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Unisexual flowers as a robust synapomorphy in Cariceae (Cyperaceae)? Evidence for bisexual flowers in *Schoenoxiphium*

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Abstract

Cariceae, the largest tribe within Cyperaceae, comprises about 2000 species in five genera. Cariceae is usually considered to be distinct from other Cyperaceae by the presence of exclusively unisexual flowers and by the arrangement of the pistillate flowers in single-flowered spikelets that are enclosed by the flask-like spikelet prophyll (utricle or perigynium). The nature of several morphological features of the Cariceae inflorescence remains controversial. The staminate reproductive units, as well as earlier reported bisexual reproductive units in *Schoenoxiphium* have been considered to be reduced partial inflorescences, or flowers. Aims of this study are to test both interpretations, based on a floral ontogenetic investigation. Moreover, for the first time, detailed SEM micrographs are presented of the inflorescence and floral development and of bisexual flowers in *Schoenoxiphium*. We propose that 'inhibition of bisexuality' is a more robust synapomorphy in Cariceae than 'presence of only unisexual flowers'.

1. Introduction

1.1. The Cyperaceae tribe Cariceae with emphasis on Schoenoxiphium

The tribe Cariceae comprises about 2000 species, making it the largest clade within the Cyperaceae (Goetghebeur, 1998). Molecular phylogenetic analyses have confirmed the monophyly of the Cariceae (Waterway and Starr, 2007; Muasya et al., 2009; Fig. 1) but the infratribal relationships are complex (Table 1) and not yet entirely resolved (Crins and Ball, 1988; Starr and Ford, 2009; Gehrke et al., 2010). Recent authors recognise five genera in Cariceae: *Carex*, *Cymophyllus*, *Kobresia*, *Schoenoxiphium* and *Uncinia* (Fig. 1). The latter four genera have been shown to be nested within *Carex* subgenus *Psyllophora* in molecular phylogenetic analyses (Yen and Olmstead, 2000; Starr et al., 2004; Waterway and Starr, 2007; Starr and Ford, 2009; Gehrke et al., 2010). In this study, we focus on the genus *Schoenoxiphium*, which has about 20 species with its center of diversity in the eastern part of Southern Africa, with a few species extending their distribution to East Africa, Madagascar and the Arabian Peninsula (Fig. 2). Molecular phylogenetic analyses show that the genus is monophyletic and is nested within *Carex* subgenus *Psyllophora* (Gehrke et al., 2010; Fig. 1). The genus is neither morphologically

nor taxonomically well studied (Levyns, 1945; Kukkonen, 1983; Timonen, 1989; Gordon-Gray, 1995) and a critical taxonomic revision is required. There are limited studies on reproductive structures to date: Levyns (1945) described the basic pattern of inflorescence branching in three species of *Schoenoxiphium*, and Timonen (1989) compared *S. lanceum* (Thunb.) Kük. to *Kobresia laxa* Nees. Kükenthal (1909) defined *Schoenoxiphium* as being characterised by a partially open prophyll (=utricle/perigynium) and by the presence of lateral androgynous 'spikelets' with proximal pistillate 'flowers' (which are actually spikelets) as well as terminal staminate flowers along an elongate rachilla. His view was amended by Timonen (1989), who added that the spikelets are arranged in a compound inflorescence. *Schoenoxiphium* differs from *Kobresia* by the presence of a flattened rachilla (and rachis) with scabrous or ciliate margins, and usually by large and leaf-like inflorescence bracts. In contrast, in *Kobresia*, the rachilla is ± terete and the inflorescence bracts are small and evaginate (Reznicek, 1990).

1.2. Bract, glume and prophyll

In Cariceae, as in other Cyperaceae, bracts that subtend an axis (for example a spikelet) are referred to as 'bracts', whereas bracts subtending a true flower are referred to as 'glumes'. The morphology of bracts and glumes is often scale-like, but in many cases they can be distinguished. In a spikelet, the first, adaxially positioned glume, termed 'addorsed prophyll' or just 'prophyll', is usually empty (not subtending a flower) with exception of Cariceae and Dulichieae. In these two tribes the spikelet prophyll usually subtends a ± developed female or pistillate flower (e.g. Goetghebeur, 1998; Vrijdaghs et al., 2010; Fig. 3). In Cariceae this structure is referred to as a utricle or perigynium. The prophyll at the base of a fully developed spike of spikelets is in most cases more deeply incised than those in other positions (Fig. 4) and often encloses only a sterile pistillate flower.

1.3. Spikelets and flowers in Cariceae

Cariceae are usually considered to be characterised by exclusively unisexual flowers and by the development of the spikelet prophyll (of the single-flowered female spikelets) into a partially or entirely closed flask-like structure (perigynium or utricle), enveloping both the pistillate flower and the rachilla (Kükenthal, 1909; Reznicek, 1990). In female flowers, perianth and androecium are absent, and remnants are absent even at early ontogenetic stages (Fig. 5b). This caused controversy about the interpretation of flowers or spikelets and the nature of inflorescence units in Cariceae (e.g. Smith and Faulkner, 1976; Reznicek, 1990). Pistillate flowers are reduced to a naked, trimerous or dimerous, dorsiventrally flattened pistil, arranged in single-flowered spikelets enveloped by the utricle and subtended by a glume-like bract (Goetghebeur, 1998; Kükenthal, 1909; Reznicek, 1990; Fig. 6).

