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THE *SCHOENUS* SPIKELET: A RHIPIDIUM? A FLORAL ONTOGENETIC ANSWER

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ABSTRACT

The inflorescence unit of *Schoenus nigricans* and *S. ferrugineus* consists of a zigzag axis and distichously arranged bracts, each of which may or may not subtend a bisexual flower. Each flower seems to terminate a lateral axis. These features have led to a controversy about the nature of the inflorescence unit, particularly whether it is monopodial or sympodial. It was often seen as a pseudospikelet composed of a succession of lateral axes, each subtended by the prophyll of the previous axis, as in a rhipidium. Many authors, however, consider the inflorescence units of all Cyperaceae to be indeterminate, racemose, actual spikelets. In our study, we present new SEM observations on the floral ontogeny of *S. nigricans*, corroborating a monopodial interpretation of the spikelet. Concaulescent growth of the flower primordium and the spikelet apex explains: (1) the presence of a peduncle under the flower, (2) the advanced development of the subtending glume compared to its own flower primordium, and (3) the position of the distal glume with regard to the distal flower primordium.

Key words: floral ontogeny, monopodial, rhipidium, *Schoenus nigricans*, SEM, spikelet.

INTRODUCTION

A cyperaceous inflorescence is basically a panicle of spikelets, which can be modified by elongation or contraction of internodes and various reduction trends into an anthela, a corymb, a terminal capitate—or pseudolateral—inflorescence, a single spike, or a complex compound inflorescence with several combinations of partial inflorescence types (Goetghebeur 1998). A lateral axis is subtended by a bract, and the first leaf on this axis is theoretically a two-keeled, adaxial prophyll. The inflorescence unit is a functional unit, named spikelet. Spikelets can be terminal or lateral. A lateral spikelet consists of a spikelet axis or rachilla inserted in the axil of a bract, a sterile adaxial prophyll, and one to many glumes. A glume may be sterile or—if subtending a sessile flower—fertile. A terminal spikelet has neither a bract nor a prophyll (Goetghebeur 1998).

Schoeneae sensu Goetghebeur (1998) are a tribe of subfamily Cyperoideae in Cyperaceae. Most species of *Schoenus* L. occur in Australia and Malesia and have a typical paniculate inflorescence. *Schoenus nigricans* L. and *S. ferrugineus* L. occur in the temperate zones of the Northern Hemisphere, Africa, and Southeast Asia. Both have a condensed inflorescence (Goetghebeur 1986). At the apex of the culm several involucre bracts are present. Each bract axillates a group of spikelets, each spikelet having its own peduncle. The spikelets in these two species of *Schoenus* do not have a prophyll, which makes it difficult to distinguish between lateral and terminal spikelets (Haines 1967). The spikelets of Schoeneae are characterized by the inclusion of each flower by the wings of the glume above. The empty distal glume in *S. nigricans* and *S. ferrugineus* is two-keeled, giving it a prophyll-like appearance. Haines (1967) concluded his study of the spikelet in Rhynchosporae with “the peculiarity of the tribe lies in the enwrapping glumes, not in a cymose structure.” Celakovsky (1887), following Pax

(1886), considered the inflorescences of Rhynchosporae (at that time including Schoeneae) to be sympodial. He separated Rhynchosporae from other Cyperaceae by the presence of a two- or three-flowered inflorescence unit that he called a “Fächel” (rhipidium). A rhipidium is a cymose partial inflorescence with a monochasial branching pattern out of the axil of the adaxial prophyll on each axillary shoot (Weberling 1992). The decurrent wings of each glume in *S. ferrugineus* were interpreted by Celakovsky (1887) as the result of fusion between the new lateral axis (“Achselprosse”) and the subtending bract. The zone of fusion between the bract and the lateral axis extends all over the length of the internode, up to the terminal flower, where the free part of the bract resembles a flower subtending glume. Mora (1960) used the term “Vorblatt” for the distal leaf. He considered it to be the first leaf of a lateral axis that, theoretically, could subtend a new lateral axis. The zigzag “rachilla of the spikelet” should be interpreted as a pseudorachilla built up by successive lateral axes, with prophyll-branching (Mora 1960). Kern (1962), who supported Mattfeld’s synanthium hypothesis (Mattfeld 1938), considered not only the inflorescence units of Rhynchosporae (sensu Kükenthal 1938) as sympodial, but he extended the sympodial interpretation to the inflorescence units of all Cyperaceae.

