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# Development and anatomical evidence of floral morphological variation in Cyperoideae (Cyperaceae): Case studies on the most species-rich genera

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ABSTRACT

Cyperaceae comprises subfamilies Mapanioideae and Cyperoideae, mainly distinguished by reproductive morphology. Whilst Mapanioideae has spicoids, reproductive units composed of reduced unisexual flowers, Cyperoideae exhibit unambiguous spikelets with mainly trimerous bisexual flowers. However, for the latter, there is considerable variation within each floral whorl, hampering taxonomic descriptions and assessing morphological homologies to better understand Cyperaceae evolutionary relationships. Therefore, we focused on species from the most species-rich genera of Cyperoideae: *Carex, Cyperus*, and *Rhynchospora*, as potential models to explore the main floral variations reported, addressing the following questions: (1) Does the *Rhynchospora* perianth follow the typical Cyperoideae developmental pattern? (2) Are the unisexual flowers in *Cyperus* truly unisexual? (3) What processes underlie the increased number of stamens in *Carex* staminate flowers? (4) What explains gynoecium variation in Cyperoideae flowers? The results showed that the *Rhynchospora* perianth follows a distinct ontogenetic sequence, indicating independent evolutionary patterns within Cyperoideae. We confirmed the presence of bisexual and unisexual flowers in *Cyperus*, requiring taxonomic updates. In *Carex*, the increased number of stamens is due to the congenital fusion of primordia. Across species, mechanical constraints from the glume limited the development of abaxial structures, such as perianth and stamens, which may influence the positioning of the dimerous and dorsiventrally flattened pistil in Cyperoideae flowers. These findings emphasize the importance of integrating anatomical and developmental data to better understand the evolutionary processes shaping floral diversity in Cyperaceae.

## 1. Introduction

Cyperaceae, the third largest monocot family, is known for its extensive distribution, occurring in a variety of environments with the highest concentration in the Neotropics (Larridon, 2022). This places the family in a pivotal position regarding the understanding and conservation of its biodiversity. Beyond its geographic distribution, Cyperaceae exhibits remarkable morphological diversity, particularly in floral structures, making it a valuable model for ecological, physiological, morphological and molecular studies aiming to unravel macroevolutionary processes (Spalink et al., 2016a, 2016b; Demeda et al., 2018; Semmouri et al., 2019; Larridon et al., 2021; Monteiro et al., 2022). The family comprises approximately 5687 species in 95 genera (Larridon et al., 2021; Larridon, 2022), distributed across two subfamilies: Cyperoideae, with 85 genera, and Mapanioideae, with 10 genera (Govaerts et al., 2007; Larridon et al., 2021; Larridon, 2022).

The two subfamilies exhibit distinct floral characteristics. Cyperoideae typically features flowers with a trimerous floral bauplan, including two perianth whorls, one whorl of stamens and a trimerous gynoecium (Vrijdaghs et al., 2009, 2010, 2011). In this subfamily, the flowers are sessile and arise in the axil of glumes, which are arranged along an open axis to form a spikelet (Bruhl, 1995; Goetghebeur, 1998; Vegetti, 2003). In contrast, Mapanioideae is distinguished by a unique reproductive unit known as the spicoid, which has sparked debate over whether it represents a flower or an inflorescence (Simpson, 1992; Richards et al., 2006; Prychid and Bruhl, 2013; Monteiro et al., 2016,

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2020, 2022;). Whilst the nature of the spicoid in Mapanioideae remains a topic of discussion, the floral bauplan in Cyperoideae is better defined, although the flowers frequently exhibit deviations in organ morphology and number within each whorl (Vrijdaghs et al., 2009, 2010, 2011; Lucero et al., 2014; Reutemann et al., 2015).

The pronounced floral variation of Cyperoideae may be related and contribute to the extensive species richness of the subfamily, which, despite encompassing 85 genera, has 80 % of its species concentrated in just seven genera: *Carex* L. (2003 spp.), *Cyperus* L. (964 spp.), *Rhynchospora* Vahl (399 spp.), *Fimbristylis* Vahl (320 spp.), *Eleocharis* R. Br. (302 spp.), *Scleria* P.J. Begius (258 spp.), and *Bulbostylis* Kunth. (227 spp.) (Larridon, 2022). Within these genera, significant floral morphological diversity is observed, not only between species but sometimes within individual plants. This variation hampers taxonomic delimitation and species descriptions based solely on mature flowers. For example, flowers in *Cyperus* species are often described as bisexual, typically bearing a gynoecium and a single stamen (Vrijdaghs et al., 2011). However, pistillate flowers may appear along the spikelets (Araujo and Longhi-Wagner, 1996; Chen et al., 2009; Ribeiro et al., 2015), raising questions about whether such flowers are strictly unisexual or a result of the late detachment of stamens. Similarly, *Carex* species often deviate from the typical trimerous b auplan by increasing the number of stamens (Smith, 1966; Smith and Faulkner, 1976), prompting discussions towards the nature of such units as flowers or reduced inflorescences.

Moreover, floral variation in Cyperoideae extends to all floral whorls. The perianth, for instance, ranges from foliar structures to reduced bristle-like appendages, varying from three to eight parts (Bruhl, 1995; Goetghebeur, 1998; Vrijdaghs et al., 2009, 2010). Despite this diversity, the ontogenetic pattern of perianth development is generally stable, with whorls forming after the stamens and concurrently with ovary primordium initiation (Vrijdaghs et al., 2009, 2010, 2011). Deviations from this sequence, however, have been noted in certain genera, such as *Rhynchospora* (Monteiro et al., 2017) and *Oreobolus* R. Br. (Mora-Osejo, 1967). Similarly, the androecium typically consists of three stamens opposite the outer perianth whorl (two latero-adaxial and one abaxial), but reductions or increases in stamen number have been reported across different genera such as *Carex* (Smith, 1966; Smith and Faulkner, 1976) *Pycreus* P.Beauv., *Lepidosperma* Labill. (Vrijdaghs et al., 2009) and genera of tribe Schoeneae (Bruhl, 1995; Goetghebeur, 1998). The gynoecium also shows variation, ranging from trimerous to dimerous structures with diverse morphologies, such as dorsiventrally or laterally flattened pistils, particularly in flowers belonging to *Carex, Cyperus*, and *Rhynchospora* (Vrijdaghs et al., 2009, 2010; Reynders et al., 2012). These genera, therefore, represent promising models for studying floral variation patterns in Cyperaceae.

To elucidate evolutionary relationships and morphological homologies in Cyperoideae, it is essential to investigate floral morphological variation, particularly the developmental modifications occurring in its most species-rich genera. Although these genera are highly species-rich, the key floral modifications can already be observed in selected species. Here, *Rhynchospora sparsiflora* (Kunth) L.B. Sm., *Cyperus surinamensis* Rottb. and *Carex brasiliensis* A. St.-Hil. are included as potential models to explore the main variations in each floral whorl within Cyperoideae. These species are widely distributed in Brazilian ecosystems (Alves et al. 2009), where they constitute ecologically relevant components of the herbaceous stratum in plant communities. Moreover, they exhibit distinct floral morphologies that allow for a comparative analysis of developmental patterns and anatomical traits, providing insights into the morphological diversity within the group.

