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Occurrence and evolutionary inferences about Kranz anatomy in Cyperaceae (Poales)

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ABSTRACT

Cyperaceae is an angiosperm family with the greatest diversity of species with Kranz anatomy. Four different types of Kranz anatomy (chlorocyperoid, eleocharoid, fimbristylod and rhynchosporoid) have been described for this angiosperm family, and the occurrence and structural characteristics of these types are important to trace evolutionary hypotheses. The purpose of this study was to examine the available data on Cyperaceae Kranz anatomy, emphasizing taxonomy, geographic distribution, habitat and anatomy, to infer the potential origin of the Kranz anatomy in this family. The results showed that the four types of Kranz anatomy (associated with C_4 photosynthesis) in Cyperaceae emerged numerous times in unrelated phylogenetic groups. However, the convergence of these anatomical types, except rhynchosporoid, was observed in certain groups. Thus, the diverse origin of these species might result from different environmental pressures that promote photorespiration. Greater variation in occurrence of Kranz anatomy and anatomical types was observed in *Eleocharis*, whose emergence of the C_4 pathway was recent compared with other genera in the family, and the species of this genus are located in aquatic environments.

Key words: anatomy, ultrastructure, taxonomy, phylogeny, Cyperaceae.

INTRODUCTION

The Kranz anatomy represents a structural modification of photosynthetic tissues, generally two distinct concentric layers of chlorenchyma cells, associated with C_4 metabolism, the main function in plants with suppressed photorespiration, induced through decreased levels of CO_2 and

increased levels of O_2 (Sage 2004, Lundgren et al. 2014). Several factors, such as water stress, high temperature and lightness, and the salinity and high density of plants, influence the reduction of CO_2 (Sage et al. 2012).

The structural modification (Kranz anatomy) was initially reported in Cyperaceae species (Haberlandt 1914). Since then, several studies using different approaches have examined the Kranz structure and the C_4 pathway in this family (e.g.

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Carolin et al. 1977, Takeda et al. 1985, Bruhl et al. 1987, Ueno and Samejima 1989, Bruhl 1995, Bruhl and Perry 1995, Soros and Dengler 2001, Martins and Alves 2009, Martins and Scatena 2011). The Kranz structure varies in the Cyperaceae family, and four anatomical types have been described: chlorocyperoid, eleocharoid, fimbristyloid and rhynchosporoid. These types anatomically differ in the number and continuity of the vascular bundle sheath and in the presence of chloroplasts in the bundle sheath (Carolin et al. 1977, Soros and Dengler 2001, Martins and Scatena 2011).

Representatives of the Cyperaceae family with Kranz anatomy are restricted to four of the 13 tribes of the Cyperoideae subfamily: Abildgaardieae, Cypereae, Eleocharideae and Rhynchosporae (Goetghebeur 1998). Among these, only Abildgaardieae and Eleocharideae are closely related in phylogenetic studies (Ghamkhar et al. 2007, Muasya et al. 2008). The Kranz Cypereae species present a Kranz anatomy of the chlorocyperoid type, while the Abildgaardieae species present a Kranz anatomy of the fimbristyloid type (Bruhl and Wilson 2007). Chlorocyperoid, eleocharoid and fimbristyloid types have been described in the Eleocharideae tribe (Murphy et al. 2007, Martins and Scatena 2015), and chlorocyperoid and rhynchosporoid types have been reported in Rhynchosporae (Martins and Scatena 2011, Ueno 2013).

Therefore, it has been suggested that the origin of Kranz anatomy emerged four times in Cyperaceae, one type in each tribe (Soros and Bruhl 2000). In subsequent studies using molecular markers, five potential appearances of Kranz anatomy were reported: two types in Eleocharideae and one type in each of the remaining Kranz tribes (Besnard et al. 2009). Phylogenetic studies of Abildgaardieae (Ghamkhar et al. 2007) and Eleocharideae (Roalson et al. 2010) indicated multiple origins of C_4 photosynthesis.

The variations of Kranz anatomy observed in this family have generated important taxonomic, ecological and evolutive interpretations. Therefore, the aim of the present study was to review taxonomic, ecological, structural and phylogenetic data associated with the structural analyses performed with Cyperaceae species of the four Kranz types (Martins and Scatena 2011, Martins and Scatena 2015, Martins et al. 2015) to develop potential hypotheses concerning the origins of these plants.

MATERIALS AND METHODS

The species used to illustrate anatomical and ultrastructural features are listed in Table I. The voucher materials were deposited at the Herbarium of the Department of Botany, Universidade Estadual Paulista (HRCB). The data collected here added to the literature are given in Table II.

To anatomically illustrate the different Kranz types, portions of at least three fully expanded leaf blade or scapes were fixed in FAA 50 and stored in 70% ethanol (Johansen 1940) and subsequently dehydrated in an ethyl alcohol series and embedded in Historesin (Leica Historesin Embedding Kit, Nussloch, Germany) (Feder and O'Brien 1968). Transverse sections of the mid-region were obtained using a microtome, and the sections were stained with periodic acid-Schiff's reagent and toluidine blue (Feder and O'Brien 1968) and mounted in Entellan (Merck Darmstadt, Germany). The images were obtained using Leica DFC 290 digital camera on a Leica DM LB microscope using IM50 software.