Many Cyperaceae specialists, however, do not agree with this interpretation. Holtum (1948) stated that Celakovsky made an “unnecessary assumption,” when considering the *Schoenus* spikelet as a recaulescent rhipidium. Referring to Pax’s floral diagrams of *Asterochaete* Nees and *Elynanthus* P. Beauv. ex Lestib. (Pax 1886), which indicate a two-keeled prophyll accompanying the second flower, he examined *S. calostachyus* (R. Br.) Poir. but did not find any prophyll in the spikelet. Hence, he rejected the possibility of prophyll-branching in the spikelet of *Schoenus*. He compared it with *Cyperus* L., where the bases of each glume are often also

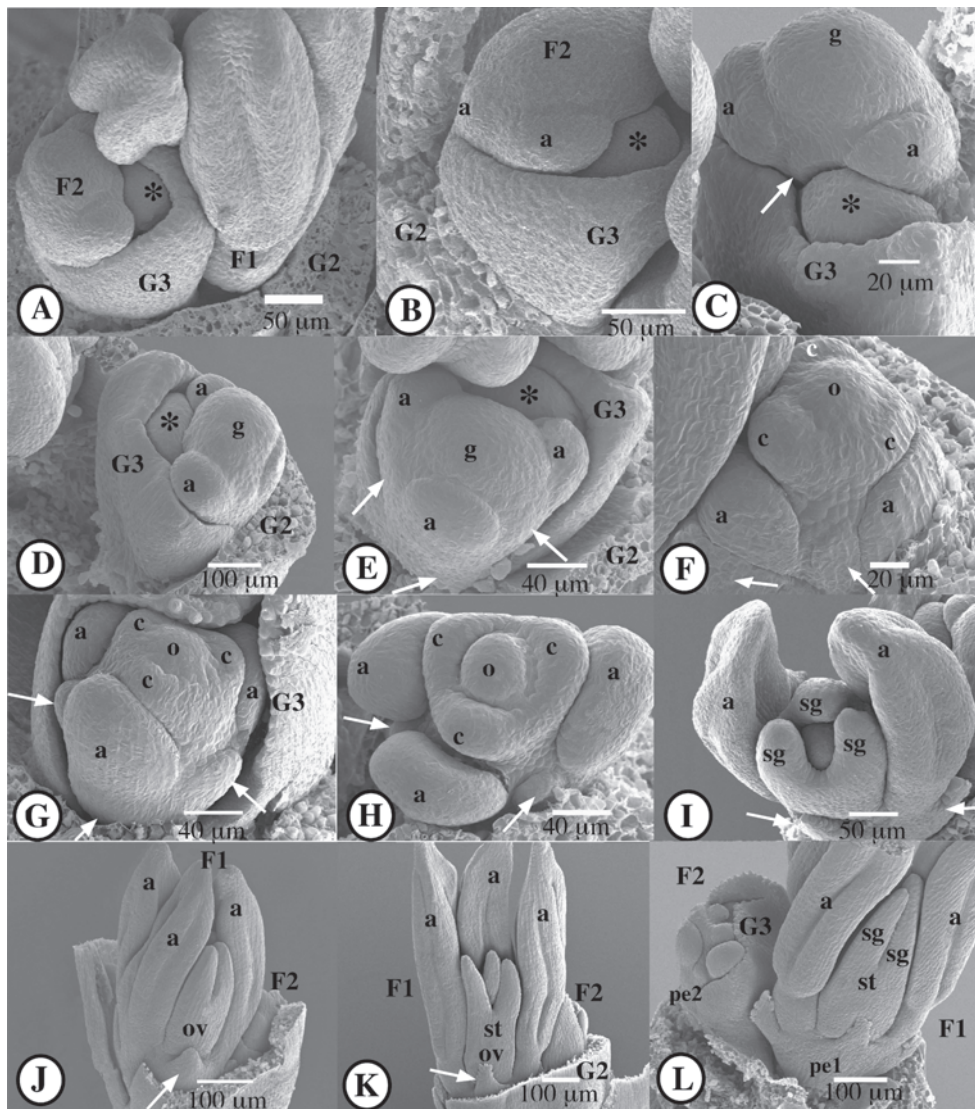


Fig. 1.—Floral ontogeny of *Schoenus nigricans*.—A. Lateral-apical view of the spikelet of *S. nigricans* with rachilla (*), distal (F2), and underlying (F1) flower and distal glume (G3). The glume subtending the distal flower primordium (G2) has been removed.—B. Adaxial view of the distal flower primordium (F2) behind the rachilla apex (*), and enclosed by the distal glume (G3). Stamen primordia (a) are initiated.—C. Adaxial view of the distal flower primordium (arrow) with two stamen primordia (a) and the gynoecium primordium (g).—D. Lateral-apical view of the distal flower primordium.—E. Abaxial-apical view of the distal flower primordium with tepal primordia (arrows).—F. Lateral view of the distal flower primordium with differentiating gynoecium primordium and two tepal primordia (arrows). Carpel primordia (c), as well as ovule primordium (o), become visible.