Male reproductive units usually consist of a glume-like structure subtending three stamens (Fig. 5), and have been interpreted either as an extremely reduced staminate spikelet or as a reduced flower (Kükenthal, 1909; Smith and Faulkner, 1976; Timonen, 1998). The interpretation of the male reproductive structure as an extremely reduced male spikelet, i.e. three staminate flowers, each reduced to a single stamen positioned along a congested axis subtended by a glume-like bract, led Timonen (1998) to conclude that in Cariceae, staminate, pistillate, and bisexual 'spikelets' are each homologous with a compound partial inflorescence. However, Vrijdaghs et al. (2010) argued that no remnants of spikelet structures or floral parts have been found in any floral ontogenetic study and neither is any transition species known, so that it seems improbable that the staminate reproductive units in Cariceae are reduced spikelets. Consequently, they concur with Goetghebeur (1998) and Egorova (1999), who stated that the staminate structures consist of a reduced staminate flower subtended by a glume.

In Cariceae, the occasional occurrence of bisexual flowers has been reported (Kükenthal, 1909; Börner, 1913; Martens, 1939; Smith and Faulkner, 1976; Kukkonen, 1984). However, Timonen has, to our knowledge, been the only person to have shown evidence in the form of photographic images of the presence of bisexual flowers in *S. lanceum* (Timonen, 1989) and *K. laxa* (Timonen, 1985).

1.4. Inflorescence structure in Cariceae

Female spikelets and staminate flowers in Cariceae are usually arranged in compound inflorescences, comprising ± complex compound spikes, which in turn can be arranged in higher order partial inflorescences sometimes referred to as lateral inflorescence units (Reznicek, 1990). Unfortunately, in Cariceae, the term 'spikelet' has been used by different authors to refer to non homologous structures, thus creating confusion about the exact meaning of 'spike', 'spikelet', and 'flower' (e.g. Kükenthal, 1909). In this study, we follow the concept of a spikelet as the ultimate branching of the inflorescence (e.g. Weberling, 1992; Kukkonen, 1994; Goetghebeur, 1998; Vrijdaghs et al., 2010).

The arrangement of spike(let)s differs among the different (sub-)genera in Cariceae (Kükenthal, 1909; Smith and Faulkner, 1976; Reznicek, 1990). In *Carex*, the female spikelet is usually reduced to a single-flowered spikelet and consequently, its axis (rachilla) remains rudimentary. In some species such as *C. microglochin* Wahlenb. (*Carex* subgenus *Psyllophora*), the rachilla is ± well developed (Table 1). In *Uncinia*, the rachilla carries a distal empty glume that extends into a hook-like structure protruding from the utricle. In *Kobresia* and *Schoenoxiphium*, the rachilla can have an additional distal florescence of staminate flowers (Fig. 3) that can be considered to be a terminal spike of male flowers or a terminal spikelet (Goetghebeur, 1998; Vrijdaghs et al., 2010). In *Schoenoxiphium*, spikes with a proximal female flower and distally female spikelets and male flowers or male florescence can occur additionally (Fig. 4).