To illustrate the ultrastructural features of the four Kranz types, samples from the mid-region of at least three fully expanded leaf blades or scapes were fixed in 2.5% glutaraldehyde solution in 0.1 M phosphate buffer, pH 7.3, for 24 h at 5°C, post-fixed with 1% osmium tetroxide in the same buffer for 1 h at 25°C, dehydrated with an acetone

series and embedded in Araldite resin (Machado and Rodrigues 2004). Ultrathin transverse sections were obtained using a Diatome diamond knife, and the sections were subsequently stained with uranyl acetate and lead citrate (Reynolds 1963). The samples were examined using a Philips EM 301 transmission electron microscope (MET).

To illustrate the occurrence of the Kranz anatomical types in Cyperaceae, these data were plotted onto cladograms from previously published phylogenetic analyses for each tribe: Abildgaardieae (Ghamkhar et al. 2007), Cyperaceae (Muasya et al. 2009), Eleocharideae (Roalson et al. 2010) and Rhynchosporae (Thomas et al. 2008).

RESULTS

Abildgaardieae tribe – This tribe has six genera with Kranz anatomy, *Abildgaardia*, *Bulbostylis*, *Crosslandia*, *Fimbristylis*, *Nelmesia* and *Nemum* (Tab. II), and two non-Kranz (C_3) species,

Abildgaardia hygrophila and *Fimbristylis variegata*. This tribe is non-monophyletic, and representatives of the non-Kranz Arthrostylideae tribe emerge as the sister group of the clade *Fimbristylis-Abildgaardia-Crosslandia* (Fig. 1e). The Kranz taxa of Abildgaardieae possess the fimbristyloid type, characterized by vascular bundles surrounded by three sheaths, an outer sheath (Os), a continuous middle sheath (Ms), and a discontinuous inner sheath (Is) in the major bundles, interrupted by only one or two metaxylem vessels (Fig. 1a-b). The outer bundle sheath originates from the ground meristem, while the middle and inner sheaths develop from the procambium. The chloroplasts in the outer-sheath cells present well-developed grana, similar to the mesophyll cells. The middle-sheath cells do not show chloroplasts, and the inner-sheath cells show centrifugal chloroplasts without grana (Fig. 1c) and with convoluted and parallel thylakoids (Fig. 1d).

TABLE I
Cyperaceae species used to illustrate the anatomical and ultrastructural features with Kranz types and vouchers, respectively.

Tribes and species	Kranz anatomical type	Voucher
Abildgaardieae		
<i>Bulbostylis conifera</i> L.	fimbristyloid	<i>S. Martins</i> 329
<i>Bulbostylis scabra</i> (J. Presl. & C. Presl.) C.B. Clarke	fimbristyloid	<i>S. Martins</i> 408
<i>Fimbristylis autumnalis</i> L.	fimbristyloid	<i>V.L. Scatena</i> 343
<i>Fimbristylis complanata</i> (Retz.) Link	fimbristyloid	<i>V.L. Scatena</i> 344
<i>Fimbristylis dichotoma</i> (L.) Vahl	fimbristyloid	<i>S. Martins</i> 398
Cyperaceae		
<i>Cyperus compressus</i> Jacq.	chlorocyperoid	<i>S. Martins</i> 228
<i>Cyperus ligularis</i> L.	chlorocyperoid	<i>S. Martins</i> 330
<i>Cyperus maritimus</i> Poir.	chlorocyperoid	<i>S. Martins</i> 226
<i>Kyllinga brevifolia</i> Rottb.	chlorocyperoid	<i>S. Martins</i> 288
<i>Pycnus flavescens</i> (L.) Rchb.	chlorocyperoid	<i>S. Martins</i> 327
Eleocharideae		
<i>Eleocharis minima</i> Kunth	eleocharoid	<i>S. Martins</i> 405
Rhynchosporae		
<i>Rhynchospora barbata</i> (Vahl) Kunth	chlorocyperoid	<i>S. Martins</i> 313
<i>Rhynchospora globosa</i> Lindl.	rhynchosporoid	<i>S. Martins</i> 305
<i>Rhynchospora terminalis</i> Kunth	rhynchosporoid	<i>S. Martins</i> 302