Therefore, combining anatomical and developmental analyses we aim to answer the following questions: (1) Does the perianth of *Rhynchospora* follow the typical developmental pattern described for Cyperoideae flowers? (2) Are the unisexual flowers in *Cyperus* truly unisexual? (3) What processes underlie the increased number of stamens in *Carex* staminate flowers? (4) What morphological evidence explains the gynoecium variation in Cyperoideae flowers? These questions underscore the potential of Cyperaceae as a model for studying floral diversity and evolution.

## 2. Material and methods

### 2.1. Morphological sampling

Spikelets of *Rhynchospora sparsiflora* (Kunth) L.B. Sm. were collected in August 2015 in the *Reserva Florestal Adolpho Ducke* (Manaus, Amazonas, Brazil), in the humid understorey of the Amazon rainforest. Spikelets of *Carex brasiliensis* A. St.-Hil. were collected in highland grasslands (*campos de altitude*) in the *Parque Nacional do Itatiaia* (Itatiaia, Rio de Janeiro, Brazil) in February 2017. Spikelets of *Cyperus surinamensis* Rottb. were collected in a secondary forest at the University of São Paulo *campus* (São Paulo, SP, Brazil), in February 2017. The studied species are widely distributed in Brazilian vegetation and represent distinct floral morphologies, enabling comparative analyses of developmental patterns and anatomical traits. For all species, spikelets originating from prophyll axils were examined. For each species, we sampled at least five individuals from a minimum of two distinct populations, analyzing an average of 10 spikelets and 50 flowers per species. This approach was designed to capture potential intraspecific variation and ensure that the morphological patterns observed are representative, rather than artifacts of individual or population-level anomalies. Vouchers were deposited in the herbarium SPF (University of São Paulo – Brazil) (*Rhynchospora sparsiflora* – MM/AG/JE 248; *Carex brasiliensis* – MM/LL 257; *Cyperus surinamensis* –MM 259).

### 2.2. Light and scanning electron microscopy

Inflorescences and flowers at different developmental stages were fixed in FAA (formaldehyde, glacial acetic acid, 50 % ethanol, 1:1:18 v/v) (Johansen, 1940) and stored in 70 % ethanol for morphological and anatomical studies. Inflorescences with mature flowers were dissected under a Leica EZ4 stereomicroscope (Leica Microsystems, Wetzlar, Germany) and photographs were taken using a Leica DFC 320 camera device coupled to stereomicroscope Leica MZ8, using Leica IM50 software (Leica Microsystems, Wetzlar, Germany).

Fixed spikelets at different developmental stages were dissected under a Zeiss Stemi SV6 stereomicroscope (Zeiss, Oberkochen, Germany). The material was dehydrated through an ethanol-acetone series (Johansen, 1940), critical-point dried using $CO_2$ in a k850 KPD critical-point drier (Quorum Technologies, Kent, UK), coated with platinum using an Emitech k575x Sputter Coater (Quorum Technologies, Kent, UK) and examined with a LEO Supra 55VP scanning electron microscope (Zeiss, Oberkochen, Germany). In addition, transverse anatomical sections of the flowers were made; the samples were subjected to a *tert*-butyl alcohol dehydration series and embedded in Paraplast® (Leica Microsystems Inc., Heidelberg, Germany). The embedded material was sectioned at 8–12 μm on a Leica RM2145 rotary microtome (Leica Microsystems, Wetzlar, Germany), stained with astra blue and safranin (Gerlach, 1984) and mounted on slides with Permount resin (Fisher Scientific, Pittsburgh, US). Light microscope micrographs were taken using a Leica DFC 320 camera coupled to a Leica DMLB microscope, using a IM50 (Leica Image Manager V.5.0) digital imaging system. The diagrams illustrating the spikelet architecture of each species were made using the program Corel Draw Graphics Suite X7 (Corel Corporation, Ottawa, Canada).

### 2.3. Terminology

The description of floral structures in Cyperoideae often involves conflicting terminology (Bruhl, 1995; Goetghebeur, 1998; Vrijdaghs et al., 2009). To maintain clarity and consistency in the present study, we adopted the following terms and definitions:

*Bract:* a leaf-like structure subtending a partial inflorescence; in Cyperaceae it is typically found subtending a spikelet, or in some cases, a compound spike (See definitions below).

*Glume*: a scale-like structure that belongs to the spikelet rachilla, which may subtend a flower (floral glume) or remain empty (sterile glume). In Cyperaceae, the lowermost two or three glumes in a spikelet are commonly empty.

*Perianth part*: Structures derived from the outermost whorls of the flower, also referred as bristles or tepals, due to the absence of clear differentiation between petals and sepals.

*Prophyll*: The first glume of the spikelet rachilla.

*Spikelet:* The ultimate unit of the inflorescence, composed of a rachilla (spikelet axis) bearing several glumes, which may or may not subtend a flower.

*Spikelet-subtending bract*: A bract from which an entire spikelet arises in its axil.

*Spike-subtending bract*: A bract from which a partial inflorescence arises in its axil, associated with a higher order branch of the inflorescence. In Cyperaceae, it may subtend an axis of a compound spike, which bears several spikelets, as commonly observed in the pistillate inflorescences of Cariceae.

## 3. Results

### 3.1. *Rhynchospora sparsiflora*

Lateral spikelets in this species are composed of an indeterminate rachilla in the axil of a subtending bract, where the most proximal glume of the axis is a sterile prophyll followed by five to nine sterile glumes and further five to six distal glumes with flowers arising in their axils (Fig. 1a, b). The flowers are bisexual and possess a perianth consisting of two whorls of three bristles each, one whorl of three stamens and a dimerous dorsiventrally flattened pistil (Fig 1c). The glumes emerge in a spiral sequence on the rachilla (Fig. 2a). The flower primordium arises in the axil of a glume and has an elliptical shape with flattened adaxial and lateral sides and rounded abaxial side, acquiring a triangular-like shape (Fig. 2a– coloured).

Two latero-adaxial perianth primordia appear followed by the third one in abaxial position on the early developing flower that keeps a triangular shape (Fig. 2b– arrows). The abaxial one remains undeveloped during the appearance of subsequent organs (Fig. 2c, d, F– arrow). The outer perianth is followed by the emergence of a larger adaxial inner perianth primordium (Fig. 2b– arrowhead), followed by two less developed abaxial ones (Fig. 2c–e– arrowhead). Two adaxial stamen primordia appear slightly before the abaxial stamen and after the emergence of the outer perianth whorl (Fig. 2b–d). The development of the inner perianth whorl is delayed compared to the stamens (Fig. 2e, F), and the perianth parts are visible as small floral appendages. The abaxial perianth parts and the abaxial stamen also have a delayed development as compared to the adaxial ones (Fig. 2 g). Each stamen differentiates into a basifixed anther and a filament (Fig. 2h). The abaxial outer perianth part is underdeveloped and visible as a small appendage at maturity (Fig. 2i– asterisk). Following the initiation of perianth and stamens, the floral apex differentiates into an elliptical ovary wall

