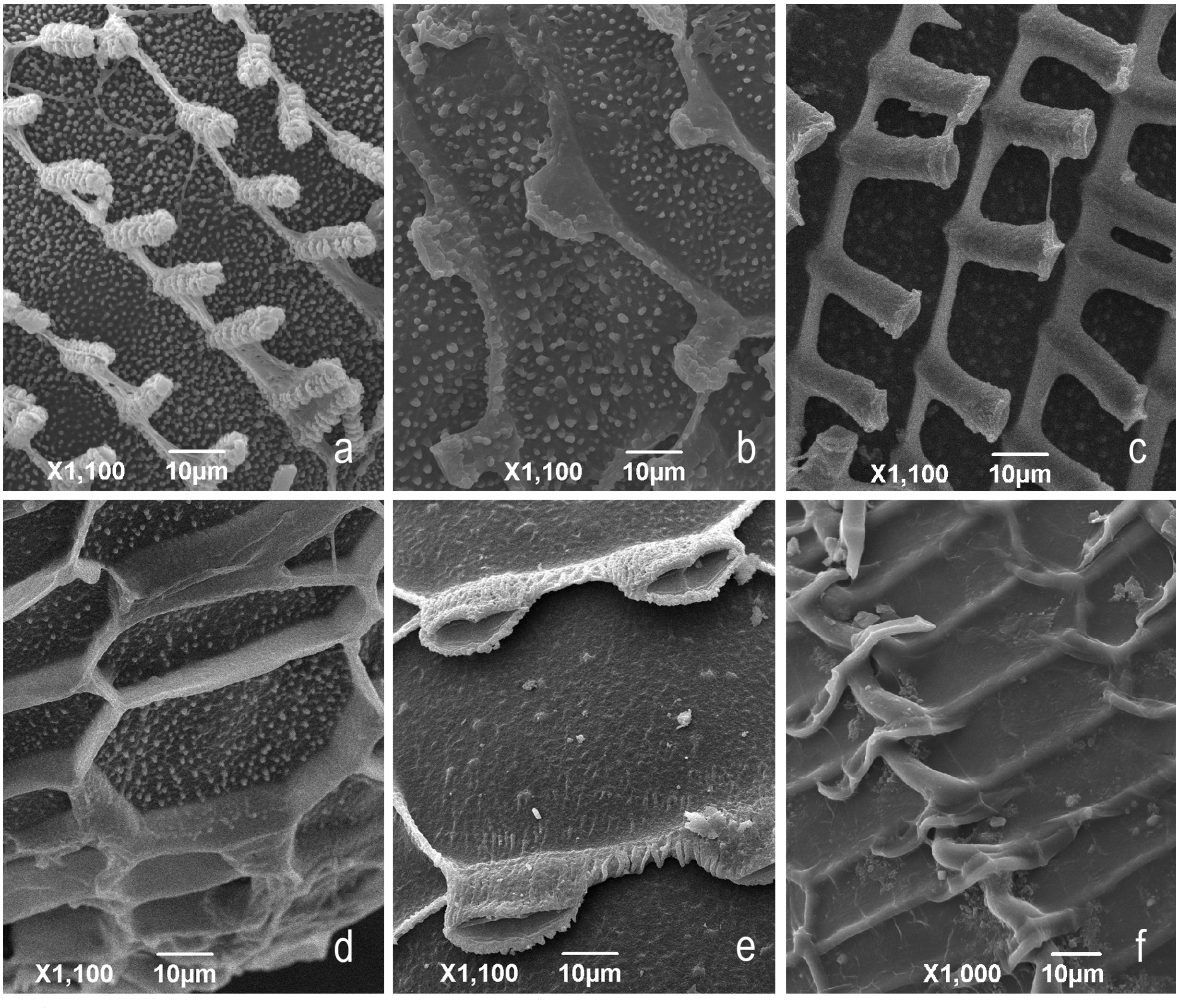

Fig. 9. The shape of secondary projections in *Eriocaulon*. **a.** post shape projection of *E. transvaalicum*; **b.** belt-shaped projection of *E. araguaiense*; **c.** belt-shape projection of *E. sellowianum*; **d.** Thick ribbon-like projections of *E. microcephalum*; **e.** double belt shape projection of *E. papillosum*; **f.** T-shape projection of *E. palustre*.

nudiscupe and *E. heleochariodes* are sister taxa. In Larridon *et al.* (2019), *E. heleochariodes* emerges as a sister to *E. decemflorum* Maxim. and *E. alpestre* Hook.f. & Thomson ex Körn., and in Darshetkar *et al.* (2021), *E. alpestre* emerges independently. In our analysis, these Asian species form a clade that also includes *E. palustre,* the only species from South America. Our results indicate the monophyly of species with pistillate flowers and fused sepals, corroborating previous phylogenies (Zhang, 1999; Larridon *et al.*, 2019).