TABLE II

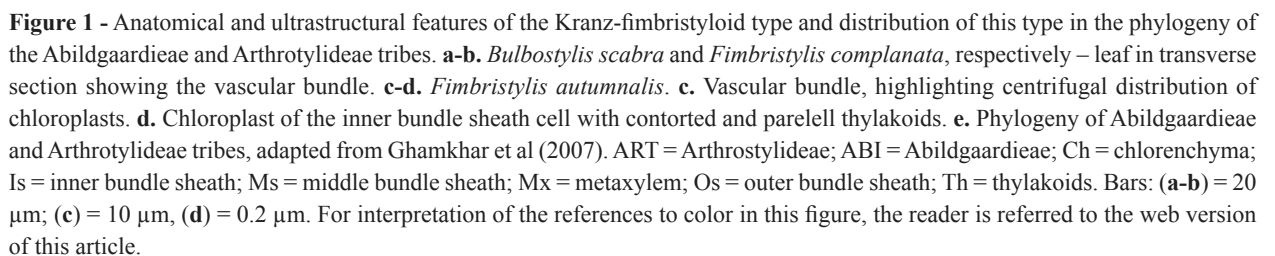
Cyperaceae genera with Kranz anatomy (C_4 photosynthesis), detach to taxonomical classification, Kranz anatomical types, biochemical subtypes, habitat and distribution (K-C = chlorocyperoid; K-E = eleocharoid; K-F = fimbristylloid; K-R = rhynchosporoid).

Tribes and genera (number of C_3 and C_4 species)	Kranz type	Biochemical type	Habitat	Distribution
Abildgaardieae				
<i>Abildgaardia</i> (1 C_3 /16 C_4) ^{1,2,3,5,6}	K-F	NADP-ME	Dry field and disturbed area	Tropical and subtropical
<i>Bulbostylis</i> (150 C_4) ^{1,2,3,4,5,6}	K-F	NADP-ME	Dry field, rare moist area	Tropical
<i>Crosslandia</i> (4 C_4) ^{2,4,6}	K-F	NADP-ME	Dunes and dry field	Tropical (Australia)
<i>Fimbristylis</i> (1 C_3 /300 C_4) ^{1,2,3,4,5,6}	K-F	NADP-ME	Dry fields and disturbed area	Tropical (Asia e Australia)
<i>Nelmesia</i> (1 C_4) ^{2,4,6}	K-F	NADP-ME	Field moist	Tropical (Africa)
<i>Nemum</i> (10 C_4) ^{2,4,6}	K-F	NADP-ME	Field moist	Tropical (Africa)
Cypereae				
<i>Alinula</i> (4 C_4) ^{2,4,6}	K-C	NADP-ME	Field moist	Tropical (Africa)
<i>Ascolepis</i> (20 C_4) ^{2,4,6}	K-C	NADP-ME	Field moist	Tropical
<i>Cyperus</i> subg. <i>Cyperus</i> (260 C_4) ^{1,2,3,4,5,6}	K-C	NADP-ME	Field moist and disturbed area	Tropical, rare subtropical
<i>Kyllinga</i> (75 C_4) ^{1,2,3,4,5,6}	K-C	NADP-ME	Field moist and disturbed area	Tropical, rare subtropical
<i>Lipocarpa</i> (35 C_4) ^{2,4,6}	K-C	NADP-ME	Field moist	Tropical, rare subtropical
<i>Pycurus</i> (120 C_4) ^{1,2,3,4,5,6}	K-C	NADP-ME	Field moist and disturbed area	Tropical
<i>Queenslandiella</i> (1 C_4) ^{2,4,5,6}	K-C	NADP-ME	Dunes	Tropical (Africa, Asia and Australia)
<i>Remirea</i> (1 C_4) ^{2,4,5,6}	K-C	NADP-ME	Dunes	Tropical
<i>Sphaerocyperus</i> (1 C_4) ^{2,4,5,6}	K-C	NADP-ME	Dry field	Tropical (Africa)
<i>Volkiella</i> (1 C_4) ^{2,3,4,5}	K-C	NADP-ME	Dunes	Tropical (Africa)
Eleocharideae				
<i>Eleocharis</i> (244 C_3 /8 C_4) ^{1,2,3,4,5,6,8}	K-E; K-C; K-F	NAD-ME	Border of river and lakes	Tropical (America)
Rhynchosporae				
<i>Rhynchospora</i> grupo <i>Capitatae</i> (5 C_3 /28 C_4) ^{1,2,3,4,5,7}	K-C; K-R	NADP-ME	Dry and moist fields	Neotropical

¹Bruhl and Perry (1995), ²Bruhl and Wilson (2007), ³Bruhl et al. (1987), ⁴Goetghebeur (1998), ⁵Martins and Scatena (2011), ⁶Soros and Bruhl (2000), ⁷Ueno (2013), ⁸Martins and Scatena (2015).

Cypereae tribe – This tribe possesses 19 genera, 10 of which are Kranz species, including nine exclusively Kranz (C_4) species (*Alinula*, *Ascolepis*, *Kyllinga*, *Lipocarpa*, *Pycurus*, *Queenslandiella*, *Remirea*, *Sphaerocyperus* and *Volkiella*) and in *Cyperus* restricted to *Cyperus* subg. *Cyperus* (Tab. II). This tribe is monophyletic, and the Kranz taxa emerge in a separate clade from non-Kranz taxa (Fig. 2e). Cypereae present chlorocyperoid type

Kranz, characterized by two sheaths surrounding the vascular bundles: a continuous outer sheath (Os) and a discontinuous inner sheath (Is) in the major bundles (Fig. 2a). Both bundle sheaths develop from the procambium. The outer-sheath cells do not have chloroplasts (Fig. 2b), and the inner-sheath cells are generally centrifugal (Fig. 2b), with inconspicuous grana and convoluted and contorted thylakoids (Fig. 2c-d).