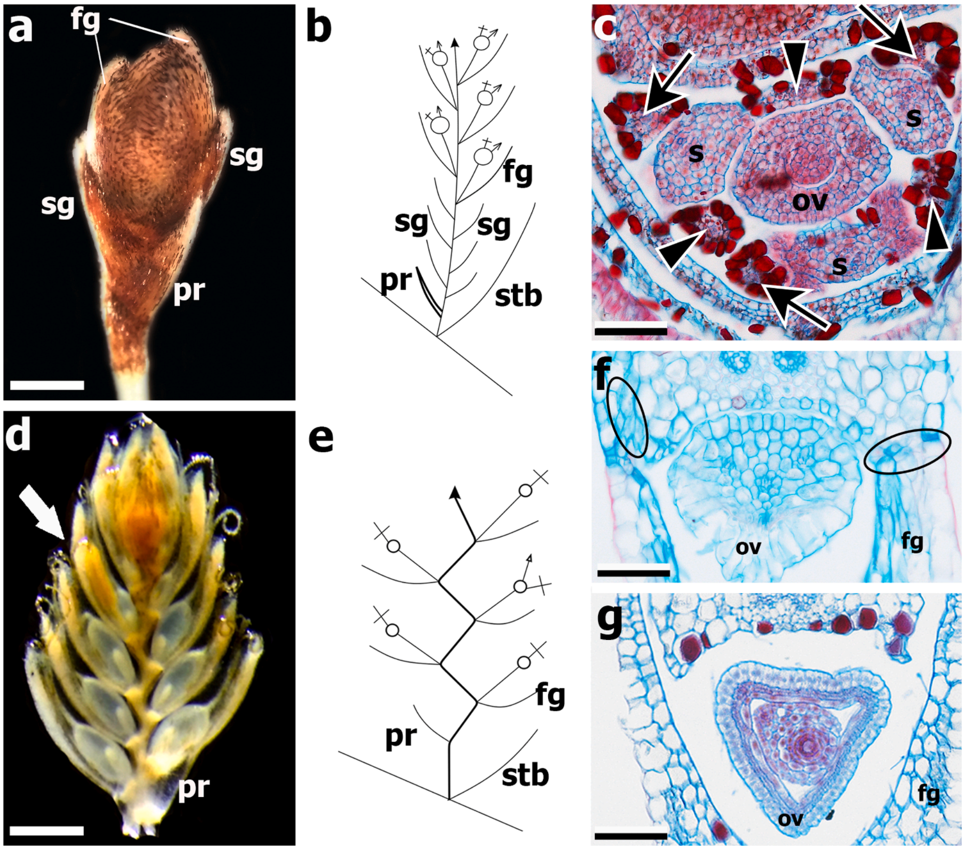

**Fig. 1.** Structure of spikelets and cross-section of flowers of cyperoid species. (a-c) *Rhynchospora sparsiflora*. (a) Lateral view of spikelet with glumes showing the presence of a prophyll and glumes. (b) Lateral presentation of a spikelet showing the position of subtending bract, prophyll and glume. (c) Cross-section in the pedicel level of bisexual flower with outer (arrow) and inner (arrowhead) perianth parts, the abaxial outer perianth part displaced towards the abaxial inner one, three stamens and a gynoecium. (d-g) *Cyperus surinamensis*. (d) Lateral view of spikelet with glumes showing the presence of a prophyll, the arrow points to a single bisexual flower among the pistillate flowers. (e) Lateral presentation of a spikelet showing the subtending bract, the prophyll and fertile glumes. (f) Cross-section in the ovary level of pistillate flower; note the region of fusion of glume lobes with the rachilla (circle). (g) Pistillate flower subtended by a glume. fg, fertile glume; ov, ovary; pr, prophyll; s, stamen; sg, sterile glume; stb, spikelet-subtending bract. Scale bars: 1 mm (a, d); 100 μm (c, f, g).

