Symantic structure of spikelets in the tribe Schoeneae (Cyperaceae)[1]

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Spikelet morphology of 250 specimens of 47 species of Schoeneae was examined using light microscopy and scanning electron microscopy. We confirmed that spikelet structure in Schoeneae is cymose with a sympodial ''rachilla.'' Monopodial spikelets, as described by most current literature, were not found in Schoeneae. Prophylls are not always present in sympodial spikelets and cannot be used to determine whether a spikelet is sympodial or monopodial. Spikelets of Schoeneae develop acropetally, and the uppermost glume may or may not produce a flower. The last feature may be variable within species and within individual plants, so presence or absence of this flower is not an indication of sympodial or monopodial spikelet structure in Schoeneae. Relative position of flower, glume, and axis is a reliable criterion to judge whether spikelets are sympodial or monopodial. In some species of *Schoenus* and in *Ptilothrix*, formation of the arch-shaped base of the fertile glume relates to the shape of the inclined nodes on which the glume grows. This study highlights the need to reinvestigate spikelet structure in other tribes of Cyperaceae.

Key words: Cyperaceae; monopodial; prophyll; rachilla; Rhynchosporeae; Schoeneae; spikelet; sympodial.

The branching pattern of spikelets is an important character in determining systematic arrangements within Cyperaceae. The spikelets, however, are extremely contracted, leading to different interpretations of spikelet morphology in Cyperaceae, especially in the tribe Schoeneae (Goetghebeur, 1998), and consequently to different classifications. For example, the Schoeneae, previously commonly named Rhynchosporeae (Bentham, 1883; Koyama, 1961; Schultze-Motel, 1964; Hooper, 1973; see Zhang, 2002, for a review of Schoeneae) was placed (as Rhynchosporeae) in the same subfamily as Scirpeae by Bentham (1883), but Pax (1887) removed the tribe to the subfamily Caricoideae because of the sympodial structure of the spikelet. Later, Schultze-Motel (1964) considered the spikelets of the tribes Rhynchosporeae, Scirpeae, and Cypereae to be sympodial and put them in the same subfamily, while Eiten (1976) insisted all these tribes had racemosely branched spikelets. The crucial dispute is whether spikelet structure is cymose (or a rhipidium, which is a sympodial structure) or racemose (a monopodial structure). Currently most literature, including floras, treats spikelets in Schoeneae (or Rhynchosporeae) as monopodial structures (e.g., Haines and Lye, 1983; Kukkonen, 1986; Wilson, 1993).

Since Wilhelm Hofmeister (1824–1877), it has been customary to classify inflorescences as racemes (racemose inflorescences) or as cymes (cymose inflorescences) (Weberling,

1989). A raceme is defined as an inflorescence characterized by a monopodial axis on which flowers are lateral. The cyme is constructed sympodially, and flowers are terminal (Guédès, 1979; Weberling, 1989; Bell, 1991). The cymose inflorescence can be subdivided into a monochasium, dichasium, or pleiochasium. The monochasium can be further characterized as a rhipidium, drepanium, cincinnus, or bostryx (Bell, 1991). A rhipidium is constructed sympodially, with alternate lateral branches, each of which terminates with a flower (Fig. 1a–c). This type of inflorescence is also called a scorpioid cyme (Radford et al., 1974; Eiten, 1976).

The spikelet structure in tribe Schoeneae (or Rhynchosporeae) was first proposed to be cymose and its rachilla sympodial by Pax (1886, 1887); this interpretation was supported by some later authors (Celakovský, 1887; Hamlin, 1956; Kern, 1962; Schultze-Motel, 1964). They interpreted the spikelet structure of this tribe as follows: the proximal flower terminates the main axis of the spikelet, and the second flower terminates a secondary axis arising from the axil of the uppermost glume on the main axis, with the secondary axis bearing only one glume, from which further branching may proceed (Fig. 1a–c). In this case, the flowers are terminal, not axillary to a glume; the glume, which apparently subtends a flower, really subtends the new branch forming the next rachilla internode. This view was also supported for *Rhynchospora macrostachya* Torr. ex A. Gray (Blaser, 1941), *Cladium* (Mora, 1960; Richards, 2002), *Schoenus* (Mora, 1960), the Schoeneae of Clarke (1908) (Schönland, 1922), *Trianoptiles* (Levyns, 1943; Phillips, 1951), *Epischoenus* (Leighton et al., 1947; Levyns, 1959), and *Costularia* (Browning, 1994). In this view, Pax (1886, 1887), Celakovský (1887), and Mora (1960) identified the distal bracts as prophylls subtending the axillary continuation axis of the sympodial spikelet, while Schönland (1922), Blaser (1941), Levyns (1943, 1959), Leighton et al. (1947), Phillips (1951), Hamlin (1956), Schultze-Motel (1964), and Kern (1962) did not mention any prophyll structure in their description of sympodial spikelet structure.