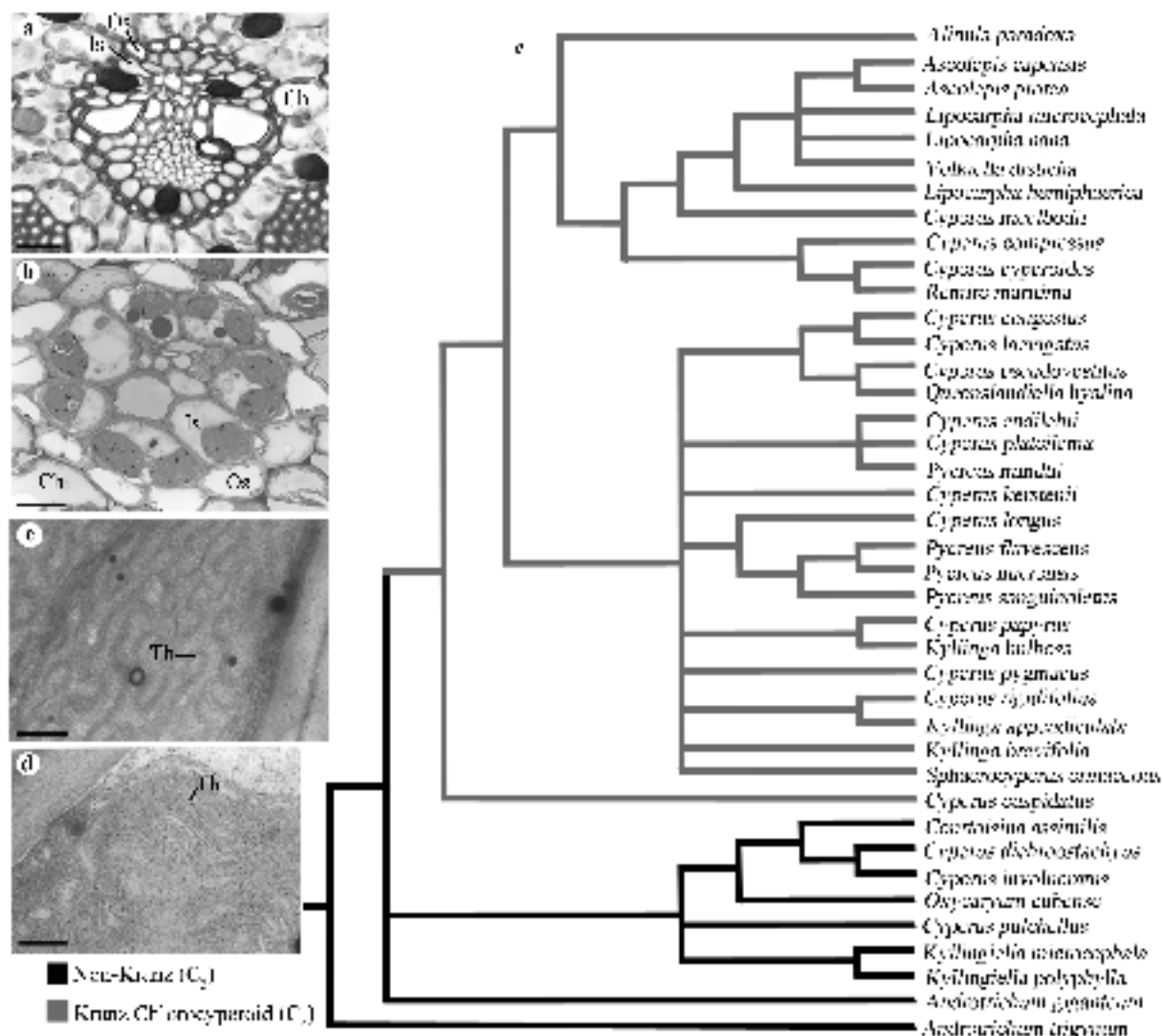


Figure 2 – Anatomical and ultrastructural features of the Kranz-chlorocyperoid type and distribution of this type in the phylogeny of the Cyperaceae tribe. **a.** *Kyllinga brevifolia* – leaf in transverse section showing the vascular bundle. **b.** *Cyperus compressus* – vascular bundle, highlighting centrifugal distribution of chloroplasts. **c-d.** *Cyperus maritimus* and *C. ligularis*, respectively – chloroplast of the inner bundle sheath cell with convoluted and contorted thylakoids, respectively. **e.** Part of phylogeny of Cyperaceae tribe, detach to Kranz species, adapted from Muasya et al. (2008). Ch = chlorenchyma; Is = inner bundle sheath; Os = outer bundle sheath; Th = thylakoids. Bars: **(a)** = 20 μ m; **(b)** = 5 μ m; **(c-d)** = 0.5 μ m. For interpretation of the references to color in this figure, the reader is referred to the web version of this article.