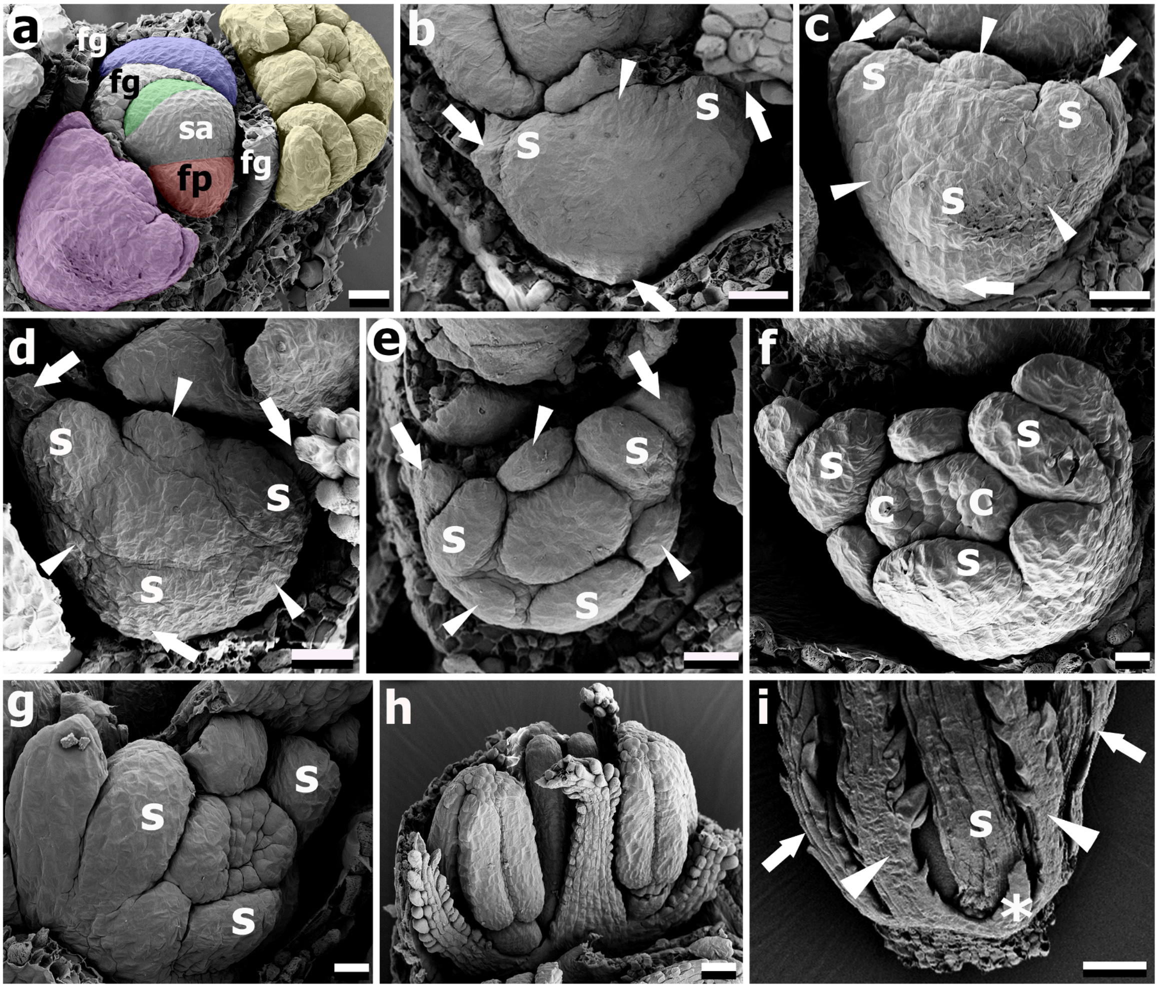

**Fig. 2.** Scanning electron micrographs of the bisexual flower of *Rhynchospora sparsiflora* at different developmental stages. (a) Spikelet axis with spirodistichous fertile glumes, each subtending a floral primordium (different colours). (b) Initiation of the outer perianth parts (arrows), the adaxial inner perianth part (arrowhead) and the adaxial stamen primordia. (c-d) Initiation of the abaxial inner perianth parts (arrowheads) and simultaneous inception of the abaxial stamen primordium. In c) the arrowheads indicate both adaxial and abaxial inner perianth parts. The outer perianth parts are formed (arrows); note that the abaxial outer perianth part is delayed relative to the adaxial ones. (e) Stamen primordia surrounding a gynoecium. (f-g) Development of the ovary wall primordium surrounding the central ovule. (h) Mature flower without glume viewing from spikelet axis showing stamens with basifixed anthers and papillose structures on the perianth parts. (i) Mature flower showing the outer (arrows) and inner (arrowheads) perianth parts and a weakly developed abaxial outer perianth part (asterisk). c, carpel lobe; fg, fertile glume; fp, flower primordium; s, stamen primordium; sa, spikelet axis. Scale bars: 20 μm (a); 10 μm (b-h); 100 μm (i).

primordium surrounding a central depression from which a central ovule develops, and two stigmas appear as two lateral projections (Fig. 2e–g). The gynoecium assumes a dorsiventrally flattened shape during development. Later in development, the perianth parts develop into papillose bristles (Fig. 2h, i).

### 3.2. *Cyperus surinamensis*

A hyaline prophyll occurs at the base of the spikelet, which is smaller and thinner than the distal glumes (Fig. 1d, e). In the spikelet, most of the flowers are solely pistillate, composed of one pistil (Fig. 1f, g). Bisexual flowers, composed of one stamen and one pistil, occur randomly in the spikelet (Fig. 1d- arrow). The glumes are distributed in a distichous arrangement on the rachilla (Fig. 3a). The flower primordium arises in the axil of a glume in which the lateral sides expand at the base and not only envelop but also fuse to the rachilla (Fig. 1f– asterisks; 3a, b – arrow). During development, the glumes elongate and partially envelop the alternate subsequent glumes (Fig. 3c– arrow). In the pistillate flower, the floral development starts with the appearance of an elliptical flower primordium, flattened adaxially and rounded laterally and abaxially (Fig. 3c– coloured). In the bisexual flower, a lateral stamen becomes visible during gynoecium formation (Fig. 3d). The gynoecium primordium differentiates into a circular ovary wall surrounding a central depression from which a central ovule develops (Fig. 3e). On this ring the stigmas appear as three projections (Fig. 3d). The three stigmas are lifted upwards by the growth of the ovary wall, progressively enclosing the central ovule, with the abaxial stigma slightly less developed (Fig. 3f– arrowhead). Papillose protuberances appear along the developed stigmas (Fig. 3 g).

### 3.3. *Carex brasiliensis*

The inflorescence is composed of two to three pistillate compound spikes and a more distal staminate spikelet (Fig. 4a). The staminate spikelet is inserted on the axil of a spikelet-subtending bract, and each staminate flower is subtended by a floral glume (Fig. 4b). The pistillate inflorescence is a lateral compound spike; the spike axis arises in the axil of a spike-subtending bract. The spike axis bears several spikelet-subtending bracts, each one subtending a single-flowered pistillate spikelet (Fig. 4c, dotted circle). On the spikelet axis, the first glume is a modified tubular prophyll that subtends a single pistillate flower in an undeveloped rachilla. In both staminate and pistillate inflorescences, the

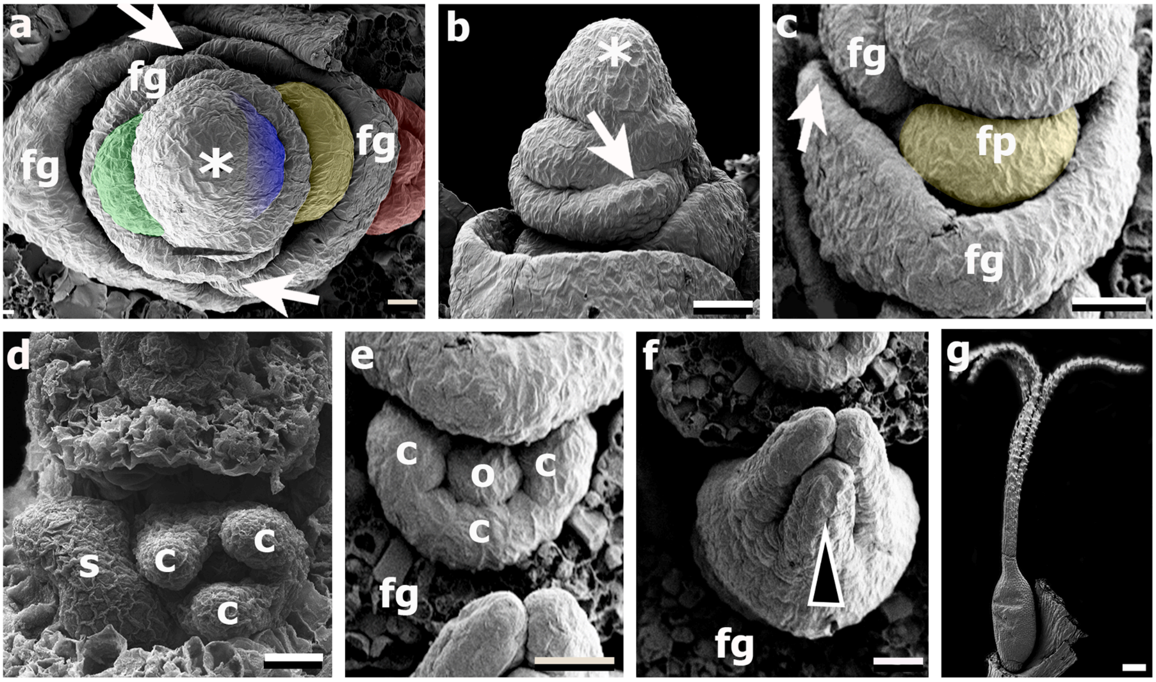

**Fig. 3.** Scanning electron micrographs of the bisexual and pistillate flower of *Cyperus surinamensis* at different developmental stages. (a) Spikelet axis (asterisk) with distichously arranged fertile glumes enveloping the flower primordia (different colours). The glumes exhibit expanded margins that envelop one another (arrow). (b) Lateral view of the spikelet, showing the base of the glume fused to the rachilla and expanding towards the lower flower primordium (arrow). (c) Flower primordium subtended by a fertile glume showing the expanded margins of the opposite new glume formed in contact with the laterals of the flower primordium (arrow). (d) Bisexual flower showing a single lateral stamen and the trimerous pistil. (e) Carpel lobes developing above the ovary wall surrounding the central ovule. (f) Development of the ovary wall and stigmas. Note the less developed abaxial stigmatic lobe (arrowhead) towards the glume. (g) Mature flower with glume removed, showing papillose structures on the stigmas. c, carpel lobe; fg, fertile glume; fp, flower primordium; o, ovule; s, stamen. Scale bars: 10 μm (a, c-f); 20 μm (b); 100 μm (g).

phyllomes are arranged spirally in the main inflorescence axis (Fig. 4d, e).