1.5. Aims of this study

In this study, nine species of *Schoenoxiphium* were investigated ontogenetically in order to test the following hypotheses: (1) sporadically occurring bisexual reproductive structures are
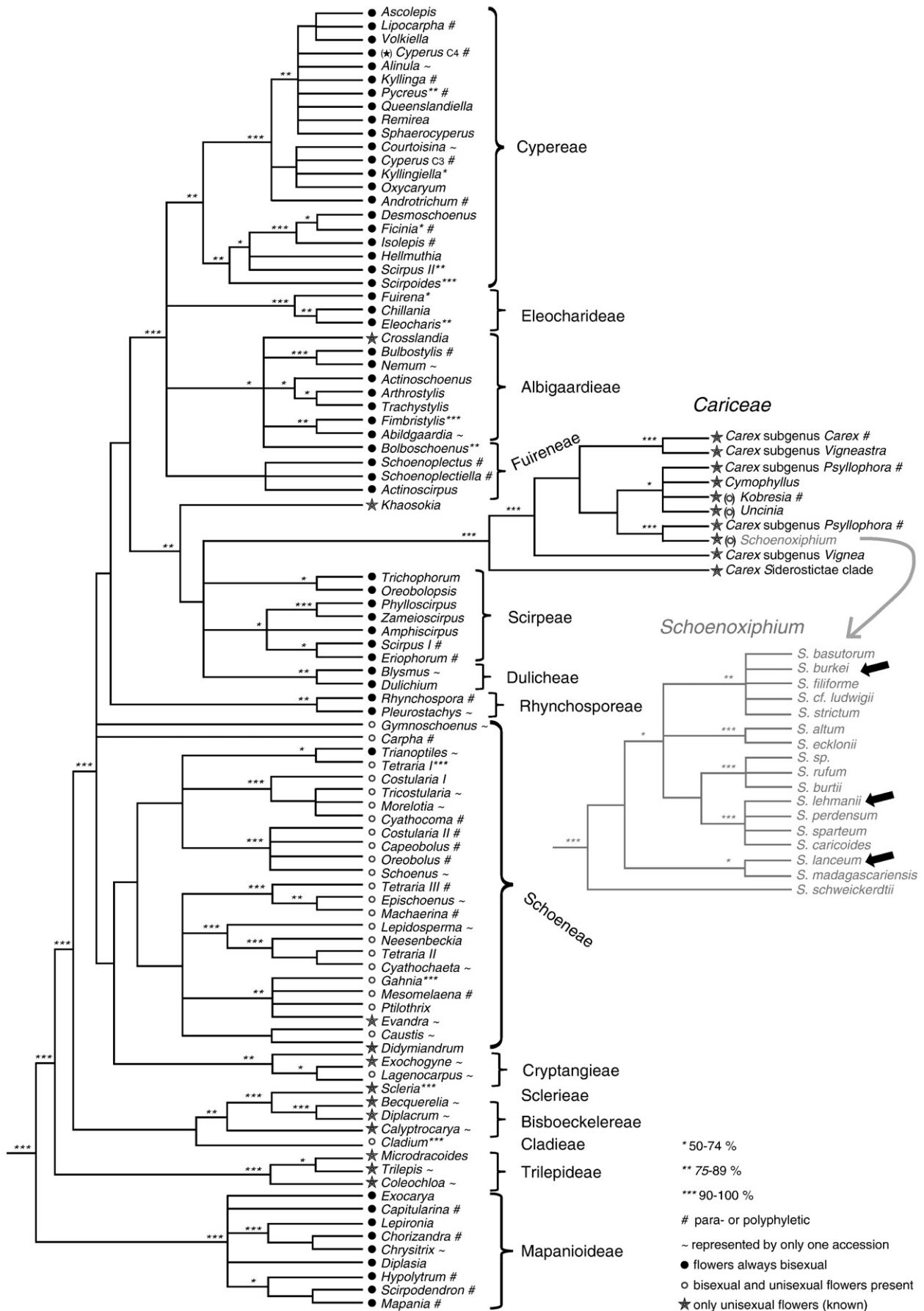
Table 1
Main taxonomic groups in Cariceae and their morphological features modified from Gehrke et al. 2010.

Taxonomic group	No. of species	Main morphological features	Distribution
Carex L. subg. **Carex** (monophyletic)	~1400	Inflorescence usually racemiform, with usually peduncled, unisexual spikes; rachilla extremely reduced, rarely more developed; stigmas (2-)3.	Worldwide (center of diversity in the temperate and cold regions of the northern hemisphere)
Carex subg. **Vigneastra** (Tuck.) Kük. (status unknown)	~100	Inflorescence compound, with androgynous, more or less sessile spikes; rachilla extremely reduced; stigmas 3.	Mainly tropical and subtropical regions, especially tropical Asia
Carex subg. **Vignea** (P. Beauv. ex T. Lestib.) Peterm. (monophyletic)	~400	Inflorescence frequently spiciform, with bisexual, sessile spikes; rachilla extremely reduced; stigmas 2(−3).	Worldwide (mainly in the northern hemisphere)
Subg. **Psyllophora** (Degl.) Peterm (paraphyletic)	~70	Inflorescence unispicate; rachilla reduced to developed; stigmas 2–3.	Mainly in temperate and cold regions
Cymophyllus Mack.	1	Inflorescence unispicate, with androgynous spikes; rachilla absent; stigmas 3.	Southeastern North America
Kobresia Willd. (polyphyletic)	~40	Inflorescence unispicate or spiciform; rachilla present and sometimes well developed; spike of spikelets absent; stigmas usually 3.	Arctic and mountainous areas (mainly Himalayas)
Schoenoxiphium Nees (monophyletic)	~20	Inflorescence unispicate to compound; cladoprophyll and inflorescence prophyll absent; rachilla usually present and well developed; spike of spikelets generally present; stigmas 3.	Africa and Madagascar to Yemen (center of diversity in eastern South Africa)
Uncinia Pers. (monophyletic)	~50	Inflorescence unispicate; rachilla present, topped by a hooked scale; spike of spikelets absent; stigmas 3.	Southern hemisphere (center of diversity in South America)

reduced partial inflorescences (Smith and Faulkner, 1976: 63–64), (2) male reproductive structures are reduced partial inflorescences (Timonen, 1998) and (3) the development and structure of spikelets and flowers in *Schoenoxiphium*, as a representative of Cariceae is cyperoid (Vrijdaghs et al., 2009, 2010). Moreover, for the first time, scanning electron microscopical (SEM) observations of the presence of bisexual flowers in two species of *Schoenoxiphium* are presented. The spikelet and floral morphology in *Schoenoxiphium* (with extension to Cariceae in general) is reinterpreted and the use of bisexual flowers as a robust synapomorphy in Cariceae is discussed.