Eleocharideae tribe – This tribe only includes the genus *Eleocharis* (250 spp.), presenting Kranz (C_4) and non-Kranz species (C_3) (Tab. II) and facultative C_3/C_4 and intermediate C_3 - C_4 species. These species possess leaf lamina reduced to a tubular basal sheath, and the scape is the principal photosynthetic organ. The Kranz species of *Eleocharis* present eleocharoid, fimbristyloid and chlorocyperoid types (Fig. 3d-e). The eleocharoid

type shows two continuous vascular bundle sheaths (Fig. 3a): an outer sheath (Os) without chloroplasts and an inner sheath (Is) with chloroplasts that do not show a constant location and have parallel thylakoids, occasionally forming grana (Fig. 3b-c). The fimbristyloid and chlorocyperoid types in *Eleocharis* are anatomically similar to those previously described for Abildgaardieae and Cyperaceae.

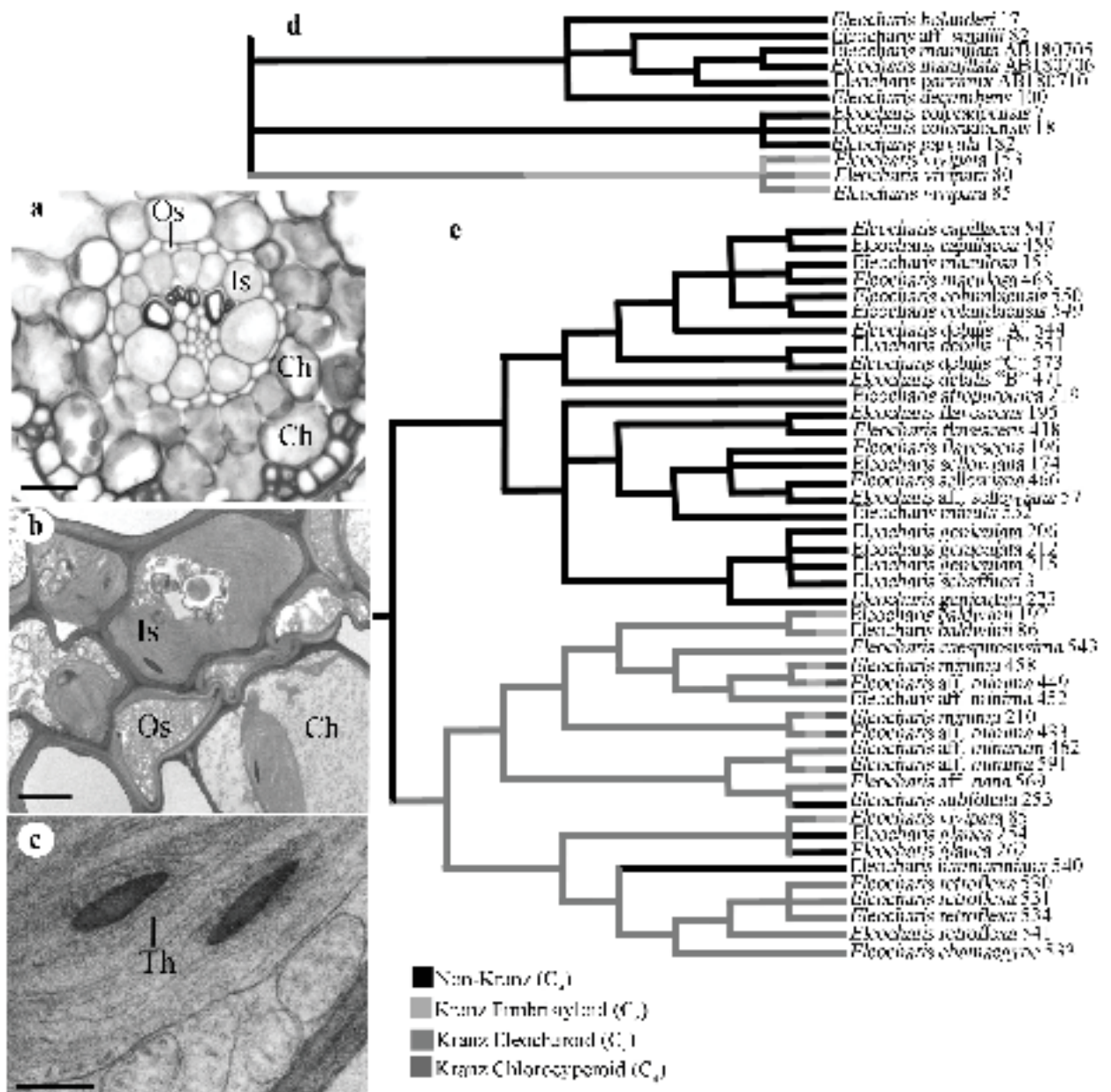


Figure 3 - Anatomical and ultrastructural features of the Kranz-eleocharoid type and distribution of this type in the phylogeny of the Eleocharideae tribe. **a-c.** *Eleocharis minima*. **a.** Scape in transverse section showing the vascular bundle. **b.** Vascular bundle, detach to chloroplast without Constant location in the inner bundle sheath. **c.** Chloroplast with parallel thylakoids in the inner bundle sheath. **d-e.** Part of phylogeny of the Rhynchosporeae tribe, highlighting the Kranz species, adapted from Roalson et al. (2010). Ch = chlorenchyma; Is = inner bundle sheath; Os = outer bundle sheath; Th = thylakoids. Bars: (a) = 20 µm; (b) = 2 µm; (c) = 0.5 µm. For interpretation of the references to color in this figure, the reader is referred to the web version of this article.