On the other hand, the interpretation of spikelet structure in Schoeneae (or Rhynchosporeae) as racemose with a monopodial rachilla is preferred by many authors (Holttum, 1948;
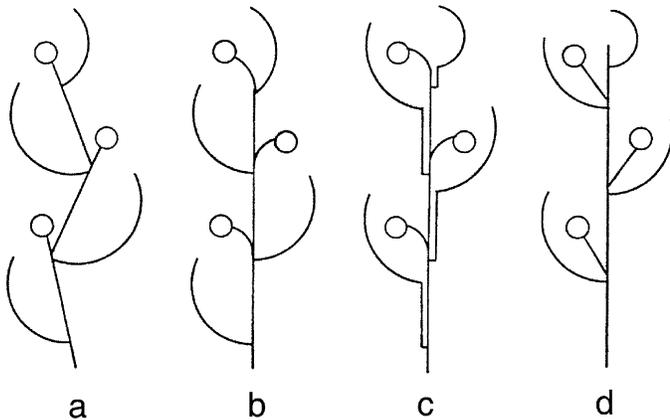
Fig. 1.   Schema of spikelet structure. a. Sympodial structure (rhipidium). b. Sympodial structure with straight ''rachilla,'' flowers displaced to a lateral position. c. Sympodial structure with ''rachilla'' internodes adnate to basal part of each subtending glume. d. Monopodial structure. (Adapted from Eiten, 1976, p. 87.)

Koyama, 1961; Haines, 1967; Raynal, 1971; Eiten, 1976; Haines and Lye, 1977; Kukkonen, 1986; Browning and Guthrie, 1994). They considered the spikelet structure of this tribe to be as follows: the flowers are lateral (they do not terminate the rachilla, which continues growing to produce further glumes and flowers), and each flower is situated in the axil of the subtending glume (i.e., between the glume and the rachilla) (Fig. 1d). These authors used different evidence to support this view. Holttum (1948, p. 535) stated that the two-keeled pro-phyll of *Asterochaete*, *Elynanthus*, and *Gahnia*, supposed by Pax to accompany the second flower, does not exist: ''Such a prophyll is normally present at the base of every branch in Cyperaceae and would be clear indication that branching had occurred . . . and in the absence of a prophyll there seems no evidence that branching occurred.'' Koyama (1961) proposed Rhynchosporoid-type spikelets (a reduced Scirpoid spikelet structure) for Rhynchosporeae (= Schoeneae), and the ar-rangement of glumes in the Scirpoid spikelet supported this interpretation as a racemose structure. The explanation of Haines (1967) was not based on the absence of prophylls. He explained that each flower was enwrapped by the winglike margins of the glume above in *Rhynchospora*, *Cladium*, and *Schoenus*. Haines and Lye (1977) also held the same view in *Trianoptiles*. Eiten (1976, pp. 87–88) supported the interpre-tation of the spikelet structure as racemose by her ''prelimi-nary observation that there is no anatomical evidence for re-caulescence and therefore sympodiality,'' i.e., ''the glumes are really on the same side of the rachilla as their flowers, ap-pearing to subtend them.'' Kukkonen (1986, p. 118) supported the view of a monopodial spikelet structure in Rhynchosporeae and argued that ''in the inflorescence of *Schoenus ferrugineus* the glume extends to the opposite side of the inflorescence axis, between the glume and flower, and embraces the flower as well as the axis.'' Browning and Guthrie (1994, p. 151) would not accept the spikelet structure in *Carpha* as cymose despite finding that spikelets in *Carpha* had the same structure as described by Levyns for the sympodial spikelet structure of *Trianoptiles* and *Epischoenus*. They interpreted ''the floret as occupying considerable space and appearing pseudo-terminal, making further rachilla growth possible only as a slightly elon-

gated extension that must curve to accommodate the expand-ing floret with its maturing fruit.''

How to distinguish the two types of spikelets in Schoeneae is a controversial issue. Mora (1960) stated that the decisive indication for cymose structure (the rachilla is sympodial) is a terminal flower at the apex of the rachilla. Racemose struc-ture (the rachilla is monopodial) lacks this terminal flower. Eiten (1976, p. 87) pointed out ''An apparent terminal position of a flower in the Cyperaceae is no indication that it really is so; rather, it may well be pseudoterminal, that is, lateral.''

Browning and Gordon-Gray (1995b) suggested that a more convincing explanation of spikelet structure should be sought. Based on their observations on *Rhynchospora gracillima* subsp. *subquadrata*, they considered the flowers not to be ax-illary to the glumes, yet they considered that an interpretation of sympodial construction for the spikelet was not acceptable. However, they did not pursue this issue further.

In this study, we address these controversial issues through a comparative study of spikelet structure in tribe Schoeneae. Our aims are to document and clearly describe spikelet struc-ture in Schoeneae and to resolve differing interpretations and clarify relevant concepts of spikelet structure in Schoeneae.