2. Materials and methods

Young spikelets of nine species of *Schoenoxiphium* were collected in South Africa by Berit Gehrke, and vouchers are deposited at the Bolus Herbarium (BOL) at the University of Cape Town, South Africa (*S. burkei* C.B.Clarke [BG-F7], *S. caricoides* C.B.Clarke [BG-F3], *S. filiforme* Kük. [BG-F2], *S. lanceum* [BG-F16], *S. lehmanii* (Nees) Kunth ex Steud. [BG-F 17], *S. madagascariense* Cherm. [BG-F14], *S. rufum* Nees [BG-F5], *S. sparteum* (Wahlenb.) C.B.Clarke [BG-F4], *S. schweickherdtii* Merxm. & Podlech [BG-F9]). Spikelets were either investigated fresh or preserved in 70% ethanol and later transferred to FAA (70% ethanol, acetic acid, 40% formaldehyde, 90:5:5). Floral buds

were dissected in 70% ethanol at Department of Botany (University of Cape Town, Rondebosch, South Africa) or at the Laboratory of Plant Systematics (K.U. Leuven, Leuven, Belgium).

For SEM observations, the material was washed twice with 70% ethanol for 5 min and then placed in a mixture (1:1) of 70% ethanol and dimethoxymethane (DMM) for 5 min. Subsequently, the material was transferred to 100% DMM for 20 min, before it was dried using a CPD 030 critical point dryer (BALTEC AG, Balzers, Liechtenstein). The dried samples were mounted on aluminium stubs using Leit-C and coated with gold with a SPI-ModuleTM Sputter Coater (SPI Supplies, West-Chester, PA, USA). Images were obtained using a JEOL JSM-5800 LV (JEOL, Tokyo) scanning electron microscope at the Laboratory of Plant Systematics (K.U. Leuven).

3. Results

3.1. Spikelet arrangement

Flowers in *Schoenoxiphium* are arranged in ± complex compound (co-)florescences in which a rachis (Fig. 3, R1) of a spike of spikelets (Fig. 3I) carries proximal an incompletely closed prophyll (Fig. 3P1) that also encloses a gynoecium (Fig. 3O), as well as proximal female spikelet(s) (Fig. 3II) and/or bisexual spikelet(s) (Fig. 3III) and distal male spikes of

Fig. 1. Phylogenetic position of *Schoenoxiphium* (Cyperaceae phylogeny modified from Muasya et al., 2009, with additional Cariceae and *Schoenoxiphium* inserts modified from Gehrke et al., 2010) and mapping of bisexual flowers across Cyperaceae. Names of tribes are given after the large bracket. Bootstrap support values are indicated by asterisk above branches in the phylogenetic tree. The number of asterisks indicates the strength of support. Lineages that are para- or polyphyletic in the molecular analyses are indicated by a hash. Where monophyly was not tested due to the representation of the taxon by a single accession a~was added after the lineage name. The presence of exclusively bisexual flowers is indicated by a filled circle in front of the taxon name. The presence of bisexual and unisexual flowers in a clade is represented by an open circle. Exclusively unisexual flowers are marked by a star. Bold arrows indicate *Schoenoxiphium* species in which bisexual flowers were found. Rare and exceptionally reported bisexual flowers are mapped using an open circle in parenthesis.
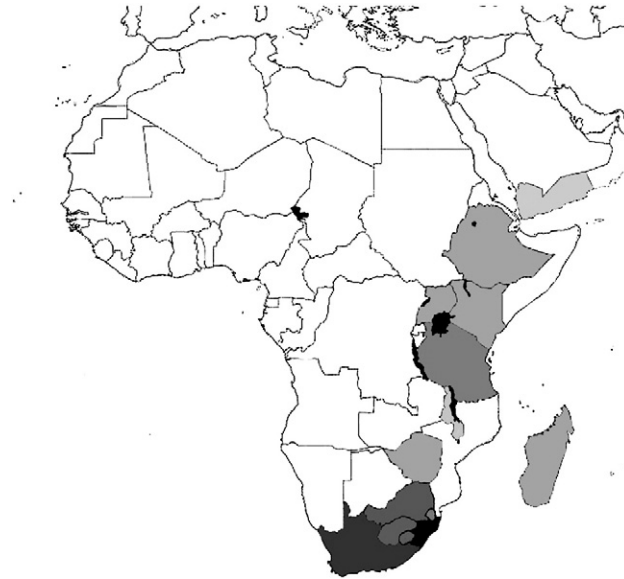
Fig. 2. Distribution of *Schoenoxiphium* in Africa mapped on botanical countries according to the Taxonomic Databases Working Group (TDWG-level3) as recorded in the Monocot checklist (http://www.kew.org/wcsp/). Species number between 0 (white) and 13 (KwaZulu-Natal: very dark grey) are indicated by grey scale. Major lakes are given in black.