Rhynchosporeae tribe – This tribe possesses two genera, *Pleurostachys* and *Rhynchospora*, and only *Rhynchospora* has species with Kranz anatomy (C_4) restricted to *Pauciflorae* (Pau) and *Pluriflorae* (Plu) sections from the Capitatae group

(Tab. II). This species presents chlorocyperoid and the rhynchosporoid Kranz types that occur in distinct clades in the phylogenetic analysis (Fig. 4e). The chlorocyperoid has two sheaths surrounding the vascular bundles, wherein the outer (Os) is

continuous and the inner (Is) is discontinuous in the major bundles (Fig. 4a). Similar to the chlorocyperoid type in Cyperaceae, both sheaths (outer and inner) originate from the procambium. The chloroplasts are absent in the outer sheath cells (Os), whereas these organelles are centrifugal or without pattern, with convoluted and parallel thylakoids in the inner sheath cells (Fig. 4b). The rhynchosporoid present a unique continuous bundle sheath (Ss – single sheath) (Fig. 4c), originating from the procambium and presenting cells with chloroplasts located centrifugally or without pattern, with inconspicuous grana and parallel thylakoids (Fig. 4d).

DISCUSSION

The data obtained from the present study and previously published studies suggest that multiple origins of Kranz anatomy occurred in Cyperaceae due to different environmental factors that promote photorespiration. The Kranz anatomy is uniform in Abildgaardieae Cyperaceae tribes, showing only one anatomical type, and varied in Rhynchosporae and Eleocharideae tribes, showing more than one type.

In Abildgaardieae, the Kranz anatomy (C_4) likely had only one origin, before the occurrence of a single anatomical (fimbristyloid) and biochemical (NADP-ME) type, with possible reversion to the C_3 pathway (not Kranz) in *Abildgaardia hygrophila*, *Fimbristylis variegata* and representatives of the Arthrostylideae tribe. This hypothesis is confirmed by phylogenomic and phylogenetic studies (Besnard et al. 2009, Ghamkhar et al. 2007), suggesting the initial onset of C_4 photosynthesis in *Bulbostylis* (ca. 19.6 ± 4.9 Ma), followed by *Fimbristylis* (ca. 12.3 ± 3.8 Ma). Moreover, the species of Abildgaardieae is primarily observed in xeric environments (open fields, rocky outcrops, dunes), and the C_4 pathway must have arisen in this environment, where this biochemical pathway is more advantageous (Sage 2004, Sage et al. 2012).

In the Cyperaceae tribe, the Kranz anatomy likely derived from a single source, as the Kranz species in this tribe emerged in the same clade (Muasya et al. 2002, 2009) and have the same anatomical (chlorocyperoid) and biochemical (NADP-ME) types and similarities in the structure of the chloroplasts. The emergence of C_4 in this tribe is indicated ca. 10.9 ± 3.8 Ma (Besnard et al. 2009), initially in mesophyte species (with C_3 mesophytes ancestors) and subsequently in xerophytes (with C_4 mesophytes ancestors), as most of the C_4 species primarily occur in mesic environments and a minority of these species are observed in xeric areas. This hypothesis has also been postulated for the C_4 species of Poaceae (Osborne and Freckleton 2009). The occurrence of C_4 metabolism in mesic environments with high water availability is associated with the high density, high temperature and increased luminosity, which reduce the absorption of CO_2 and carbohydrate production in plants (Bowes et al. 2000, Sage et al. 2012).

The plasticity of the C_4 pathway makes it difficult to interpret the origin of this pathway in Eleocharideae, with the possibility of two sources with reversals for C_3 or multiple origins. The Kranz types in this tribe vary between individuals of the same species (Ueno 1996, 2004, Murphy et al. 2007) and even in the same individual (Martins and Scatena 2015). As eleocharoid types are considered more related to C_4 metabolism, and the fimbristyloid types are considered C_3 - C_4 intermediates (Murphy et al. 2007), it is likely that the aquatic environment of these plants promotes anatomical plasticity, such as the number of vascular bundles and the presence and development of aerenchyma (Martins and Scatena 2015), as observed in other anatomical structures.