MATERIALS AND METHODS

Materials—We examined spikelets of 250 herbarium and fresh specimens (Appendix, see Supplemental Data accompanying the online version of this article) of 47 (of about 380–700) species in 15 (of 27–29) genera of Schoe-neae (Bruhl, 1995; Goetghebeur, 1998; see Zhang, 2002, for a review of Schoeneae). Specimens with many spikelets were chosen for examination (Appendix, see Supplemental Data accompanying the online version of this article). The number of spikelets examined varied from two to several for each specimen until the spikelet structure of the specimen could be unambig-uously determined. The herbarium specimens were from the following her-baria: B, BM, BOL, CANB, EA, HO, K, MEL, MO, NE, NSW, NU, NY, P, and PRE. Herbaria abbreviations follow Holmgren and Holmgren (1990). Fresh material was collected and fixed in FAA or FPA (Prakash, 1986) in the field in Australia (Kosciuszko National Park, the south coast of New South Wales, and National Parks in the New England region of NSW, and Tasmania). After a few weeks, material was transferred to Kew Mix (1% glycerine in 70% ethanol) for long-term preservation. Vouchers have been lodged at NE and NSW and replicate specimens distributed widely.

Dissection—Glumes were carefully removed from the proximal to the distal end of a spikelet under a Stemi 2000 Zeiss (Jena, Germany) or a Leica MZ75 (Heerbrugg, Switzerland) dissecting microscope. Spikelets from herbarium specimens were observed either directly or after softening in boiling water with a drop of detergent. Some dissections were stained with toluidine blue to assist in viewing.

Scanning electron microscopy—Spikelets from herbarium specimens, after removal of selected glumes and fruits, were mounted on stubs with double-sided tape, sputter-coated with gold using a Polaron E5100 coating unit (Wat-ford, England), and viewed with a JEOL JSM-5800LV (Tokyo, Japan) scan-ning electron microscope (SEM) at 15 kV. For species with rachillas that break easily if dissected directly, the spikelets were hydrated by boiling in water with a drop of detergent. After dissection, they were dehydrated using an ethanol dehydration series and mounted on stubs. Pickled material, after re-moval of selected glumes and fruits, was dehydrated using the same alcohol dehydration series, and then mounted on stubs. The SEM images were scanned to disk at high resolution, and electronic plates were constructed using Adobe Photoshop and Illustrator (San Jose, California, USA).

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Spikelet—A spikelet (e.g., Fig. 1) is usually defined as a small spike (typically the smallest repeated unit of an inflo-

rescence, unless the inflorescence is reduced to a single spikelet), that is, a racemosely branched structure consisting of an axis bearing lateral, sessile flowers each subtended by a bract (Lawrence, 1951; Eiten, 1976; Weberling, 1989; Harris and Harris, 1994; Kukkonen, 1994). As discussed earlier, the spikelet of Schoeneae has been interpreted as monopodial by some authors (Holttum, 1948; Koyama, 1961; Haines, 1967; Raynal, 1971; Eiten, 1976; Haines and Lye, 1977; Kukkonen, 1986) and as sympodial by others (Pax, 1886, 1887; Celakovský, 1887; Hamlin, 1956; Mora, 1960; Kern, 1962; Schultze-Motel, 1964). When the spikelet in Schoeneae is interpreted as a monopodial structure, it is a true spikelet as defined, but does not fit the definition when the spikelet is interpreted as a sympodial structure. However, most authors who interpreted the Schoeneae spikelet to be a sympodial structure still called it a spikelet (Levyns, 1943, 1959; Leighton et al., 1947; Phillips, 1951; Hamlin, 1956; Kern, 1962, 1974; Browning, 1994), although some used ''partial inflorescence,'' ''Scheinährchen'' (pseudospikelet), or ''spikelet'' (in quotes) (Pax, 1886, 1887; Celakovský, 1887; Schönland, 1922; Blaser, 1941; Schultze-Motel, 1964).

In this study, a spikelet is defined as the smallest inflorescence unit that is easily identified by the unaided eye, including both sympodial- and monopodial-branching structures. Spikelets with sympodial branching are called sympodial spikelets, and spikelets with monopodial branching are called monopodial spikelets.

Rachilla and "rachilla"—A rachilla is defined as ''a diminutive or secondary axis, or rachis'' (Lawrence, 1951, p. 767). In this study, monopodial spikelets have a single (simple) rachilla (Fig. 1d); sympodial spikelets have successive axes, resulting in a ''rachilla'' consisting of a succession of single rachillas or axes (Fig. 1a–c).

Glume—Most authors have used the term ''glume'' for parts of the spikelet in Cyperaceae, but Haines and Lye (1983) used both ''glume'' and ''scale'' to describe the spikelets of *Carpha* and its relatives, and Bruhl et al. (1992) and Bruhl (1995) used ''floral bracts'' in describing the spikelet in Cyperaceae. In this study ''glume'' is still used, in accordance with traditional usage in this family. To avoid including the spikelet bract as a glume (see Bruhl, 1995; Goetghebeur, 1998), ''glume'' in this study is defined as a small bract in the spikelet, including any proximal sterile and any distal empty ones, but not the bract subtending the spikelet.

Fertile glume—A glume that directly encloses or partly encloses an adjacent male, female, or bisexual flower, as indicated in Figs. 2–6.

Sterile glume—A glume that does not have a flower directly associated with it.