Submerged species with developed stems were placed in *Eriocaulon* sect. *Setaceae* Fyson, *E.* sect. *Macrocaulon* Ruhl and in section IV (Ansari & Balakrishnan, 1994). These sections are characterised by an aquatic submerged habit, an elongated stem, and filiform leaves. Additionally, some species of section XII (Ansari & Balakrishnan, 1994) (e.g., *E. mitophyllum*) are submerged, characterized by narrow leaf blades and the absence of secondary projections in the seed coat. In previous phylogenetic analyses, *E. setaceum* L. has been identified as a distinct lineage (Zhang, 1999; Larridon *et al.*, 2019; Darshetkar *et al.*, 2021). In our study, submerged species with developed stems and one-nerved leaves are found within the clade B6a, being a monophyletic group.

The present study suggests the possibility of two subgenera: *Eriocaulon* subg. *Eriocaulon* that corresponds to clade B, including *E. decangulare.* The other subgenera correspond to clade A, with the species that retained more plesiomorphic states of characters. Some existing categories correspond to clades and show clear synapomorphies. *Eriocaulon* subg. *Spathopeplus* is a smaller clade within clade B, and in the future, it will need to be reclassified as a section with a new circumscription that includes other species. *Eriocaulon* sect. *Macrocaulon* is also monophyletic, encompassing one nerved, submerged species. It is likely that the sections will need a new delimitation and circumscription to include synapomorphies. However, it is too early to propose taxonomic changes in *Eriocaulon,* and molecular and combined analyses are necessary to corroborate this hypothesis.

Ecology and Evolution

A recent anatomical study focusing *on Eriocaulon* (Khoshnaw *et al.*, 2022) demonstrated that the life forms of aquatic species are closely linked to their anatomical features. Our morphology-based cladistic analysis corroborates this hypothesis, indicating an evolutionary anatomical pattern, rather than a result of phenotypic plasticity. Natural selection likely played a role in the conquest of the aquatic environment by the species of clade B, the emergent and generally annual, living in temporarily flooded places; these species disappear in dry periods.

Conclusion

We presented a cladistics-based hypothesis for morphological evolution in *Eriocaulon* with species from across the geographic range and diverse morphological variation. Although far from a holistic approach, our results bring a better understanding of morphological evolution in the genus. Characters such as leaf shape, spathe integrity, and the colour of involucral bracts are important for reconstructing the evolution in *Eriocaulon.* Additionally, micromorphological characters, such as seed projection shape, leaf and scape anatomy, provided a better understanding of the group. Future phylogenetic analysis using a combined data set may produce a more robust phylogenetic hypothesis to clarify the relationships in the genus.

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Appendix 1: Terminal taxa (based on taxonomic descriptions, drawings, and herbarium sheet (digital image consultation).

Terminal species as per Körnicke (1863)

Eriocaulon L.

1. **Subgenus *Astole* Körn.**

E. guyanense Körn.
E. pygmaeum Körn.
E. stramineum Körn.

2. **Subgenus *Euriocaulon* Körn.**

E. angustifolium Körn.
E. aquatile Körn.
E. benthami Kunth
E. brevifolium Klotzsch
E. crassiscapum Bong.
E. dictyophyllum Körn.
E. ehrenbergianum Klotzsch ex Körn.
E. gibbosum Körn.
E. gomphrenoides Kunth
E. helichrysoides Bong.
E. humboldtii Kunth
E. kunthii Körn. (*E. ligulatum*)
E. laxifolium Körn.
E. leptophyllum Kunth
E. linearifolium Körn.
E. macrobolax Körn.
E. melanocephalum Kunth
E. microcephalum Kunth
E. modestum Kunth
E. papillosum Körn.
E. paraguayense Körn.
E. rosulatum Körn.
E. schiedeanum Körn.
E. sellowianum Kunth
E. tenuifolium Klotzsch
E. vaginatum Körn.