Structurally, the difference between the eleocharoid and fimbristyloid types is the size and shape of the cells of the inner layer chlorenchyma (Ch) (both originate from the ground meristem), which is slightly larger and elongated in the first

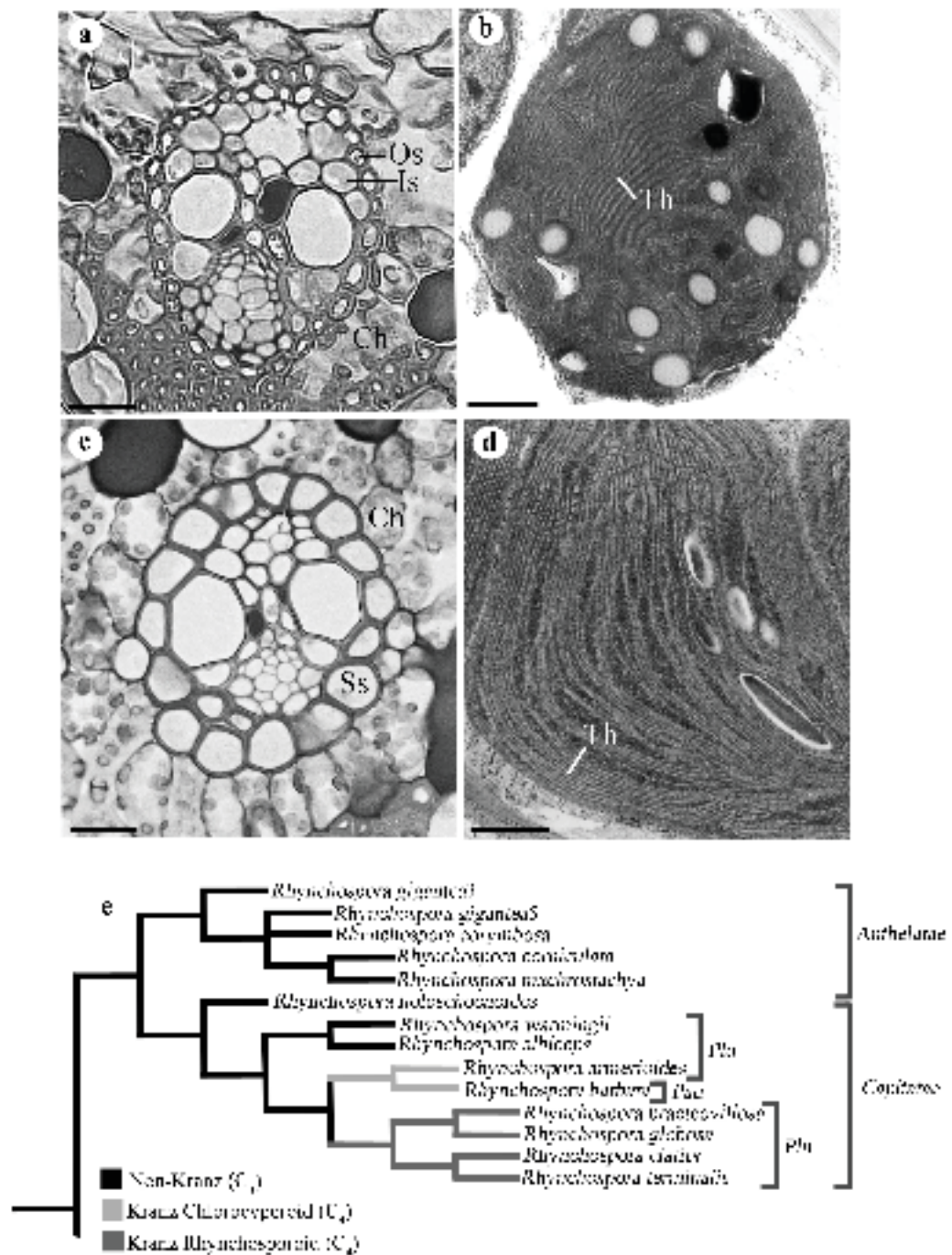


Figure 4 - Anatomical and ultrastructural features of the Kranz-chlorocyperoid and Kranz-rhynchosporoid types and distribution of these types in the phylogeny of the Rhynchosporeae tribe. **a-b.** *Rhynchospora barbata*. **a.** Leaf in transverse section showing the vascular bundle. **b.** Chloroplast of the inner bundle sheath cell with parallel thylakoids. **c-d.** *Rhynchospora globosa*. **c.** Leaf in transverse section showing the vascular bundle. **d.** Chloroplast of the inner bundle sheath cell with parallel thylakoids. **e.** Part of phylogeny of Rhynchosporeae tribe, detach to Kranz species, adapted from Thomas et al. (2008). Ch = chlorenchyma; Is = inner bundle sheath; Os = outer bundle sheath; Pau = *Pauciflorae*; Plu = *Pluriflorae*; Ss = single bundle sheath; Th = thylakoids. Bars: (**a, c**) = 20 μ m; (**b, d**) = 0.5 μ m. For interpretation of the references to color in this figure, the reader is referred to the web version of this article.

type, and rounded and smaller in the second type. These types also differ in the continuity of the inner sheath in the major vascular bundles, being continuous only in the eleocharoid type (Soros and Bruhl 2000). However, the continuity of the inner sheath might vary along the scape and can be interrupted in the apical region, as indicated for *Eleocharis minima* (Martins and Scatena 2015), described as Kranz eleocharoid (Murphy et al. 2007, Martins and Scatena 2011).