Basal shape of glumes—Most species observed have glumes with a typically slightly curved, more or less truncate base (see Fig. 4b). However, the fertile glumes in some species of *Schoenus* and in *Ptilothrix deusta* have an arch-shaped base (see Figs. 2b, c, 3c, 4c, 6; also see Browning and Gordon-Gray, 1995a, fig. 5).

Line of attachment and point of attachment—Line of attachment refers to a line on the node of rachilla/''rachilla''

where a glume grows/is attached. Point of attachment refers to a point on the node of rachilla/''rachilla'' where a flower grows/is attached.

Prophyll—The monocot prophyll, as seen in Cyperaceae, is defined as a foliar organ with two more or less equally developed main vascular bundles each with its own keel, rather than having the single main bundle and single keel seen in other bracts and glumes. When present, it is the first foliar organ on a lateral axis, that is, proximal on the lateral shoot, and it is adaxial to the lateral shoot (Haines, 1967; Kern, 1974; Haines and Lye, 1983; Bruhl et al., 1992; Kukkonen, 1994).

Bisexual flower—This refers to a flower in which both pistil and stamens develop.

Male flower—This refers to a flower with stamens but without a developed pistil.

RESULTS

Spikelet structure in Schoeneae can be classed as one of the 22 types illustrated in Fig. 7 according to the specimens examined (Appendix, see Supplemental Data accompanying the online version of this article). They differ in flower number (1–3(–5)), presence or absence of an empty uppermost glume and a proximal male flower, whether the ''rachilla'' is elongated or not, whether or not the base of each fertile glume is adnate to the ''rachilla'' above it, and whether a prophyll exists or not. All spikelets observed develop acropetally and are bisexual, having sessile (or very contracted stalk) flower(s) and several distichous to subdistichous glumes, with a few of the proximal glumes sterile (Figs. 2c, d, 3d, 4e, 5a–d, 6c–d, 7). Each fertile glume is on the opposite side of the ''rachilla'' from the point of attachment of its flower, encloses or partly encloses the ''rachilla'' and the flower (Figs. 2a–d, 3c, d, 4a, d, e, 5a–c, 6a–d) and subtends the new branch forming the next ''rachilla'' internode (Figs. 2a–d, 3c, d, 4a, d, e, 5a–c, 6a–d, 7) regardless of differences in spikelet type, i.e., the spikelet structure in the specimens examined is consistently sympodial.

In some species (*Carpha alpina*, *C. angustissima*, *C. borbonica*, *C. capitellata*, *C*. cf. *nitens*, *C. nitens*, *C. perrieri*, *Cyathochaeta avenacea*, *C. diandra*, *Cyathocoma hexandra*, *Mesomelaena graciliceps*, *Ptilothrix deusta*, *Schoenoides oligocephalus*, *Schoenus calostachyus*, *S. maschalinus*, *S. rhynchosporoides* and *S. turbinatus*), spikelets vary in flower number (Fig. 7; Appendix, see Supplemental Data accompanying the online version of this article), and this variation sometimes occurs on the same plant, such as in specimens of *Carpha alpina* (MEL 252110), *C. angustissima* (P 199386), *C. borbonica* (I. B. Balfour s.n.), *C. capitellata* (Drège 1840), *C*. cf. *nitens* (I. B. Balfour s.n.), *C. nitens* (C. Barclay 1920), *C. perrieri* (H. Humbert 6146), *Cyathocoma hexandra* (B. Sonnenberg 477), and *Schoenus rhynchosporoides* (R. Santesson 1224) (Fig. 7; Appendix, see Supplemental Data accompanying the online version of this article).