—G. Abaxial view of the developing distal flower primordium. Notice the inner tepals [two visible: arrows at left and lower right] alternating with the stamens and an outer tepal [arrow at lower left] opposite the abaxial stamen.—H. Apical view of the distal flower. The carpel primordia (c) fuse postgenitally at the base. The stamen primordia (a) start differentiating into filament and anthers. Note the growing tepals (arrows).—I. Adaxial view of the distal flower. Stigma lobes (sg) develop. Anthers of the two lateral stamens (a) can be distinguished. The abaxial stamen has been removed. Note the adaxial and one lateral tepal (arrows).—J. Adaxial view of the well-developed proximal flower (F1). Note the adaxial tepal (arrow). At right hand side, there is the distal flower (F2).—K. Same view as in J, successive stage. The style (st) develops. The surface of the adaxial tepal (arrow) of the proximal flower (F1) becomes papillose.—L. Maturing proximal flower (F1). At left-hand side, the distal glume (G3) encloses the rachilla and the upper flower (F2). Notice the pedicels (pe) under the proximal and distal flowers. Abbreviations: a = stamen/anther (primordium), c = carpel (primordium), F1 = proximal flower (primordium), F2 = distal flower (primordium), G = glume (G1 subtending the proximal flower, G2 subtending the distal flower, G3 = distal glume), g = gynoecium (primordium), o = ovule (primordium), ov = ovary, pe = pedicel, pe1 and pe2 = pedicels of flower1 and flower 2, respectively, sg = stigma (primordium), st = style, * = rachilla apex.