The staminate flowers exhibit a variation on the number of stamens ranging from four (Fig. 4d– circle, f), five (Fig. 4 g) to six stamens (Fig. 4h). In flowers with four stamens, the stamens are entirely free; in flowers with five to six stamens, two or three stamens may be fused by their filaments (Fig. 4 g, h– arrow). Flowers with four and six stamens are the most common conditions. Regardless of the number of stamens, in all examined flowers the vascularization initially shows the divergence of the glume vascular trace, leaving a central vascular plexus at the flower receptacle (Fig. 5a, b), from which the staminal vascular traces subsequently arise (Fig. 5c, d). In flowers with four stamens (Fig. 5e–g), the anatomy shows the presence of four distinct vascular traces, each independently supplying one stamen. The two lateral vascular traces diverge first, followed by the abaxial and adaxial that remain in the center (Fig. 5e), each observed in separated filaments (Fig. 5f) that will supply an anther (Fig. 5 g). In flowers with a higher number of stamens (i.e., five stamens), the divergence of the vascular traces follows the same initial pattern, diverging first to the lateral stamens, leaving a central vascular plexus with one abaxial and two adaxial vascular traces (Fig. 5h– arrowhead). At a higher level four filaments are observed; the adaxial filament contains two vascular bundles (Fig. 5i– arrowhead), which indicates that it represents two stamens with their filaments fused. This filament with two vascular traces later divides into two separated anthers (Fig. 5j– arrowhead, k). Along development, the staminate spikelet exhibits a rachilla with flowers developing in the axil of glumes, which exhibit a narrowing apex (Fig. 6a– arrows). The flower primordium is dome-shaped, rounded both abaxially and adaxially, from which two lateral stamens appear first (Fig. 6b), followed by an abaxial and an adaxial stamen primordium (Fig. 6c). All staminate flowers investigated develop four androecial primordia (Fig. 6b, c), which in some cases give rise to four individual stamens of conventional structure. In other mature flowers, five or six anthers are formed—three borne on individual filaments and two or three others attached to a common stalk.

The pistillate spikelets exhibit a dome-shaped spikelet primordium, rounded abaxially and adaxially, arising in the axil of a spikelet-subtending bract (Fig. 6d– arrow). A prophyll primordium appears as a discontinuous ring expanding around the dome-shaped spikelet primordium (Fig. 6e– coloured). The two margins of the prophyll connect on the adaxial side (Fig. 6f) and expand as a tube (Fig. 6 g, h, j). From the peripheral region of the floral primordium apex an annular ovary wall differentiates and the three stigmas appear as two latero-adaxial and one abaxial projections (Fig. 6f). These projections surround a central ovule that appears to originate from a distinct central domain within the primordium (Fig. 6f) and develops before being completely enclosed by the ovary wall (Fig. 6 g). The prophyll develops as a tubular structure, enclosing the entire gynoecium, except for the tips of stigmas (Fig. 6h). When removing the prophyll, it is possible to observe an undeveloped rachilla (Fig. 6i). Later in development, the style and stigmas emerge beyond the tubular prophyll (Fig. 6j).

## 4. Discussion

Anatomical and developmental evidence supports the observed floral morphological variations in all studied species. In *Rhynchospora sparsiflora*, we identified a distinct ontogenetic sequence for perianth formation, revealing a developmental pattern that deviates from the typical model described for Cyperoideae (Vrijdaghs et al., 2009). For *Cyperus surinamensis*, the presence of both bisexual and unisexual flowers within the same spikelet was documented, the latter confirmed as strictly unisexual rather than resulting from the late detachment of stamens, contrasting with previous taxonomic descriptions (e.g., Araujo and Longhi-Wagner, 1996; Chen et al., 2009; Ribeiro et al., 2015).