Whether spikelets have an empty uppermost glume or not is also variable within some species (*Carpha angustissima*, *C. borbonica*, *C. capitellata*, *C*. cf. *nitens*, *C. eminii*, *C. nitens*, *C. perrieri*, *C. schlechteri*, *C. schoenoides*, *Cyathochaeta clandestina*, *Cyathocoma hexandra*, *Schoenoides oligocephalus*, *Schoenus maschalinus*, *S. rhynchosporoides*, *Tetraria capil-*
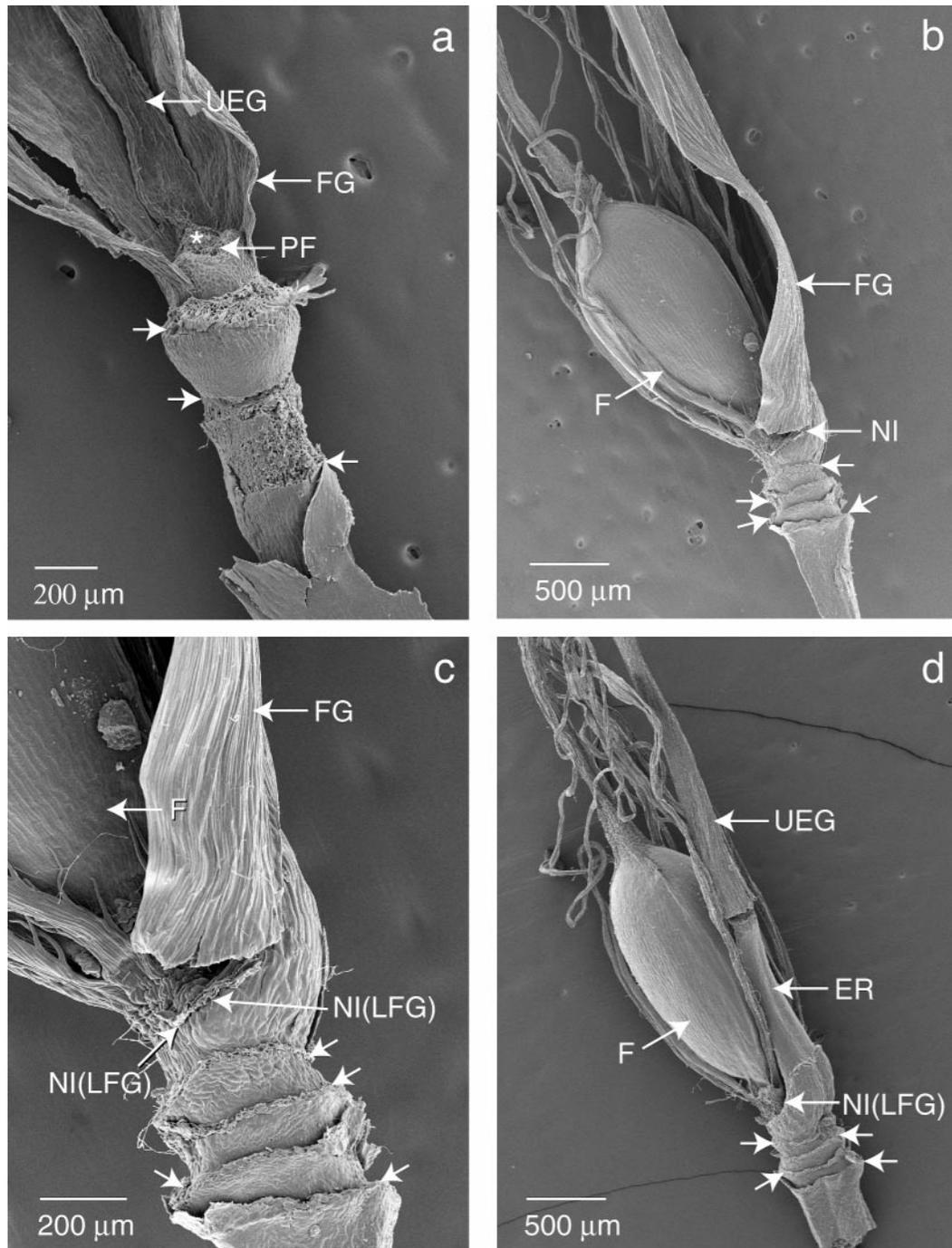
Fig. 2.   Scanning electron micrographs of spikelet structure in Schoeneae. a. *Carpha curvata* (HO 53801). Spikelet with four proximal sterile glumes (lines of attachment of three of these indicated by short arrows) and single terminal flower removed (PF, point of attachment). Fertile glume (FG) subtends the contracted axis (indicated by asterisk) that bears the empty uppermost glume (UEG, which is the unexpanded first leaf on a bud in the axil of FG). Line of attachment of FG is lower than the flower attachment point. FG encloses the internode and the flower. b–d. *Schoenus andinus* (S. Laegaard 12532). b. Spikelet with four proximal sterile glumes removed (lines of attachment indicated by short arrows). A flower (F, the arrow indicates the maturing nut and perianth bristles of F) with mature nut present terminates the main axis of the spikelet and is partly enclosed by the fertile glume (FG). A new "rachilla" internode arises between FG and F (hidden in Fig. 2b, but visible in Fig. 2d, ER). The fertile node is inclined (NI). c. Close-up of Fig. 2b. The line of attachment of FG (LFG) is lower than F, and FG has an obvious demarcation line from the "rachilla." The inclined fertile node (NI) makes the arch-shaped