staminate flowers (Fig. 3IV). The bract that subtends a spike of spikelets is usually green and leaf-like (Fig. 3B1), while the bract subtending bisexual or female spikelets are glume-like
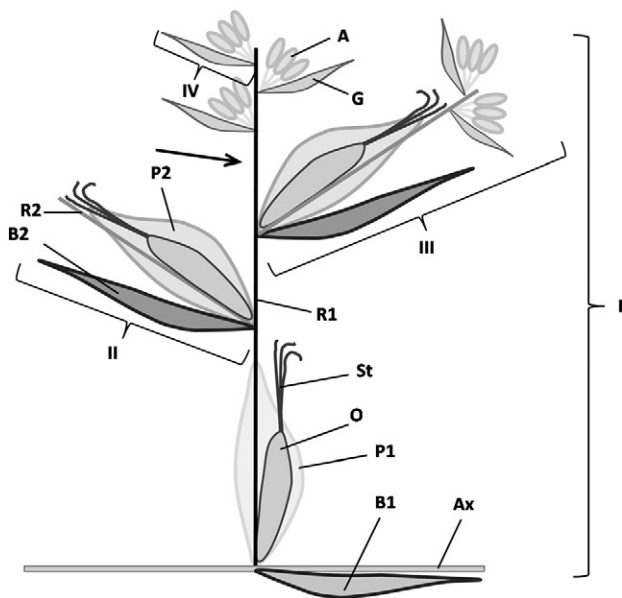

Fig. 3. Schematic outline of the inflorescence structure in *Schoenoxiphium*: I) spike of spikelet with a proximal female flower enclosed by a utricle followed distally by pistillate spikelet, a bisexual spikelet, and a spike of staminate flowers; II) pistillate spikelet resembling a 'female flower'; III) bisexual spikelet with a proximal pistillate flower enclosed by a prophyll and two distal staminate flowers; IV) staminate flower subtended by a glume. Abbreviations: A = stamens, Ax = main inflorescence axis, B1 = leaf-like bract of the spike of spikelet, B2 = glume-like bract of the spikelet, G = glume of the staminate flower, O = ovary, P1 = tubular spike of spikelet prophyll, P2 = flask-like spikelet prophyll (=utricle), R1 = rachis of the spike of spikelet, R2 = spikelet rachilla, St = tristigmatic style. The black arrow indicates the position where bisexual flowers were most frequently found.
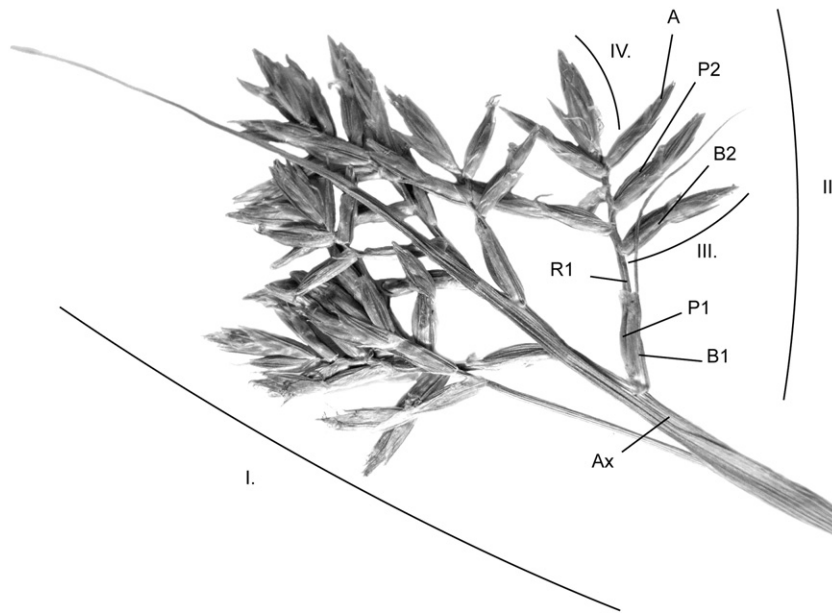
(Fig. 3B2). Female flowers and rachilla are enclosed by the spikelet prophyll (=utricle) (Fig. 3P1, P2, Fig. 7b). The terminal spike(let) of staminate flowers is not subtended by a bract but each male flower is subtended by a glume (Fig. 3G). We were able to identify and document three different flower types, male flowers, female flowers arranged as spikelets and bisexual flowers.

3.2. Male flowers

The staminate flowers consist of three stamens with basifixed anthers in the axil of a glume-like bract (Fig. 7a; see also Fig. 3IV). The anthers fall off shortly after anthesis leaving long hyaline filaments (Fig. 7c). One to six staminate flowers are usually arranged in a florescence (spikelet) terminating a bisexual spikelet and/or a bisexual spike of spikelets (Fig. 3, 7a).

3.3. Female spikelets/flowers

The pistillate flowers consist only of a gynoecium (Fig. 6a). The gynoecium and associated flattened, often scabrous rachilla (Fig. 6) are together enclosed by the spikelet prophyll with ± fused margins, thereby forming a flask-like structure (=utricle or perigynium; Fig. 7b). All female flowers observed have a trimerous, trigonous gynoecium with three stigma branches (Fig. 6a). The gynoecium develops into a somewhat trigonous nutlet (not shown).