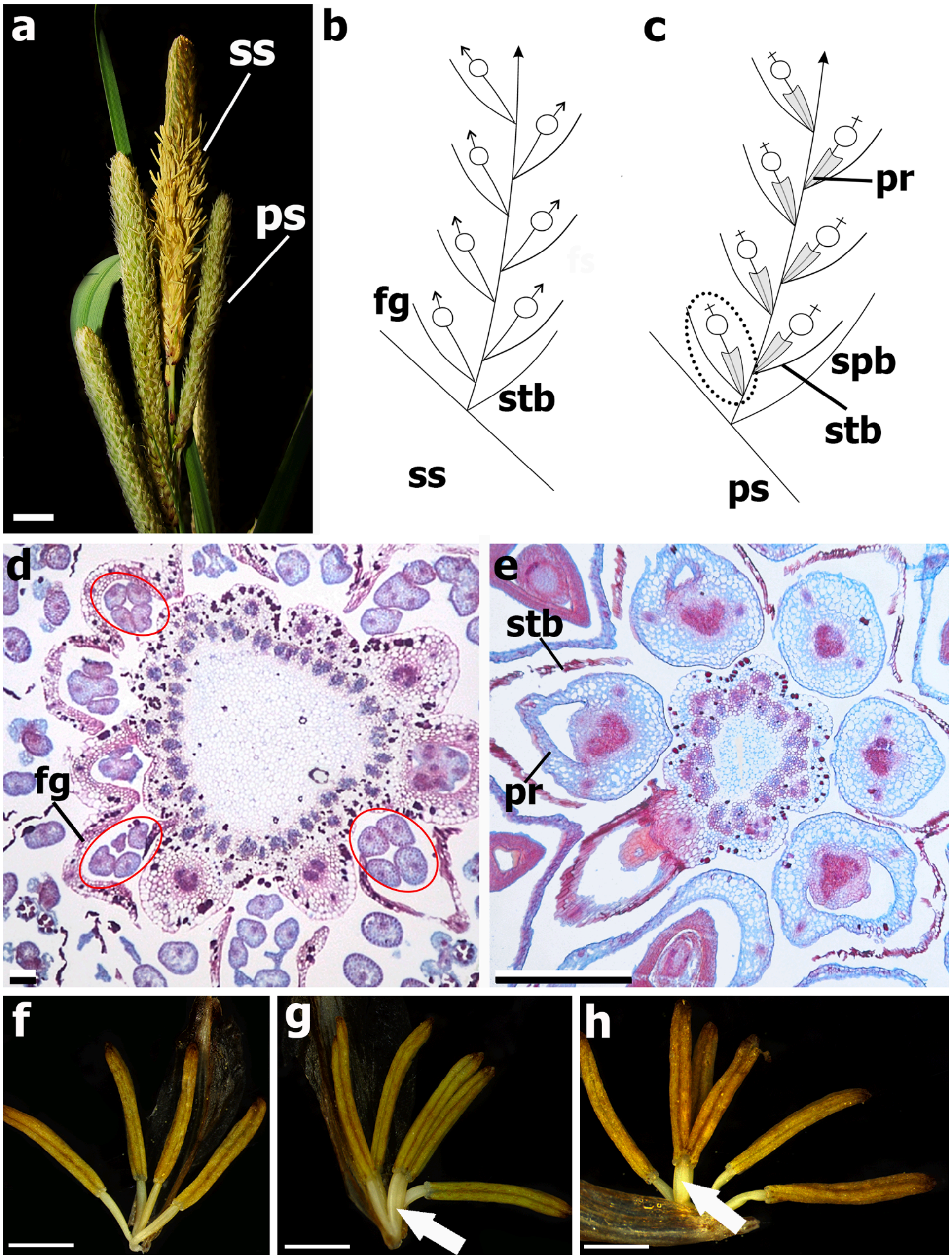

**Fig. 4.** Morphology, diagram and cross-section of the inflorescence and mature flowers of *Carex brasiliensis*. (a) Lateral view of inflorescence showing the staminate spikelet in the center surrounded by pistillate compound spike composed of several spikelets. (b) Staminate spikelet showing the fertile glumes subtending the flowers. (c) Pistillate compound spike subtended entirely by the spike-subtending bract, constituted by several spikelets (dotted circle). Each spikelet is enveloped by a spikelet-subtending bract and the modified prophyll subtends each flower. (d) Staminate spikelet with flowers spirally arranged. Note the presence of a single vascular bundle per stamen in flowers with four stamens (red circles). (e) Pistillate compound spike with spikelets spirally arranged. (f) Mature staminate flower with four stamens. (g-h) Mature staminate flower with (g) five and (h) six stamens; note the fused filament (arrow) with two (g) and three anthers (h). fg, floral glume; ps, pistillate compound spike; ss, staminate spikelet; pr, prophyll; spb, spike-subtending bract; stb, spikelet-subtending bract. Scale bars: 1 mm (a); 200 µm (d, e).

Additionally, the variation in stamen number in the staminate flowers of *Carex brasiliensis* was particularly notable, with evidence suggesting that this variation arises from the congenital fusion of primordia, as corroborated by the analysis of staminal vasculature. These findings underscore the importance of anatomical and developmental studies in elucidating floral variation, as they provide critical insights into the processes shaping each floral whorl. The detailed discussion of these variations is presented below.

### *4.1. Perianth*

The presence, absence and variation in the number of perianth parts are generally stable character states for Cyperoideae tribes. For instance, the absence of a perianth is a consistent feature in the tribes Cypereae (Vrijdaghs et al., 2009, 2011; Bauters et al., 2014; Reutemann et al., 2014), Cariceae (Smith, 1966; Smith and Faulkner, 1976; Gehrke et al., 2012) and Abildgaardieae (Reutemann et al., 2015). Conversely, in Eleocharideae, the presence of a perianth is generally observed (Vrijdaghs et al., 2009; San Martin, 2014). However, within tribe Rhynchosporeae, the presence or absence of a perianth is notably labile, deviating from the stability seen in other tribes (Vrijdaghs et al., 2009; Lucero et al., 2014; Monteiro et al., 2017). This lability extends to the number of perianth parts as well. This is the case of *Rhynchospora sparsiflora,* previously placed in *Pleurostachys* and described as

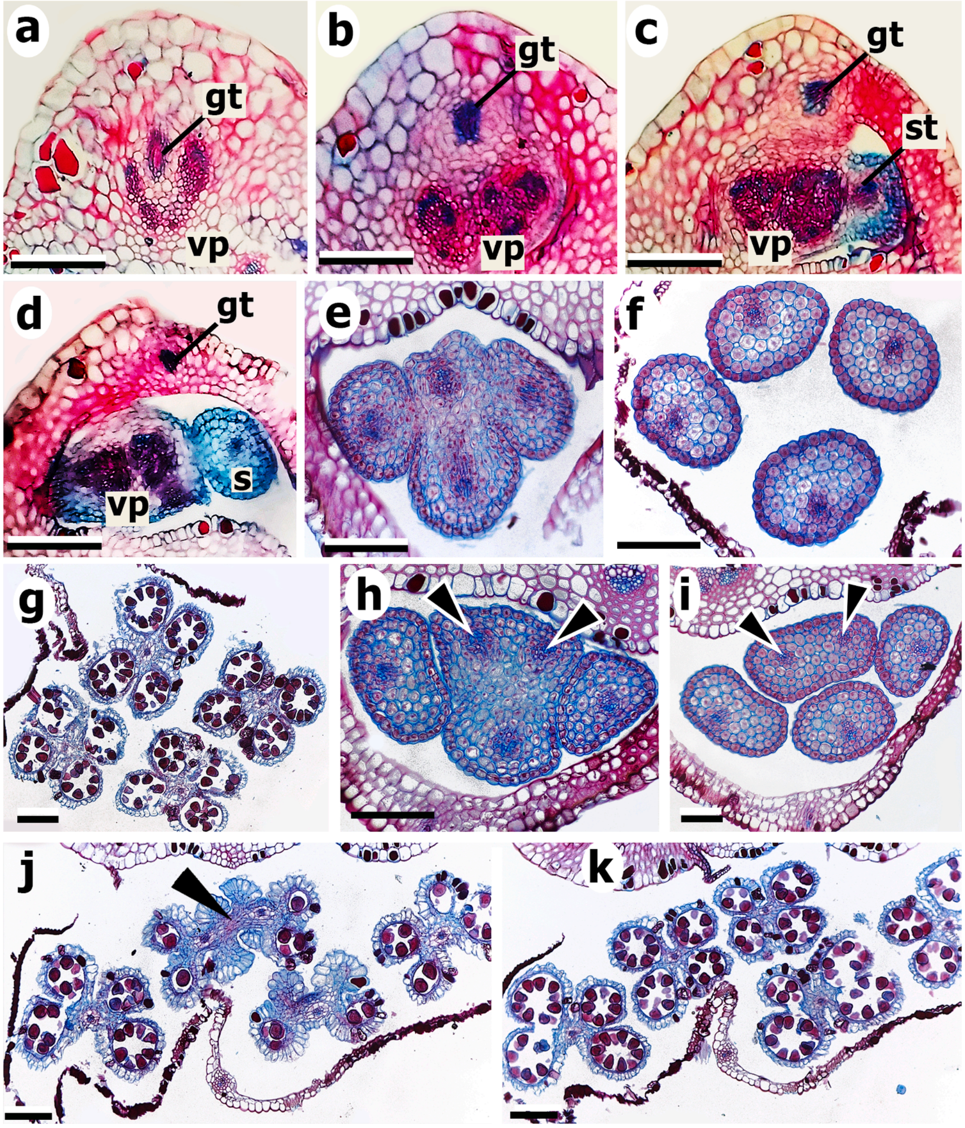

**Fig. 5.** Cross-sections of mature staminate flowers of *Carex brasiliensis*. (a–d) Cross-sections at the receptacle level (a–c) showing the divergence of the glume vascular trace and the remaining central vascular plexus, from which the staminal vascular traces (c, d) arise. (e) Staminate flower with four stamens, showing the floral receptacle initially splitting toward the lateral stamens, followed by the abaxial and adaxial vascular traces that remain in the center; (f) these traces will then split into four filaments. (g) Four anthers with a single vascular bundle each. (h) Cross section of a mature staminate flower with five stamens showing the lateral stamens separating first, leaving an abaxial and two adaxial vascular traces (arrowhead) in the center, (i) which will split into four filaments, one of them with two vascular bundles (arrowhead) indication the fusion of two filaments. (j) The filaments remain attached up to the level of the anthers, (k) before completely separating in five stamens. Scale bars: 1 mm (a-c); 200 μm (d, i-k); 100 μm (e-h).

exhibiting five perianth parts (Thomas and Alves, 2008; Thomas et al., 2013; Alves and Thomas, 2015). However, in the present study we observed the development of six perianth bristles, although the outer abaxial bristle is weakly developed. The absence or underdevelopment of the outer abaxial perianth part may result from the physical pressure exerted by the subtending glume on the floral meristem, as previously suggested by other authors (Lucero et al., 2014; Silva et al., 2023). This finding underscores the importance of developmental studies in refining taxonomic descriptions, particularly in families like Cyperaceae, where reduced and variable structures are common. Silva et al. (2023), in their study on floral anatomy and vasculature in *Fuirena robusta* Kunth, *Cyperus sesquiflorus* (Torr.) Mattf. & Kük., *Rhynchospora panicoides* Nees ex L.B. Sm. and *Schoenoplectus californicus* (C.A. Mey.) Soják, show that the losses of perianth parts and stamens do not always occur in the same way in the different species, providing evidence that the reduction processes observed in Cyperoideae are not homologous, having probably occurred independently during the evolution of the subfamily.