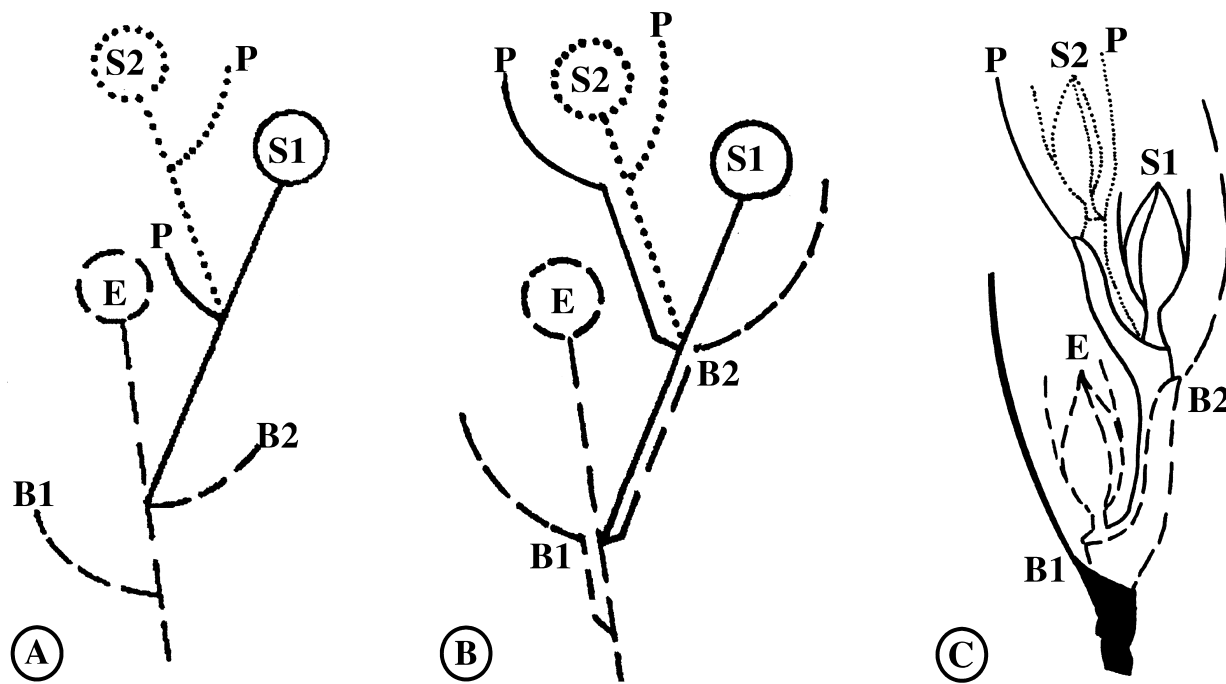


Fig. 2.—Comparison of three representations of the spikelet in *Schoenus*.—A. Theoretical interpretation of the *Schoenus ferrugineus* spikelet as a rhipidium.—B. The same, with recaulescent prophylls.—C. Drawing after Celakovsky (1887). (Dotted line = most recent lateral axis with terminal flower S2. Solid black line = previous lateral axis of which the prophyll [P] axillates the distal, most recent lateral axis, with its terminal flower S1. Broken line = main axis with terminal flower [E = “Endblüte”], and two bracts of which the second one [B2] axillates a lateral axis. The proximal bract [B1] is empty.)

decurrent as wings along the lower internode. According to Holtum (1948) such wings are probably the result of the distichous arrangement of the glumes in the spikelets of *Schoenus* and *Cyperus*. Raynal (1971) examined cross sections of the rachilla, and he concluded that the *Schoenus* spikelet cannot be cymosely branched. This conclusion was corroborated by Eiten (1976), who made a detailed anatomical study on the rachilla of three species of *Rhynchospora* Vahl and one of *Cyperus* in order to determine whether there is anatomical evidence for recaulescency. In a sympodial recaulescent axis there should be traces of the bract running parallel to the central strand through the internode, before leaving the axis to enter the free part of the bract. Eiten (1976) did not find such traces and she concluded that there is no anatomical evidence for recaulescency or sympodality. Kukkonen (1986: 109) examined the spikelet structure of *S. ferrugineus* and observed that each spikelet is indeterminate since “they were found to be open (or ending in a bud . . .).” Starting from the narrow definition of a prophyll being two-keeled and positioned adaxially, he concluded that prophylls redefined by Mora (1960) must be glumes. According to him, a monopodial interpretation of the *Schoenus* spikelet is more likely, a view also supported by Bruhl (1991) and Goetghebeur (1986). Recently, Zhang et al. (2004b) reopened the discussion, presenting results of a detailed study of a large variety of inflorescence units of Australian *Schoenus* species, which, according to the authors, argues in favor of a sympodial interpretation. Most of their observations are based on studies of mature spikelets, in which each achene indeed seems to terminate a lateral axis.

We study the ontogeny of the inflorescence unit and the

floral ontogeny of *S. nigricans* in order to evaluate sympodial and monopodial interpretations.