3.4. Bisexual flowers

Bisexual flowers were sporadically found in *S. lehmanii* and *S. burkei* (Fig. 7c–f). Bisexual flowers consist of a whorl of three stamens, two adaxially and the third abaxially (with

Fig. 4. Illustration of inflorescence of *Schoenoxiphium filiforme:* I. = Inflorescence of several spikes of spikelets; II. = spike of spikelets; III. = bisexual spikelet; IV. = spike(let) of male flowers; Abbreviations: A = stamens, Ax = main inflorescence axis, B1 = bract of the spike of spikelet, B2 = bract of the spike of spikelet, P1 = tubular spike of spikelet prophyll, P2 = prophyll of the spikelet (=utricle), R1 = rachis of the spike of spikelet.

respect to the spikelet rachilla) positioned around a single dimerous, dorsiventrally flattened and distigmatic gynoecium. The ovary is biconvex. Bisexual flowers were always subtended by a glume (7c–f). All bisexual flowers observed were positioned in the spike of spikelets either at a transitional position between the proximal bisexual spikelets and the male
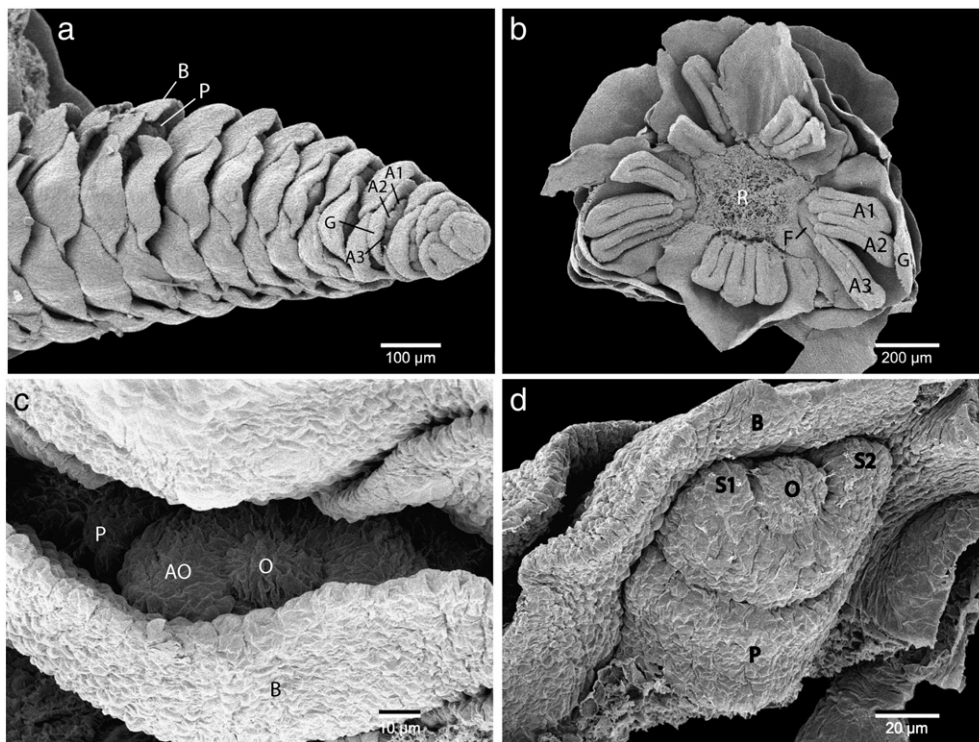

Fig. 5. Illustration of Cariceae spike (*Carex elata*): (a) spike primordium with distal staminate florescence zone (glumes subtending staminate flower primordia at different developmental stages can be seen) and proximal zone with pistillate spikelets; (b) view onto transversally broken rachis in the florescence zone, with adaxial view on developing staminate flowers; (c) very early developmental stage of a pistillate spikelet; (d) later developmental stage of a pistillate spikelet. *Carex elata* has dorsiventrally compressed pistils with proximally positioned stigma branch primordia. Abbreviations: A1–A3 = stamens; AO = annular ovary wall primordium; B = glume-like bract; F = filament, G = glume; O = ovule primordium; P = spikelet prophyll (=utricle) primordium; R = rachis; S1 and S2 = stylar primordia of the annual ovary wall.
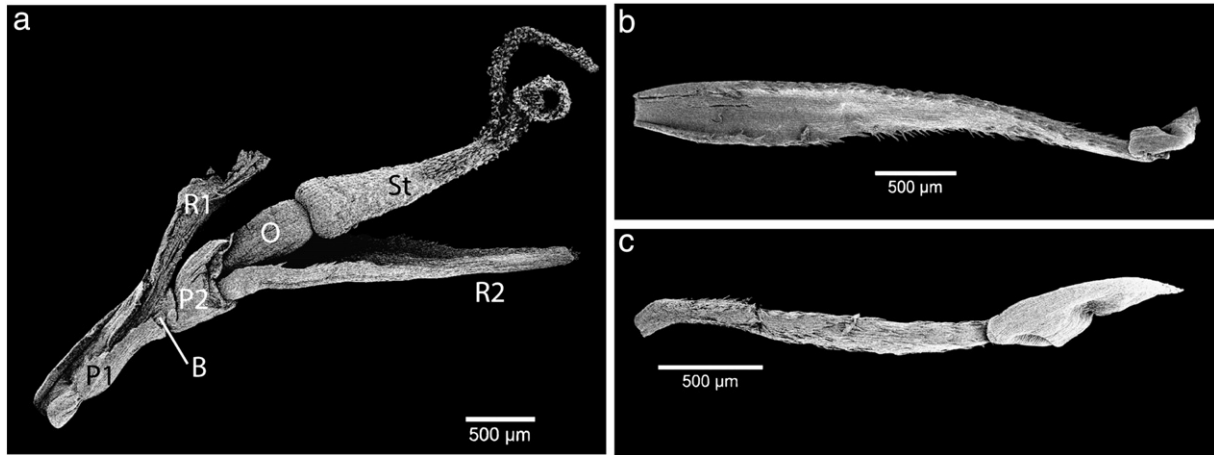
Fig. 6. Illustration of position and shape of rachilla of *Schoenoxiphium*: (a) *S. sparteum*; (b) and (c) rachilla of *S. madagascariensis* with distal remnants of scales; (b) abaxial view, (c) adaxial view. Abbreviations: B = remnant of the bract of the spikelet, O = ovary, P1 = tubular spike of spikelet prophyll, P2 = remains of the spikelet prophyll (=utricle) enclosing a pistillate spikelet consisting of a rachilla and a gynoecium, R1 = spike of spikelet rachilla (axis of the spike of spikelet with distal pistillate spikelets and staminate flowers), R2 = spikelet rachilla without distal fertile parts, St = tristigmatic style with a distinct style head.