base of FG (only one side is visible here). d. FG removed (LFG, line of attachment) from a spikelet similar to that in Fig. 2b, c. FG subtends an elongated "rachilla" internode (ER), which grows between the FG and F. The empty uppermost glume (UEG) is borne distally on ER.
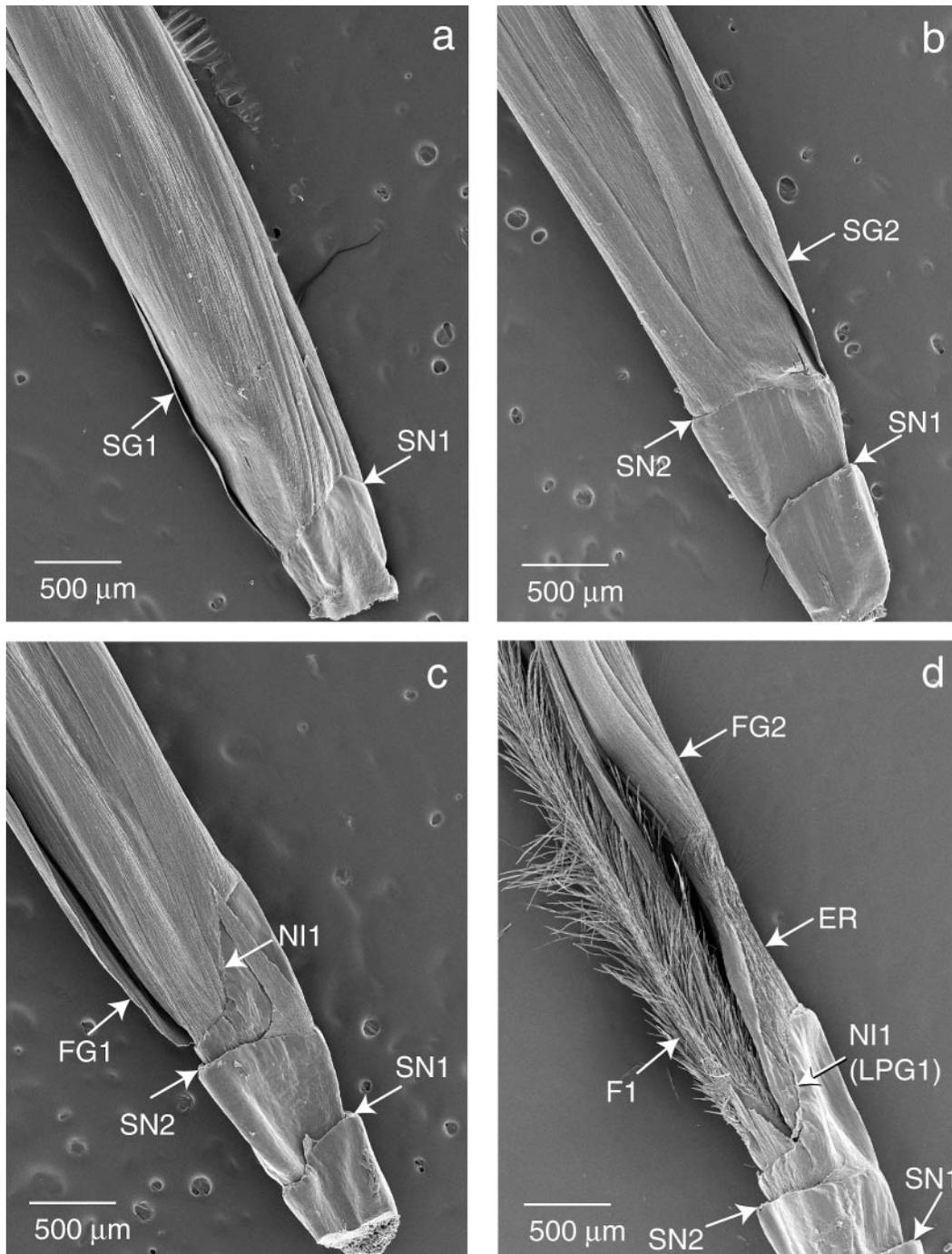
Fig. 3. Scanning electron micrographs of spikelet structure in Schoeneae. a–d. *Ptilothrix deusta* (X. Zhang 1). a. Lower half of a spikelet. SN1 indicates the first sterile node, attached to which is the proximal sterile glume (SG1; the arrow points to the left margin of this glume, which envelops the rest of the spikelet) with slightly curved, more or less truncate base (also see Fig. 4b). b. SG1 removed from a spikelet similar to that in Fig. 3a, showing SN2, the second sterile node. SG2 is the second sterile glume with slightly curved, more or less truncate base (seen more clearly in Fig. 4b). c. SG2 removed from a spikelet similar to that in Fig. 3b. NI1 indicates the inclined node (i.e., the proximal fertile node). FG1 is the proximal fertile glume with an arch-shaped base (seen more clearly in Fig. 4c). A torn remnant of SG2 is present on the right side of the spikelet, attached at SN2 and beneath the arrow for NI1. d. FG1 removed (LPG1, line of attachment) from a spikelet similar to that in Fig. 3c. Proximal flower (F1; the arrow indicates the plumose perianth bristles of this flower) terminates the main axis of the spikelet and is surrounded by FG1 (removed). A new elongated ''rachilla'' internode (ER) arises in the axillary position between FG1 and F1, and bears FG2, the distal fertile glume, at its apex.