3. **Subgenus *Spatopeplus* Körn.**

Type: *E. palustre* Salm-Dyck ex Steud.
E. palustre Salm-Dyck ex Steud.

4. **Subgenus *Trichopeplus* Körn.**

Type: *E. griseum* Körn.
E. griseum Körn.

Classification as per Zhang (1999).

Eriocaulon L.

1. Subgenus *Trimeranthus* Nakai

1.1. *E.* subg. *Trimeranthus* sect. *Macrocaulon* Ruhland
Type: *E. setaceum* L.
E. setaceum L.

1.2. *E.* subg. *Trimeranthus* sect. *Simplices* Fyson
E. achiton Körn.
E. boni Lecomte
E. brownianum Mart.
E. collinum Hook.f.
E. eglandulatum Z.X. Zhang
E. ermeiense W.L. Mae ex Z X. Zhang
E. heterolepis Steud.
E. kunmingense Z.X. Zhang
E. laosenese Moldenke
E. leianthum W.L. Ma
E. luzulaefolium Mart.
E. nantoense Hayata
E. nepalense Prescott ex Borg.
E. oryzetorum Mart.
E. parvum Körn.
E. pseudonepalense Satake
E. quinquangulare Heyne ex Mart.
E. robusto-brownianum Ruhland
E. rockianum Hand.-Mazz
E. schochianum Hand.-Mazz

E. smitinandi Moldenke

E. sollyanum Royle

E. tailândiaicum Moldenke

E. wightianum Mart.

E. xenopodium Koyama

E. xeranthemum Mart.

1.3. Subg. *Trimeranthus* sect. *Anisopetalae* Fyson

Type: *E. cristatum* Mart.

E. bassacense Moldenke

E. kradungense Satake

E. cristatum Mart.

E. nautiliforme Lecomte

E. eberhardtii Lecomte

E. siamense Moldenke

E. henryanum Ruhland

E. tanakae Ruhland

E. hookerianum Stapf

1.4. Subg. *Trimeranthus* sect. *Heterochiton* Ruhland

Type: *E. sexangulare* L.

E. sexangulare L.

E. willdenovianum Moldenke

1.5. Subg. *Trimeranthus* sect. *Disepala* (Satake) Z.X.Zhang

Type: *E. truncatum* Buch.-Ham. ex Mart.

E. dipsacoides Satake

E. echinulatum Mart.

E. hamiltonianum Mart.

E. nigrum Lecomte

E. pseudotrucatum Z.X. Zhang

E. thwaitesi Körn.

E. truncatum Buch.-Ham. ex Mart.

E. zollingerianoides Z.X.Zhang

E. zollingerianum Körn.

1.6. Subg. *Trimeranthus* sect. *Leucantheae* Fyson

Type: Not specified

E. barbeyanum Ruhland

E. cinereum R. Br.

E. taishanense F.Z. Li

E. tonkinense Ruhland

1.7. Subg. *Trimeranthus* sect. *Nasmythia* Huds.

E. decemflorum Maxim.

2. Subgenus *Spathopeplus* Körn.

Type: *E. palustre* Salm-Dyck ex Steud.

2.1. Subg. *Spathopeplus* sect. *Apoda* (Satake) Z.X. Zhang

Type: *E. buergerianum* Körn.

E. alpestre Hook.f. & Thomson ex Körn.

E. atroides Satake

E. atrum Nakai

E. buergerianum Körn.

E. faberi Ruhland

E. hondoense Satake

E. japonicum Körn.

E. kusiroense Miyabe & Kudó ex Satake

E. liberisepalaum Z.X. Zhang

E. minusculum Moldenke

E. miquelianum Körn.

E. monococcon Nakai

E. nanellum Ohwi

E. sachanlianse Miyabe & Nakai

E. sekimotoi Honda

E. sphagnicola Ohwi

E. takae Koidz.

E. tenuissimum Nakai

E. zyotanii Satake

2.2. *E.* subg. *Spathopeplus* sect. *Macropoda* (Satake) Z.X. Zhang

E. heleocharioides Satake

2.3. *E.* subg. *Spathopeplus* sect. *Nudicuspa* Z.X. Zhang

E. nudicuspe Maxim.

Appendix 2. Infrageneric classifications of *Eriocaulon* and terminal species used in this study:

Eriocaulon abyssinicum Hochst., Zimbabwe, *H. Wild* 5475 (P); *E. africanum* Hochst., South Africa, *Tyson* 1203 (P); *E. albosetaceum* A.L.R.Oliveira, Brazil, *A.Oliveira, C.P. Bove et al.* 1839 (R); *E. alpestre* Hook.f. & Thomson ex Körn., Japan, *T. Kajita et al.* 559 (SP, R); *E. alto-gibbosum* Ruhland, Brazil, *A. Oliveira et al.* 257 (R). *E. aquaticum* Hill Druce (*E. septangulare* With.), United States of America, *H. C. Beardslee & C. A. Kofoid s.n.* (SP 121175); *E. aquatile* Körn., Brazil, *A. Oliveira & R. Moura* 91 (R); *E. araguaiense* A.L.R.Oliveira & C.P.Bove, Brazil, *C.P. Bove et al.* 267 (R); *E. australe* R.Br., Australia, *Baleeiro & Jobson* 543 (BRI); *E. bongense* Engl. & Ruhland, Mali, *P. Jaeger* 5126 (P); *E. brownianum* Mart., India, *Wallich* 6066 (B holótype);. *E. cabralense* Silveira, Brazil, *A. Silveira* 553 (R holótype); *E. carsonii* F.Muell., Australia, *Baleeiro & Jobson* 501 (BRI); *E. cinereum* R.Br., Brazil, *A. Carvalho & G. Martinelli* 223 (RB); *E. compressum* Lam., United States of America, *R. Kral* 57692 (SP); *E. crassiscapum* Bong., Brazil, *J. Badini s.n.* (OUPR 13106, R); *E. coniferum* Herzog., Brazil, *Luetzelburg* 455 (R); *E. cylindratum* A.L.R.Oliveira & C.P.Bove, Brazil, *C.P. Bove et al.* 596 (R); *E. decangulare* L., United States of America, *R. Kral* 84056 (SP); *E. decemflorum* Maxim., Japan, *H. Ohashi* 8767 (SP, R); *E. dimerum* (Giul. & E.B.Miranda) A.L.R.Oliveira, Brazil, *A.M. Giulietti et al.* 0781 (HUEFS); *E. ehrenbergianum* Klotzsch ex Körn., Mexico, *C.G. Pringle* 8989 (R); *E. elegantulum* Engl., Tanzania, *R. Polhill & S. Paulo* 2010 (P); *E. elichrysoides* Bong., Brazil, *A. Oliveira & R. Moura* 117 (R); *E. fistulosum* R.Br., Australia, *Baleeiro & Jobson* 518 (BRI); *E. gibbosum* Körn., Brazil; *E. gomphrenoides* Kunth, Brazil, *G.G. Hatschbach* 71670 (RB); *E. griseum* Körn., Brazil, *G. Martinelli et al.* 16307 (RB); *E. guyanense* Körn., Brazil, *A. Oliveira et al.* 245A (R); *E. heleocharioides* Satake, Japan, *B.Y. Satake s.n.* (TNS 59301); *E. herzogii* Moldenke, *Luetzelburg* 21052 (R); *E. hookerianum* Stapf., Indonesia, *R.J. Johns* 10736 (HUEFS); *E. huanchacanum* Hensold, Venezuela, *J.R.I. Wood et al.* 16552 (HUEFS); *E. humboldtii* Kunth, Brazil, *W. Rodrigues s.n.* (INPA 675); *E. iringense* S.M.Phillips, Tanzânia, *R. Polhill & S. Paulo* 1720 (K, holotype); *E. ligulatum* (Vell.) L.B.Sm., Brazil, *J. Badini s.n.* (OUPR 13111, R); *E. majusculum* Ruhland, Brazil, *G. Eiten & L. Eiten* 6642 (RB); *E. microcephalum* Kunth, Mexico, *B. Sparre s.n.* (R140367); *E. modestum* Kunth, Brazil, *R. Reitz* 1963 (R); *E. multiscapum* A.L.R.Oliveira, Brazil, *D.F. Austin et al.* 7302 (INPA); *E. nantoense* Hayata, China, *B.Y. Satake s. n.* (TNS 195816); *T. Tawakami s.n.* (TAIF, isótype); *E. naviculum* A.L.R.Oliveira, Brazil, *G.C. Argent & Richards* 6472 (UB); *E. nudicuspe* Maxim., Japan, *J. Ohwi s.n.* (TNS 267980); *E. odontospermum* G.J.Leach., Australia, *Baleeiro & Jobson* 508 (BRI); *E. palustre* Salm-Dyck ex Steud., Brazil, *T.S. Santos & L.A.M. Silva s. n.* (HUEFS 38841); *E. papillosum* Körn., Brazil, *A. Oliveira et al.* 255 (R); *E. pygmaeum Vauthier s.n.* (B); *E. sellowianum* Kunth., Brazil, *A. Oliveira et al.* 232 (R); *E. setaceum* L., Brazil, *A. Silveira* 207 (R); *E. sexangulare* L., Malaysia, *S.H. Vû-Van-Cuong* 1188 (P); *E. siamense* Moldenke, Thailand, *C.F. van Beusekom* 4571 (P); *E. silveirae* Moldenke, *A. Silveira* 723 (R); *E. singulare* Moldenke, Brazil, *J C. Lindeman & J.H. Haas* 2419 (RB); *E. sphagnicola* Ohwi, South Korea, *J. Ohwi* 2843 (KYO); *E. spruceanum* Herzog., Brazil, *Luetzelburg* 22796 (R); *E. steyermarkii* Moldenke, Brazil, *J.A. Steyermarkii & J.J. Wurdack* 341 (RB); *E. tanakae* Ruhland, Japan, *Tanaka s.n.* (B[B100106839]); *E. teusczii* Engl. & Ruhland, Tanzania, *S. Bidgood* 4098 (P); *E. texense* Körn., United States of America, *R. Kral* 57596 (SP); *E. tortuosum* F.Muell., Australia, *Baleeiro & Jobson* 461 (BRI); *E. transvaalicum* N.E.Br., Republic of Cameroon, *Audru-Boudet* 2271 (P); *E. truncatum* Buch.-Ham. ex Mart., Vietnam, *B. Balansa* 241 (P); *E. zollingerianum* Körn., Indonesia, *Zollinger* 333 (B); *Eriocaulon sp.*, Brazil, *Lima* 051 (RB); *Comanthera aurifibrata* (Silveira) L.R.Parra & Giul., Brazil, *A. Silveira* 582 (R); *Mesanthemum albidum* Lecomte, French Guinea, *M. Pobéguin* 1359 (P); *M. jaegeri* Jacq.-Fél., Serra Leon, *J.G. Adam* 22666 (P); *M. prescottianum* Körn., Guinea, *H. Scaetta* 3263 (P); *M. radicans* (Benth.) Körn., Angola, *H. Hess* 52671 (P); *Paepalanthus elatus* (Bong.) Körn., Irwin, *H.S. et al.* 22208 (UB); *Syngonanthus widgrenianus* Ruhland, Brazil, *A. Oliveira et al.* 138 (R).