florescence, or among the most proximal staminate flowers in the male florescence (Fig. 3, indicated by an arrow).

4. Discussion

4.1. Support for bisexual flowers

Our results are mostly congruent with those of Timonen (1985) and we follow her opinion in considering the observed bisexual flowers as real flowers. This view differs from that of Smith and Faulkner (1976: 63-64), who interpreted a similar structure (a reproductive structure consisting of a gynoecium with two stigma branches instead of the usual three, and two stamens) found in *C. nigra* as a female spikelet that lacks a prophyll and has 'a stamen [that] protruded from the ovary, apparently replacing the ovule'. By the current knowledge of the ABCDE-model (Coen and Meyerowitz, 1991; Fornara et al., 2003), we know that the position of sepals, petals, stamens and carpels can be exchanged, but not the position of ovules. Neither can stamens be positioned on carpels.

In our opinion, these bisexual reproductive structures are not different from the usual bisexual flowers in Cyperaceae, based on the following observations (Fig. 7):

- The whorled arrangement and positions of the stamens.
- Position of the bisexual flowers in the inflorescence:
  all bisexual flowers observed were situated at a transitional position between the proximal female/bisexual spikelets and the terminal, male spikelet (or florescence), or in between the two most proximally situated staminate flowers (indicated by an arrow in Fig. 3). This means that the bisexual flowers were found in a position where the transition is initiated between the development of female/ bisexual spikelets and staminate flowers.
- Absence of prophyll remnants and presence of a glume-like structure subtending the flower:

neither prophylls nor any remnants of prophylls were found in bisexual flowers, neither by us (Fig. 5c, 6a, 7), nor by Timonen (1985), nor by Smith and Faulkner (1976: 63). Usually, in a bisexual spike of *Schoenoxiphium*, the proximal female spikelet is enclosed by the spikelet prophyll which has a flask-like shape (utricle). However, in the observed bisexual flowers, such a structure or remnant of it was not found (Fig. 7) and instead each bisexual flower was subtended by an open, somewhat flattened glume-like structure (Fig. 7).

In all observed bisexual flowers, the gynoecium was usually dimerous, dorsiventrally flattened with two stigma branches (Fig. 7c–f). In contrast, the pistils of the flowers in the female spikelets are trimerous with three stigma branches (Fig. 3, 6a, 7b). The dimerous gynoecia are also smaller than the usual trimerous ones. No evidence for the fertility of the gynoecium in the form of fruit development was found, but too few specimens were examined and the specimens were not at fruiting stage. We are therefore unable to draw any conclusions as to the fertility of the bisexual flowers.