In Eleocharideae, the C_4 pathway is considered intermediate to recent (*Eleocharis vivipara* - ca. 10.5 ± 3.2 Ma; *E. baldwinii* - 4.4 ± 2.1 Ma) compared with the other C_4 species of this family (Besnard et al. 2009). These authors indicated that Cyperaceae species with different Kranz types do not present significant genetic modifications. Thus, before the plasticity observed in *Eleocharis*, the changing of C_3 to C_4 metabolism might have required a small number of genetic modifications, as indicated by Christin et al. (2007) for groups with high plasticity in present C_4 photosynthesis. Plasticity in Kranz anatomy was also observed in other C_4 groups, such as some species of Poaceae and Asteraceae (Araus et al. 1990, Gong et al. 2011).

In Rhynchosporae, it is likely that the Kranz anatomy arose twice, once for each anatomical type, as chlorocyperoid and rhynchosporoid occur in distinct clades (Thomas et al. 2008). Both Kranz types occur in *Pauciflorae* and *Pluriflorae* sections (Ueno and Koyama 1987), and although these types differ in the number of sheaths and chloroplast locations, similarities are observed in chloroplast distribution and thylakoid organization. Genetic markers indicate that the C_4 pathway is recent in *Rhynchospora* (ca. 7.4 ± 2.8 Ma) compared with the other species of this family (Besnard et al. 2009), and phylogenetic data show the occurrence of the C_4 pathway in derivative gender groups (Thomas et al. 2008). The Kranz (C_4) of the *Rhynchospora* species are primarily Neotropical, occurring in xeric environments, such as open fields and savannas

(Ueno and Koyama 1987), living sympatrically with non-Kranz (C_3) species of the same genus. Thus, it has been suggested that the C_4 pathway arose in some lineages of the genus as an adaptation to conditions of water stress, high temperatures and light from C_3 ancestors potentially occurring in this type of environment. However, the occurrence of different Kranz types in closer phylogenetic groups living sympatrically is intriguing and requires more detailed studies.

The variations among the Kranz types in Cyperaceae reflect essential differences in the structure, not the origin, of the tissues. The homologous chlorophyllian cells surrounding the vascular bundles arise from the ground meristem and might have an elongated (chlorophyll parenchyma) or rounded (outer sheath) shape. In chlorocyperoid, eleocharoid and fimbristylloid types, the procambium gives rise to two vascular sheaths, with chloroplasts only in the inner sheath. In the rhynchosporoid type, only one sheath has procambial origin and presents chloroplasts. This sheath is homologous to the outer sheath, which lacks chloroplasts with procambial origin.

Herein, we showed the multiple origins of Kranz anatomy in Cyperaceae in different phylogenetic groups, confirming the results of Soros and Bruhl (2000), Muasya et al. (2002, 2008, 2009), Ghamkhar et al. (2007), Thomas et al. (2008) and Roalson et al. (2010). Thus, this study represents adaptive convergence, as phylogenetic relationships are not reflected. In addition, the anatomical types are not associated with specific environmental conditions because the Kranz species of Abildgaardieae, *Rhynchospora* and some of Cypereae occur in similar xeric environments or even live sympatrically and present different Kranz types. In addition, *Eleocharis* representatives vary in relation to the occurrence and the type of Kranz anatomy in individuals of the same species.

Thus, the Kranz types in Cyperaceae likely result from ecological pressures that promote

photorespiration, even in different environmental conditions. The Kranz species of Abildgaardieae and Rhynchosporae tribes are xerophytes, whereas the Cyperaceae species are mesophytes or xerophytes and the Eleocharideae species are hydrophytes. Thus, independent of the environment, distinct lineages of Cyperaceae have similar evolutionary pathways for more efficient photosynthesis.

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RESUMO

Cyperaceae é uma das famílias de angiospermas com maior diversidade de espécies com anatomia Kranz. Para a família foram descritos quatro diferentes tipos de anatomia Kranz (clorociperoide, eleocaróide, fimbristiloide e rincosporóide) e a ocorrência e as características estruturais desses tipos são importantes para traçar hipóteses evolutivas. Este trabalho visou examinar dados disponíveis sobre anatomia Kranz de Cyperaceae com ênfase na taxonomia, distribuição geográfica, habitat e anatomia para inferir a possível origem da anatomia Kranz na família. Verificou-se que os quatro tipos de anatomia Kranz (relacionada à fotossíntese C_4) em Cyperaceae surgiram diversas vezes em grupos não relacionados filogeneticamente. Por outro lado, observou-se a convergência desses tipos anatômicos, exceto o rincosporóide, em determinados grupos. Assim, a origem diversa dessas espécies pode ser resultado de diferentes pressões ambientais que promovem a fotorrespiração. Maior variação da ocorrência da anatomia Kranz e de tipos anatômicos foi observada em *Eleocharis*, cujo surgimento da via C_4 é recente quando comparado aos demais gêneros da

família e as espécies deste gênero vivem em ambientes aquáticos.

Palavras-chave: anatomia, ultraestrutura, taxonomia, filogenia, Cyperaceae.

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