Appendix 3. Character list

Leaf, number of veins

Flowers, number of petals

Habit: **(0)** amphibian; **(1)** aquatic; **(2)** terrestrial.

Aquatic plants, life form: **(0)** emergent; **(1)** submerged; **(2)** rheophyte.

Life cycle: **(0)** perennial; **(1)** annual.

Stem, type: **(0)** rhizome; **(1)** aerial; **(2)** submerged.

Leaf, arrangement: **(0)** rosulate; **(1)** spiral; **(2)** equitant; (3) imbricate.

Leaf, shape: **(0)** narrowly linear (50-200:1); **(1)** linear (25-40:1); **(2)** lanceolate (1-20:1).

Leaf, blade, consistency: **(0)** membranous; **(1)** chartaceous; **(2)** incrassate.

Scape, trichomes: **(0)** absent; **(1)** present.

Scape, sheath, size, in relation to leaf: **(0)** longer; **(1)** shorter; **(2)** equal.

Scape, sheath, integrity: **(0)** slit; **(1)** close.

Scape, sheath, apex shape: **(0)** acute; **(1)** truncate; **(2)** laciniate.

Receptacle, trichomes: **(0)** absent; **(1)** present.

Inflorescence, flowers arrangement: **(0)** compact; **(1)** lax.

Inflorescence, arrangement: **(0)** alleatory; **(1)** umbelliform.