Whilst the presence and number of perianth parts can exhibit significant lability in Cyperoideae flowers, the sequence of perianth development is generally considered a stable pattern (Vrijdaghs et al., 2009). Typically, perianth formation begins after the stamens have formed and occurs simultaneously with the appearance of the ovary primordium (Vrijdaghs et al., 2009, 2010, 2011). However, our results challenge this generalization in *Rhynchospora*, since in *R. sparsiflora* the outer perianth parts begin to develop slightly before the stamens and prior to any indication of the ovary primordium. A similar developmental pattern has been reported for the flowers of *Oreobolus* R. Br. (Mora-Osejo, 1967), suggesting an ontogenetic sequence for perianth development distinct from the typical pattern described for Cyperoideae (Vrijdaghs et al., 2009, 2010). These findings highlight potential variation in the developmental trajectories of the perianth within Cyperoideae.

Notably, the tribes Rhynchosporeae and Oriobolineae (Schoeneae) are not phylogenetically related (Larridon et al., 2021), suggesting that

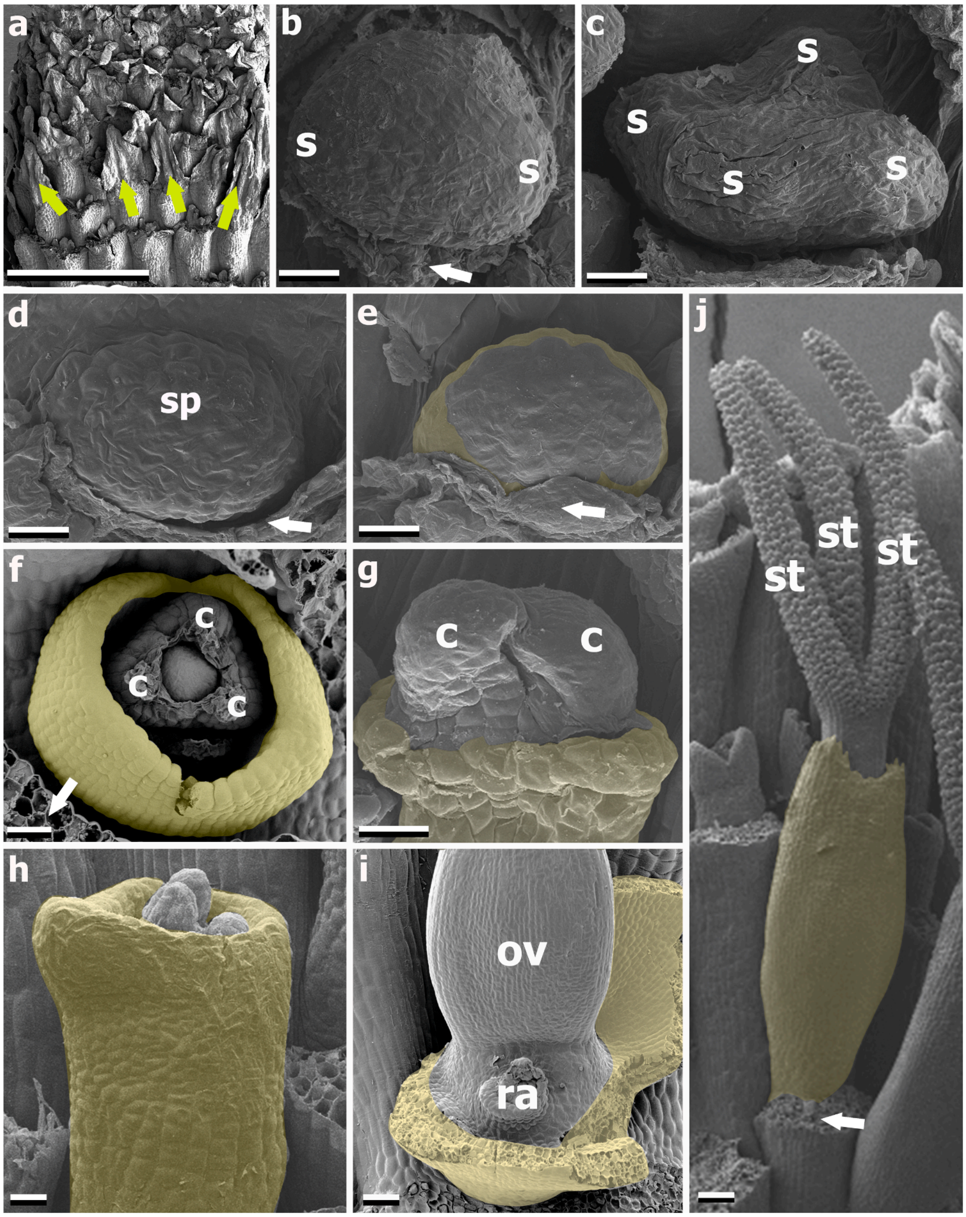

**Fig. 6.** Scanning electron micrographs of the staminate flower and pistillate spikelet of *Carex brasiliensis* at different developmental stages. (a-c) Staminate flower. (a) Spikelet axis with glumes subtending the flowers; note the narrow tips of the glumes (yellow arrow). (b) Stamens primordia initiated and subtended by a glume (arrow). (c) Flower primordium with four individual stamen primordia. (d-j) Pistillate spikelet. (d) Spikelet primordium in the axil of a spikelet-subtending bract (arrow). (e) Initiation of the prophyll or utricle (yellow) as a ring around the primordium, subtended by a spikelet-subtending bract (arrow). (f) Ovary wall surrounding the central ovule; the prophyll is highlighted in yellow. (g-h) Development of the carpels and the prophyll (yellow). (i) Prophyll removed showing an undeveloped rachilla and the ovary. (j) Mature pistillate spikelet with enclosing prophyll (yellow) and the spikelet-subtended bract removed (arrow). c, carpel; ov, ovary wall; s, stamen primordium; sp, spikelet primordium; st, stigmatic lobe; ra, undeveloped rachilla. Scale bars: 1 mm (a); 20 µm (b-i); 200 µm (j).

this developmental pattern evolved independently in each lineage. Further investigation into other Schoeneae genera could reveal whether a stable perianth developmental pattern is a consistent feature across the tribe. The differences in developmental patterns of reproductive whorls have previously been reported as defining characteristics of tribes within Mapanioideae (Monteiro et al., 2020), underscoring the importance of ontogenetic studies in clarifying evolutionary relationships within Cyperaceae.