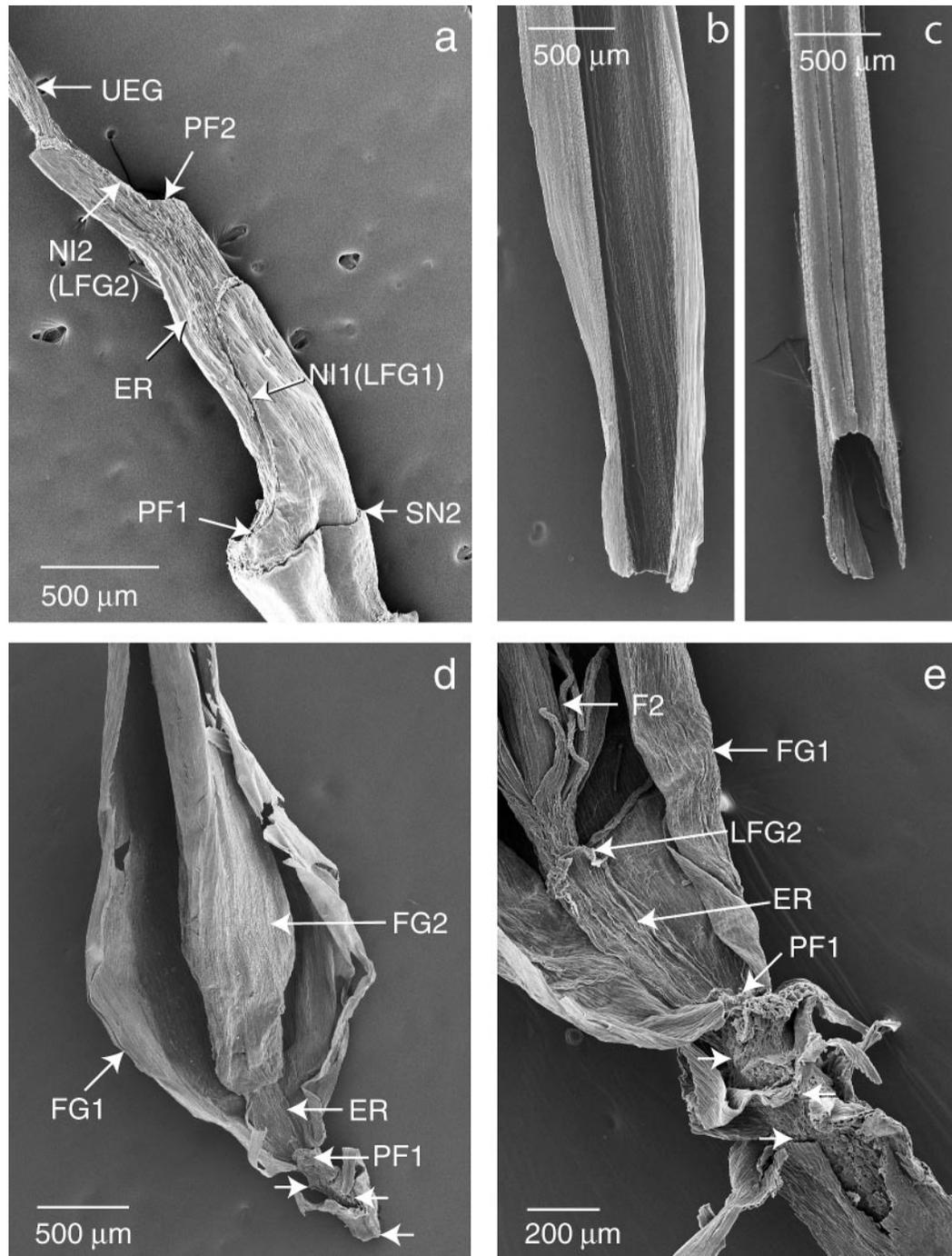
Fig. 4. Scanning electron micrographs of spikelet structure in Schoeneae. a–c. *Ptilothrix deusta* (X. Zhang 1). a. The distal fertile glume (LFG2, line of attachment) and distal flower (PF2, point of attachment) removed from a spikelet similar to, but much more developed than, that in Fig. 3d. The distal flower terminates the elongated "rachilla" internode (ER) and is surrounded by FG2. The next branch of the "rachilla" grows between FG2 and the distal flower and bears an empty uppermost glume (UEG). b. Adaxial view of a sterile glume to show slightly curved, more or less truncate base. c. Abaxial view of a fertile glume to show arch-shaped base. d, e. *Carpha bracteosa* (H. Bolus 2867). d. Spikelet with proximal sterile glumes (lines of attachment indicated by short arrows) and proximal flower (PF1, point of attachment) removed. The proximal flower terminates the main axis of the spikelet and is partly enclosed by the proximal fertile glume (FG1). A new elongated "rachilla" internode (ER) arises between FG1 and the proximal flower. The base of FG1 is partly adnate to ER. Line of attachment of FG1 is lower than the proximal flower. FG2 is the distal fertile glume. e. The distal fertile glume (LFG2, line of attachment) was removed from a spikelet similar to that in Fig. 4d to show the distal flower (F2) terminal on ER. NI1 = the proximal inclined node (i.e., the proximal fertile node); NI2 = the second inclined node (i.e., the second fertile node); LFG1 = the line of attachment of FG1; LFG2 = the line of attachment of FG2; SN2 = the second sterile node.
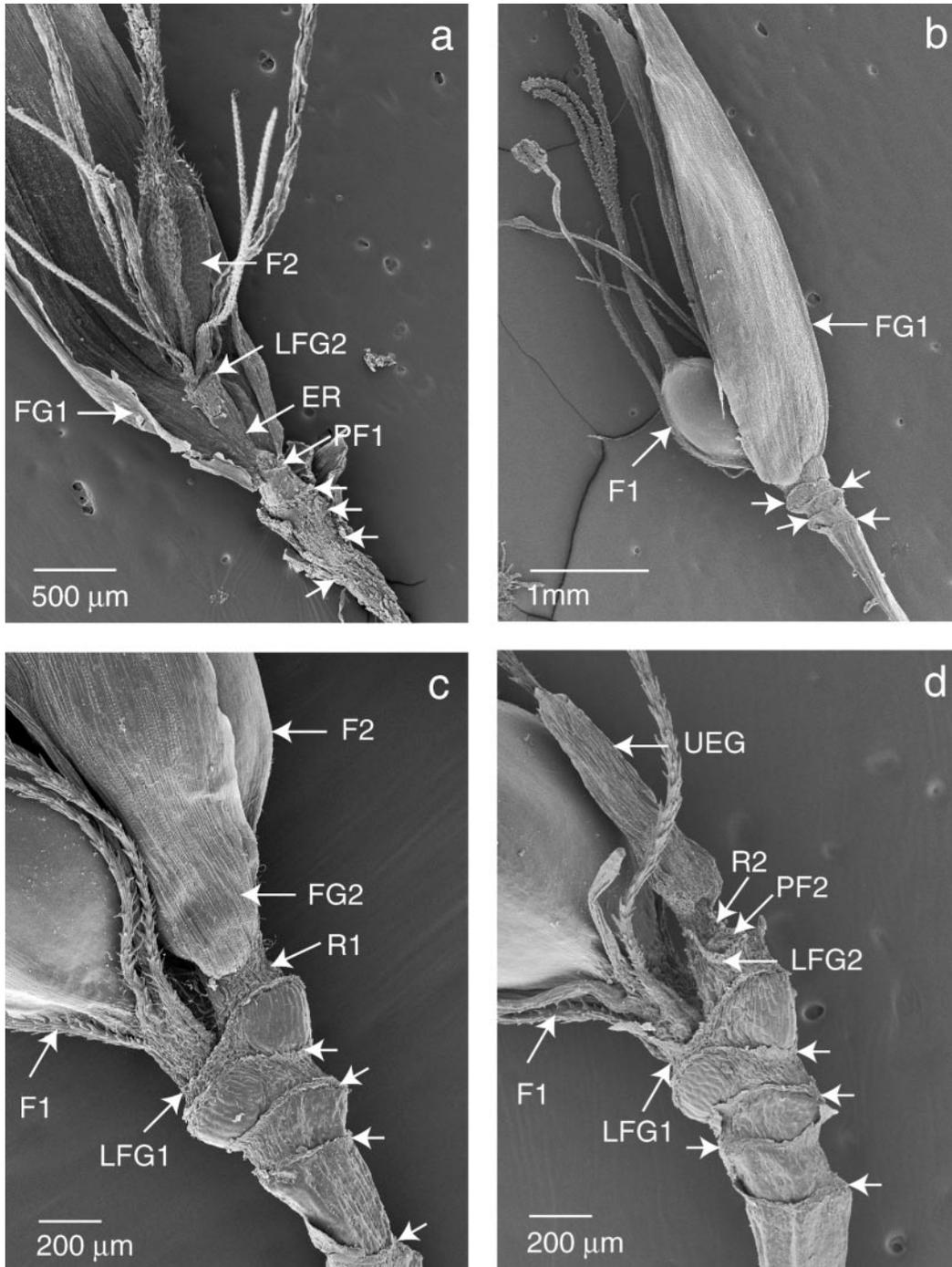