Involucral bracts series, display, relative to inflorescence: **(0)** under inflorescence with radius shorter than radius of inflorescence; **(1)** under inflorescence with radius longer than radius of inflorescence; **(2)** closing the inflorescence.

External involucral bract, shape: **(0)** ovate; **(1)** obovate; **(2)** oblong; **(3)** lanceolate; **(4)** ovate-triangulate.

External involucral bract, blade consistency: **(0)** chartaceous; **(1)** coriaceous.

External involucral bract, blade color: **(0)** dark olive; **(1)** cream; **(2)** brown.

External involucral bract, blade, abaxial face, trichomes: **(0)** absent; **(1)** present.

Floral bracts: **(0)** absent; **(1)** present.

Floral bract, type: **(0)** petaloid; **(1)** scamiform.

Floral bracts, length in relation to flowers: **(0)** shorter; **(1)** longer.

Floral bract, shape: **(0)** obtrullate; **(1)** oblong; **(2)** obovate; **(3)** spathulate; **(4)** ovate.

Floral bract, blade consistency: **(0)** membranous; **(1)** chartaceous; **(2)** coriaceous.

Floral bract, color: **(0)** dark olive; **(1)** cream; **(2)** base yellow and apex olive; **(3)** light green.

Floral bract, blade, abaxial face, trichomes: **(0)** absent; **(1)** present.

Floral bract, longitudinal posture: **(0)** concave; **(1)** keeled; **(2)** flat.

Floral vertical parts number, in relation to other verticals, stability: **(0)** absent; **(1)** present.

Staminate flower, sepal shape: **(0)** ovate; **(1)** obovate; **(2)** oblong; **(3)** elliptic; **(4)** obtrullate; **(5)** linear.

Staminate flower, sepal, blade, abaxial face, trichomes: **(0)** absent; **(1)** present.

Staminate flower, blade, sepal, consistency: **(0)** membranous; **(1)** chartaceous.

Staminate flower, sepal, color: **(0)** dark olive; **(1)** cream; **(2)** base yellow and apex olive; **(3)** green light.

Staminate flower, lateral sepal, longitudinal posture: **(0)** concave; **(1)** keeled; **(2)** flat.

Staminate flower, fusion, type: **(0)** partial with apparent fusion lines; **(1)** total without apparent fusion lines.

Staminate flowers, sepals, wing: **(0)** absent; **(1)** present.

Staminate flower, sepals, fusion: **(0)** absent; **(1)** present.

Staminate flower, petal fusion: **(0)** absent; **(1)** present.

Staminate flower, median petal, size, in relation to lateral petals: **(0)** equal; **(1)** longer.

Staminate flower, median petal, in relation to laterals, longer than: **(0)** 0.1–0.5 mm; **(1)** 1.2–1.8 mm.

Staminate flower, stamens, number: **(0)** 3; **(1)** 6; **(2)** 4.

Staminate flowers, stamens, number, in relation to the number of vertical parts: **(0)** equal; **(1)** double.

Stamens, insertion, place: **(0)** base of corolla; **(1)** petals.

Staminate flowers, stamens, anther, color: **(0)** cream; **(1)** olive.

Pistillate flower, sepal, shape: **(0)** ovate; **(1)** obovate; **(2)** obtrullate; **(3)** oblong; **(4)** elliptic; **(5)** linear.

Pistillate flower, sepal, wing: **(0)** absent; **(1)** present.

Pistillate flower, sepal, blade, abaxial face, trichomes: **(0)** absent; **(1)** present.

Pistillate flower, blade, sepal, consistency: **(0)** membranaceous; **(1)** chartaceous; **(2)** spongy.

Pistillate flower, lateral sepal, longitudinal posture: **(0)** concave; **(1)** keeled; **(2)** gibbose; **(3)** cucullate.

Pistillate flower, sepal, fusion: **(0)** absent; **(1)** present.

Pistillate flower, sepal, fusion type: (**0**) partial with apparent fusion lines; (**1**) total without apparent fusion lines.

Pistillate flower, petal, fusion: **(0)** free; **(1)** connate.

Pistillate flower, median petal, shape: **(0)** spathulate; **(1)** unguiculate; **(2)** linear.

Pistillate flower, median petal, size, in relation to lateral petals: **(0)** equal; **(1)** longer.

Pistillate flower, median petal, length, in relation to laterals: **(0)** 0.1-0.5 mm longer; **(1)** 0.8–1 mm longer.