### 4.2. Androecium

The number of stamens in Cyperoideae flowers typically varies from zero to six per flower (Vrijdaghs et al., 2009, 2010, 2011; Silva et al. 2023). This variability is further corroborated by our observations among the studied species. *Rhynchospora sparsiflora* consistently maintains a trimerous androecium, while *Cyperus surinamensis* occasionally exhibits bisexual flowers with a single stamen. In contrast, *Carex brasiliensis* shows extreme variation, with the number of stamens ranging from four to six. This instability on the number of stamens within species is remarkable and may hamper the taxonomic description of some species. This is the case of *Cyperus surinamensis*, as the species has been described in taxonomic studies as having bisexual flowers with one stamen (Araujo and Longhi-Wagner, 1996; Chen et al., 2009; Ribeiro et al., 2015). However, most of the *C. surinamensis* flowers we analysed were unisexual, consisting of a single pistil with no evidence of stamen primordia, confirming that these flowers are strictly pistillate. This pattern is consistent with previous reports for *Cyperus eragrostis* Lam., where no correlation was found between flower sex and its position within the spikelet (Barnard, 1957). Additionally, in *Carex brasiliensis*, the presence of staminate flowers with four to six stamens deviates from the typical *Carex* floral structure, which usually consists of three stamens (Smith, 1966; Smith and Faulkner, 1976; Gehrke et al., 2012). This variation appears to represent a derived condition, as the ancestral state of Cyperaceae flowers is characterized by a single whorl of three stamens, positioned opposite the outer perianth whorl (Vrijdaghs et al., 2009; Remizowa et al., 2010).

The reduction of floral parts is a common trend among Cyperoideae flowers. Therefore, the increased number of stamens in the staminate flowers of *Carex brasiliensis* is a notable exception. Regarding the development of these flowers, it is possible to observe two or more anthers sharing the same filament, however, we did not observe separate primordia fusing during later developmental stages. Similarly, during development, there was no evidence of a single primordium splitting into two equal daughter primordia. Consequently, we propose that this increase in the number of stamens does not result from the equal division of a primordium, a process known as dédoublement (Ronse De Craene and Smets, 1993). Anatomical analyses provide further insights into this phenomenon. Specifically, the vascularization of the stamens reveals two distinct patterns: 1) In flowers with four stamens, each stamen is supplied by a single vascular bundle; 2) In flowers with more than four stamens, two or three vascular bundles converge within a single filament and supply separate anthers. The latter pattern suggests that two or more stamen primordia are congenitally fused, as stamens are typically vascularized by a single vascular bundle (Puri, 1951). This pattern of vasculature has also been reported for staminate flowers of other *Carex* species, including *Carex flacca* Schreb., *Carex nigra* All., and *Carex panicea* L. (Smith, 1966; Smith and Faulkner, 1976).

Although the anatomical evidence clarifies the congenital fused nature of stamens in the staminate flowers of *Carex brasiliensis*, the underlying causes of the observed random and extreme variation remain unclear. One hypothesis is that the higher number of stamens per flower may reflect developmental anomalies or teratological events.

However, considering the high frequency with which five or six stamens are observed across multiple inflorescences and individuals from distinct populations, an alternative hypothesis is that the staminate flower of *Carex brasiliensis* represents a highly reduced and condensed spikelet, composed of several staminate flowers. This interpretation is supported by the vascular organization, since after the divergence of the glume trace, a central vascular plexus remains in the receptacle level. This pattern resembles the vascular architecture typically found in racemose inflorescences of monocots with spiral phyllotaxis (Remizowa et al., 2013) and contrasts with the more conserved vascular pattern of Cyperoideae flowers, in which three main receptacular bundles are clearly distinguishable following glume trace divergence (Blaser, 1941a, 1941b; Reynders et al., 2012; Monteiro et al., 2017). Furthermore, we observed that the stamen traces diverge at different levels. To achieve a more objective conclusion on this interpretation, additional evidence is required, particularly developmental studies focusing on stamen/anther orientation during early ontogenetic stages, as well as comparative analyses across a broader range of *Carex* species.

### *4.3. Gynoecium*

In Cyperoideae flowers, the gynoecium develops from a ring primordium surrounding a central meristematic zone (corresponding to the floral apex), resulting from the congenital fusion of carpels (Reynders et al., 2012). The annular ovary wall primordium has been interpreted as disrupting the strict positional pattern of stigma lobes, allowing shifts in the number and position of stigmas and contributing to the variation in pistil types observed in Cyperoideae, such as trimerous and dorsiventrally or laterally flattened dimerous (Reynders et al., 2012). Considering that the position of styles and stigmas is strongly fixed and predictable in the floral meristem (Ronse De Craene et al., 2002; Ronse De Craene, 2022), we propose that the emergence of new gynoecium morphs is more likely influenced by mechanical constraints exerted by the glume, which is in direct contact with the abaxial side of the primordium. In *Cyperus surinamensis*, we observed that the gynoecium develops as a ring from which three lobes emerge, with the abaxial lobe being slightly less developed than the adaxial ones. This asymmetry is likely caused by the pressure exerted on the gynoecium by the glume. A similar phenomenon is observed in *Rhynchospora sparsiflora*, where spatial constraints appear to restrict floral development on the abaxial side, which is in contact with the glume. Supporting evidence for this includes: 1) the undeveloped abaxial perianth part; 2) the delayed development of the abaxial stamen; 3) the presence of only two latero-adaxial stigmas. These observations reinforce the hypothesis that one of the factors potentially modulating the development of the dimerous dorsiventrally flattened pistil in *Rhynchospora sparsiflora* is the mechanical constraint imposed by the glume, as also demonstrated in the dimerous laterally flattened pistil of *Cyperus sesquiflorus* (Silva et al. 2023). According to Silva et al. (2023), the structure of the spikelet and consequent interference of the glumes in the development of the floral primordium seems to be one of the main factors that determine floral morphology in Cyperoideae.

## 5. Conclusions

The present study provides valuable insights into the anatomical and developmental variation of floral structures within Cyperoideae, particularly highlighting specific deviations from established patterns. The observed ontogenetic sequence of perianth formation in *Rhynchospora sparsiflora* and the presence of both bisexual and strictly unisexual flowers in *Cyperus surinamensis* challenge previous taxonomic descriptions, underscoring the need for refined morphological and developmental studies in this group. The variation in stamen number in *Carex brasiliensis* also provides new insights into the mechanisms driving floral diversification within Cyperaceae. The alternative interpretation of *C. brasiliensis* staminate flowers as potential reduced staminate inflorescences, based on the increase in stamen number and the observed vascular pattern, needs further investigation. The development of all studied species showed that mechanical constraints, applied by the glume, potentially restrict the floral development on the abaxial side, which may also modulate the dimerous and dorsiventrally flattened pistil in Cyperoideae flowers. These findings emphasize the importance of integrating anatomical and developmental data to better understand the evolutionary processes shaping floral diversity in species-rich genera of Cyperaceae.

## CRediT authorship contribution statement

**Mariana Maciel Monteiro:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Aline Oriani:** Writing – review & editing, Visualization, Methodology, Conceptualization. **Louis Ronse De Craene:** Writing – review & editing, Methodology, Conceptualization. **Diego Demarco:** Writing – review & editing, Supervision, Methodology, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Data availability

Data will be made available on request.

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