MATERIALS AND METHODS

Inflorescences of *Schoenus nigricans* were collected in the botanical garden of the Institute of Botany and Microbiology of the Katholieke Universiteit Leuven from Mar to May 2003, and the voucher AV01 is housed at the university herbarium (LV). The young spikelets were preserved in a FAA mixture (70% ethanol, acetic acid, 40% formaldehyde, 90 : 5 : 5). Floral buds were dissected in 70% ethanol under a Wild M3 stereo microscope (Leica Microsystems AG, Wetzlar, Germany) equipped with a cold-light source (Schott KL1500; Schott-Fostec LLC, Auburn, New York, USA). The material was washed twice with ethanol (70%) for 5 min and then placed in a mixture (1 : 1) of ethanol (70%) and DMM (formaldehyde dimethyl acetal; Merck-Schuchardt, Hohenbrunn, Germany) for 5 min. Subsequently the material was transferred to pure DMM for 20 min, before it was CO₂ critical point dried using a CPD 030 critical point dryer (BAL-TEC AG, Balzers, Liechtenstein). The dried samples were mounted on aluminium stubs and coated with gold with a SPI-Module[®] Sputter Coater (SPI Supplies, West Chester, Pennsylvania, USA). Scanning electron microscopy (SEM) images were obtained on a JEOL JSM-5800 LV scanning electron microscope (JEOL, Tokyo, Japan) at the National Botanical Garden of Belgium in Meise.

RESULTS

The spikelet of *S. nigricans* is an indeterminate spikelet with the apex of the rachilla enclosed by the distal glume

(referred to in the figures as G3). This glume also envelops the peduncle of the distal flower primordium (Fig. 1A–D). Each flower primordium is initiated in the axil of a subtending glume. The subtending glume appears first and develops earlier than its flower primordium. Here one abaxial and two lateral stamen primordia appear (Fig. 1B–E). Meanwhile, the distal glume is reaching its two-keeled appearance; it starts covering the rachilla and later on the developing distal flower primordium. On the top of the flower primordium the gynoecium primordium appears (Fig. 1E–F). Opposite the stamen primordia and alternating with them, two whorls of perianth part primordia can already be observed at a very early stage (Fig. 1E). The central ovule primordium and the three carpel primordia originate from the gynoecium primordium (Fig. 1F). Then the stamen primordia differentiate into filaments and anthers (Fig. 1G). The bases of the carpel primordia fuse postgenitally and rise, forming the ovary wall (Fig. 1H) and style (Fig. 1J–L). The tips of the carpel primordia differentiate into stigmas (Fig. 1H–L). The inner as well as the outer tepals remain small, bristle-like, with a papillose surface (Fig. 1L). Because of the raised position of the upper flower, the distal glume is situated in between the two flowers (Fig. 1A, 3C, 4). The inflorescence of *S. nigricans* is very compacted, which causes distortion of the positions of the flowers with respect to the rachilla (Fig. 1K–L). From the earliest stages of development, the flowers are raised on a pedicel (Fig. 1D–E, G, L).

DISCUSSION

The spikelets of *S. nigricans* are characterized by a limited number of bisexual flowers, and by the inclusion of each flower by the wings of the glume above (Goetghebeur 1998). The mature spikelet has a zigzagging rachilla and each achene seems to terminate a lateral axis. The wings of the distal and, hence, youngest glume enclose the apex of the rachilla as well as the distal flower. The distal glume also has two keels, which makes it look like a prophyll. Therefore, the mature inflorescence units of *S. nigricans* and *S. ferrugineus* were often seen as pseudospikelets, composed of successive lateral axes, each axillated by the prophyll of the previous axis, and with successive terminal flowers. In order to interpret the inflorescence unit of *Schoenus* as such a rhipidium, Celakovsky (1887) needed to assume that: (1) the distal leaf is a prophyll, (2) the pedicel of each flower is a lateral axis axillated by a prophyll and, (3) each prophyll is partly fused to the lateral axis that it axillates (Fig. 2A–C). Kern (1962), who strongly supported Mattfeld's (1938) synanthium hypothesis, attempted to derive bisexual flowers in all Cyperaceae from unisexual floral units. A cymose *Schoenus* florescence would have corroborated the synanthium hypothesis.