Pistillate flower, petal, adaxial face, trichomes: **(0)** absent; **(1)** present.

Pistillate flower, petal, consistency: **(0)** membranous; **(1)** cartilaginous; **(2)** spongious.

Petals, gland: **(0)** absent; **(1)** present.

Style, ramification: **(0)** absent; **(1)** present.

Seed, shape: **(0)** narrowly oblong (3:1-6:1); **(1)** ovoid (1.5:1-2:1); **(2)** spheroid (1:1); **(3)** obovoid (1.4:1-2:1); **(4)** widely ovoid (1.2:1-1.4:1); **(5)** oblong (1.3:1).

Seed coat, cells (primary projections), anticlinal walls, in relation to periclinal walls, height: **(0)** equal; **(1)** longer; **(2)** shorter.

Seed, coat, secondary projections: **(0)** absent; **(1)** present.

Seed, coat, secondary projections, shape: **(0)** post-shaped; **(1)** T-shaped; **(2)** ribbon jar shaped; **(3)** belt shaped larger than longer; **(4)** pyramidal (narrowly pyramidal to subulate); **(5)** J-shaped; **(6)** thick ribbon; **(7)** double belt shape longer than larger; **(8)** belt shape longer than large.

Seed, coat, secondary projections, localization: **(0)** vertices of walls; **(1)** anticlinal and periclinal walls; **(2)** middle of the anticlinal walls; **(3)** periclinal walls.

Seed, coat, tertiary projections, on secondary projections: **(0)** absent; **(1)** present.

Seed, coat, tertiary projections, on lumen: **(0)** absent; **(1)** present.

Leaf, cross-section, outline: **(0)** linear; **(1)** sinuous.

Leaf, cross-section, margin, shape: **(0)** obtuse; **(1)** acute; **(2)** acuminate.

Leaf, cross-section epidermis, adaxial surface, cells, shape: (**0**) palisade; (**1**) isodiametric.

Leaf, cross-section, epidermis, abaxial surface, stomata, chamber: **(0)** absent; **(1)** present.

Leaf, cross-section, mesophyll, adaxial surface, hypodermal chlorenchyma: **(0)** absent; **(1)** present.

Leaf, mesophyll, adaxial surface, hypodermis, cells, shape: (**0**) circular; (1) palisade.

Leaf, cross-section, mesophyll, cells, display: **(0)** continuous (not interrupted by the vascular bundle sheath); **(1)** discontinuous (interrupted by the vascular bundle sheath).

Leaf, cross-section, mesophyll, abaxial surface, hypodermal chlorenchyma: **(0)** absent; **(1)** present.

Leaf, cross-section, mesophyll, diaphragm: **(0)** absent; **(1)** present

Leaf, cross-section mesophyll, diaphragm, display: **(0)** compact; **(1)** loosely aggregate.

Leaf, cross-section, mesophyll, vascular bundle sheath composition: **(0)** collenchyma; **(1)** parenchyma; **(2)** sclerenchyma.

Leaf, cross-section, vascular bundles, localization, in relation to mesophyll: **(0)** middle; **(1)** near adaxial surface; (2) near abaxial surface.

Leaf, cross section, main, adaxial vascular bundles, sheath extension: **(0)** absent; **(1)** present.

Leaf, cross-section, main abaxial vascular bundles, sheath extension: **(0)** absent; **(1)** present.

Leaf, cross-section, secondary vascular bundles, size in relation to main vascular bundles: **(0)** equal; **(1)** smaller.

Scape, cortex, radial column, sclerenchyma: **(0)** absent; **(1)** present.

Scape, cross section, cortex, radial column, sclerenchyma, percentage: **(0)** 1/3; **(1)** 2/3.

Scape, cortex, visible endodermis, surrounding external vascular bundle: **(0)** absent; **(1)** present.

Scape, ribs, anatomical composition: **(0)** support tissue; **(1)** gas-filled cavities and diaphragm tissue.

Scape, cross section, central cylinder, pericycle in relation to vascular bundles, outline: **(0)** outlining main vascular bundles; **(1)** outlining all vascular bundles; **(2)** on main vascular bundles.

Scape, medulla, lacunae: **(0)** absent; **(1)** present.

Root, anatomy, metaxylem, number of vascular bundles: (**0**) one; (**1**) many.