4.2. Transitional position and control

In the light of our current understanding of developmental regulation, a given primordium can develop into a vegetative axis, a spike, a spikelet or a (staminate) flower, depending on the stimuli (internal and external) that trigger the developmental pathways (Smith, 1967). It is therefore likely that any given primordium in Cariceae inflorescences retains the ability (genetic and ontogenetic programming) to develop into a bisexual flower. We postulate that the presence of bisexual flowers is due to an incomplete suppression of bisexuality in the zone between female or bisexual spikelets and staminate flowers. The presence of bisexual flowers in a transitional position also supports the view of Vrijdaghs et al.
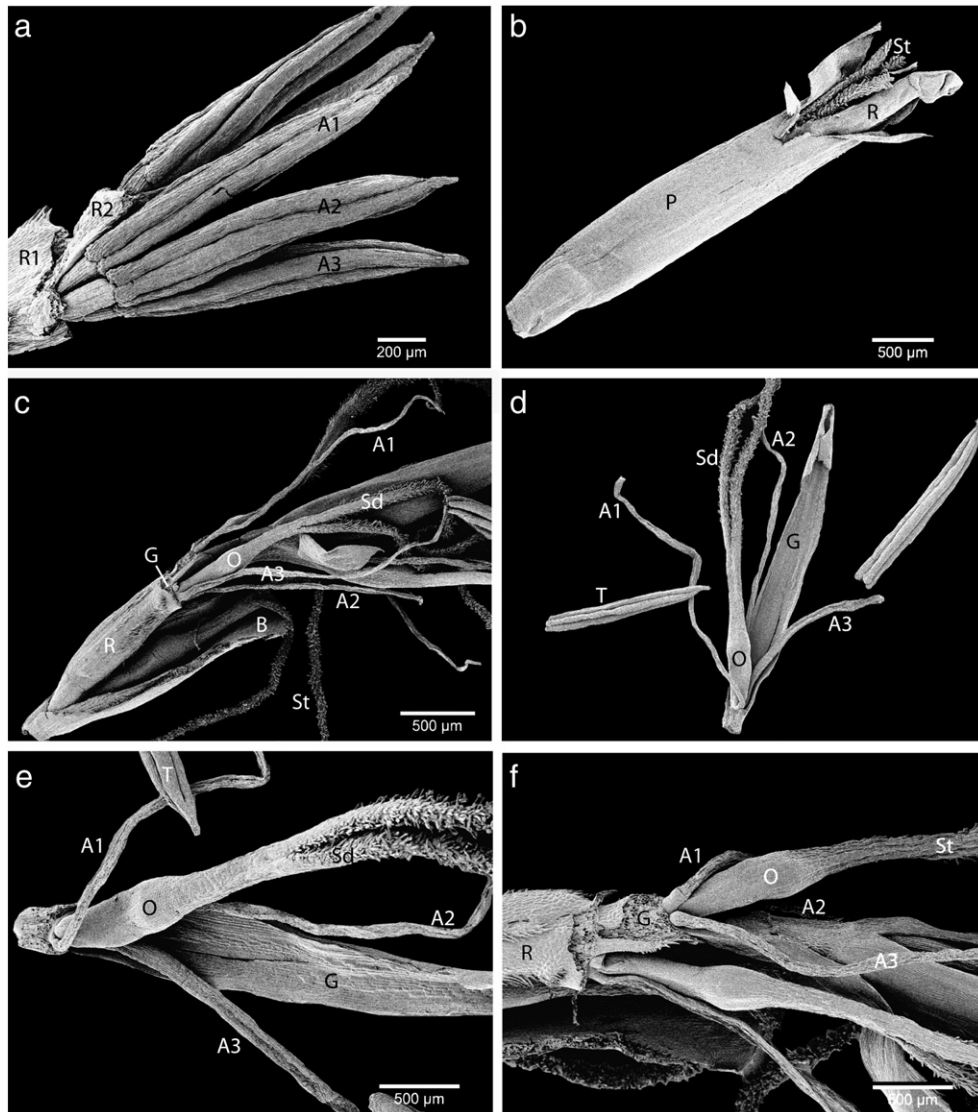
Fig. 7. *Schoenoxiphium* (a) staminate flowers of *S. sparteum* with removed glume; (b) 'female flowers' (i.e. pistillate spikelets) of *S. madagascariensis:* (c–f) bisexual flower in *S. burkei.* Abbreviations: A1–3 = stamen (only filaments present in pictures c–f); B = glume-like bract of the pistillate spikelet; O = gynoecium (ovary); P = prophyll of the pistillate or bisexual spikelet (=utricle); R1–2 = rachis; Sd = distigmatic Style; St = tristigmatic style; T = anther which was removed during the preparation process.

(2009, 2010) that the staminate reproductive units are not reduced staminate spike(-lets) as suggested by Kükenthal (1909), Smith and Faulkner (1976) or Timonen (1998), but are staminate flowers subtended by a glume. We observed within a single inflorescence in several individuals a full transition series from female spikelet or bisexual spikelet with a proximal pistillate flower and 1–6 distal staminate flowers to bisexual flowers and then to unisexual staminate flowers.

4.3. Unisexual flowers as a synapomorphy in Cariceae?

Strictly seen, the occurrence of bisexual flowers in *Schoenoxiphium*, whatever may be the explanation for it, makes the character 'unisexual flowers' unsuited as a synapomorphy for Cariceae. However, in Cyperaceae, 'bisexual flowers' is plesiomorphic (Goetghebeur, 1986; Bruhl, 1991),

and one might consider the sporadic occurrence of such flowers in *Schoenoxiphium* as a 'reversal', given that the term 'reversal' here does not mean an evolutionary process that took place in order to make bisexual flowers reappear in this genus. In our opinion, the real synapomorphy for Cariceae is therefore not 'unisexual flowers', but 'inhibition of bisexuality'. We hypothesise an underlying regulatory mechanism that usually inhibits the realisation of bisexual flowers. Apparently, this inhibition is under certain conditions incomplete, causing the development of the plesiomorphic state (i.e. the presence of a bisexual flower). A similar flexibility in sex determination is observed by Flores et al. (in review) in *Atriplex* (Chenopodiaceae). In another Cyperaceae tribe Cypereae a similar 'reversal' was observed in the genera *Dracoscirpoides* (Muasya et al., 2011), *Hellmuthia* (Vrijdaghs et al., 2006) and *Ficinia* (Schönland, 1922), where in the highly derived Cypereae clade that is

usually characterised by the synapomorphy 'absence of perianth', remnants of a perianth reappear. The 'reversal' can therefore be explained by an incomplete suppression of the perianth, making 'suppression of the perianth' the synapomorphy for the Cypereae clade similar to 'inhibition of bisexuality' being the synapomorphy for the Cariceae.

Acknowledgements

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