Our floral ontogenetic results, however, can be explained in an easier way by applying the general model of a racemose cyperaceous spikelet (Fig. 3A). In our view, the distal glume and the underlying leaves are normal glumes with decurrent wings, which each enclose the rachilla and the underlying flower, as can be observed in most genera of Schoeneae. The two-keeled form of the distal glume, which has caused so much controversy, is due to its compressed position between the distal flower and the rachilla at the one

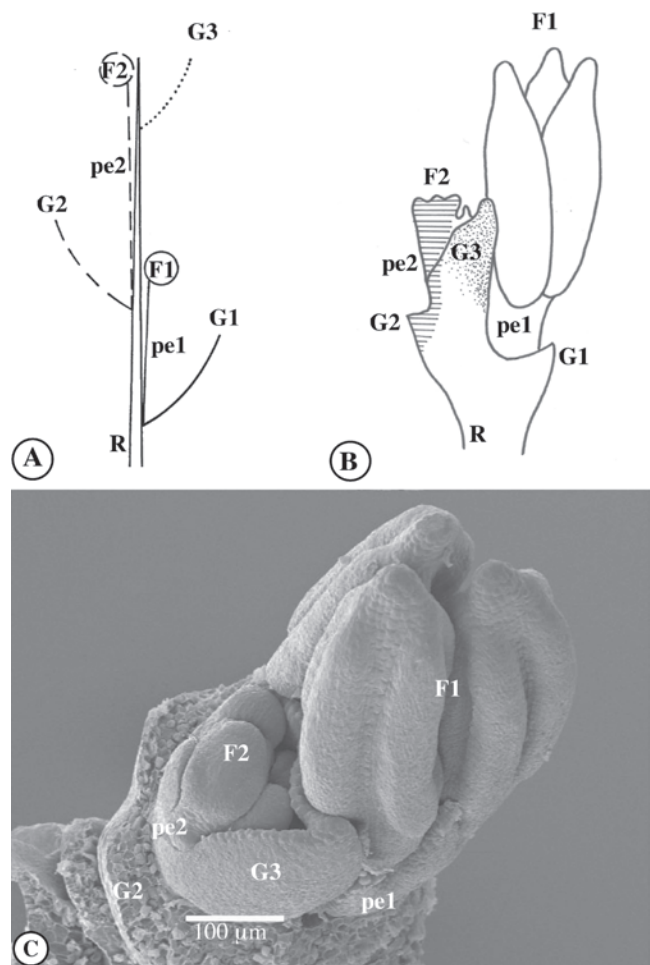


Fig. 3.—The spikelet in *Schoenus nigricans*.—A. Schematic outline of the inflorescence unit, interpreted as a racemose spikelet.—B. Diagram of the inflorescence unit interpreted as a racemose spikelet with a delay in development between the subtending glume and the flower primordium, and concaulescent growth of the rachilla apex and the distal flower primordium.—C. SEM image of the spikelet of *S. nigricans*. (Dotted line/stippled area = distal glume [G3]. Broken line/hatched area = glume [G2] subtending distal flower, and distal flower primordium [F2]. Solid black line = glume [G1] subtending proximal flower, and proximal flower [F1]. Abbreviations: pe1 and pe2 = pedicels of flower 1 and flower 2, respectively; R = rachilla.)

side, and the well-developed proximal flower at the other side, in a very condensed spikelet (Fig. 3B–C).

Blaser (1944) doubted the taxonomic value of prophylls. Within Cyperaceae there is a wide variety of structures and positions with respect to the axis, and phyllotaxy of the so-called prophylls. Zhang et al. (2004b) wrote that the presence or absence of a prophyll cannot be used to recognize different branching patterns. Moreover, examining if a fertile glume subtends a flower (monopodial) or a lateral axis (sympodial), would give reliable arguments to determine whether (in)florescences are sympodial or monopodial (Zhang et al. 2004b). This criterion, however, might cause confusion, especially on how to distinguish between a pedicel and a reduced axis. In *Schoenus* the flowers are raised on a “stalk.” The discussion in *Schoenus* is actually about the nature of

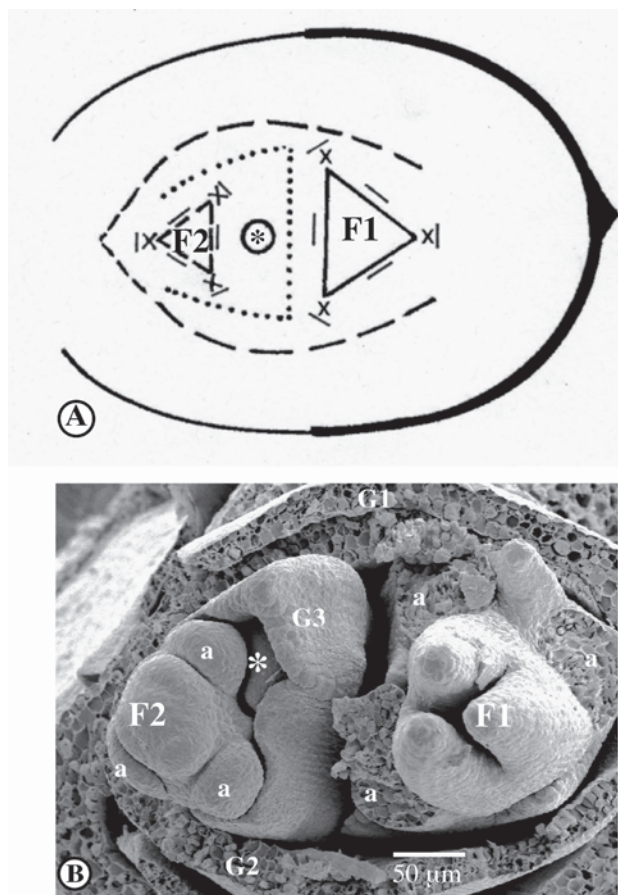


Fig. 4.—The spikelet apex in *Schoenus nigricans*.—A. Diagram of the apex of a spikelet. (Solid black line = glume subtending proximal flower [G1] and proximal flower. Broken line = glume subtending distal flower [G2] and distal flower [primordium]. Dotted line = distal glume [G3]).—B. SEM image of an apical view of the apex of a spikelet. Abbreviations: F1 = proximal flower, F2 = distal flower; X = stamen ("a" in SEM image); * = apex of the rachilla.

these stalks; are they pedicels or rather lateral axes subtended by the prophyll of the previous axis?

In Cyperoidae species we observed, flower buds are initiated in racemose inflorescences. First, the subtending glume primordium appears and starts developing. Then, a flower primordium originates in its axil. Apparently, the same scheme is followed in *S. nigricans*, but the appearance and development of the flower primordium is much more delayed. Meanwhile, the flower primordium is raised by the growing rachilla (concaulescent growth). This explains the presence of a pedicel under the flower (Fig. 3B–C), and the striking difference in developmental stage between subtending glume and flower (Fig. 1A–B, 3C). The concaulescent growth of the flower primordium, which arises above the rachilla apex, also explains the position of the distal glume apparently below the upper flower primordium (Fig. 3B–C, 4). Delay of development of flower or inflorescence parts is not uncommon in Schoeneae, and we have observed this delay in *Rhynchospora* (unpubl. data) and *Cladium* (Vrijdaghs et al. 2003). Further investigation of the floral ontogeny in other species of *Schoenus*, as well as in the other genera of Schoeneae is needed, given the non-monophyletic

status of *Schoenus* and the tribe Schoeneae (Zhang et al. 2004a; Simpson et al. 2007). Concaulescent growth of the flower primordium and the rachilla apex and a delay of the development of the flower primordium explain the presence of a pedicel and the seemingly odd positions of the distal flower (referred to in the figures as F2), its subtending glume (referred to in the figures as G2), and the distal glume (Fig. 3A–C). There is no need for other hypotheses if the inflorescence units of *S. nigricans* are interpreted as racemose spikelets.

The mature flower of *S. nigricans* has been described as a flower without perianth (Goetghebeur 1986). Our floral ontogenetic results (Fig. 1E–L), however, show that, at least in the early stages of development, two whorls of each three perianth parts are present.

CONCLUSION

The inflorescence unit of *S. nigricans* L. is an indeterminate, racemose, and (sub)distichously organized spikelet with an empty distal glume and two bisexual flowers. Each glume has decurrent wings, which enclose the rachilla and the more proximal flower. The flowers are raised on a pedicel and have a perianth with six underdeveloped, bristle-like tepals, three opposite, and three alternating with the stamens. The presence of a pedicel and the positions of the flowers and glumes can be explained by concaulescent growth of the rachilla and the distal flower primordium, and a large plastochron between the appearance of the subtending glume and the development of its flower primordium. Further investigation of the floral ontogenies in other critical genera of Schoeneae is planned.

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