Fig. 5.   Scanning electron micrographs of spikelet structure in Schoeneae. a. *Carpha capitellata* (Levyns 8391). Spikelet with proximal sterile glumes (lines of attachment indicated by short arrows), proximal flower (PF1, point of attachment), and distal fertile glume (LFG2, line of attachment) removed. The proximal flower terminates the main axis of the spikelet and is enclosed by the proximal fertile glume (FG1). Line of attachment of FG1 is lower than the proximal flower. A new elongated ''rachilla'' internode (ER) arises between FG1 and the proximal flower and is adnate to the basal part of FG1. The distal flower (F2; arrow points to immature nut of F2) terminates ER and was enclosed by the distal fertile glume (LFG2, line of attachment of that glume). b–d. *Schoenus rhynchosporoides* (A. Hollermayer 1323). b. Spikelet with four proximal sterile glumes (lines of attachment indicated by short arrows) removed. Proximal flower (F1) terminates the main axis of the spikelet and is partly enclosed by the proximal fertile glume (FG1). Line of attachment of FG1 is lower than F1. c. The proximal fertile glume (FG1; LFG1, line of attachment) removed from a spikelet similar to that in Fig. 5b. The next ''rachilla'' internode (R1) grows between FG1 and F1. Distal flower (F2) terminates R1 and is partly enclosed by distal fertile glume (FG2). Line of attachment of FG2 is lower than F2. d. Distal fertile glume (FG2; LFG2, line of attachment) and distal flower (F2; PF2, point of attachment) removed from a spikelet similar to that in Fig. 5b, c. The branch forming the next ''rachilla'' internode (R2) grows between FG2 and F2 and bears an empty uppermost glume (UEG).
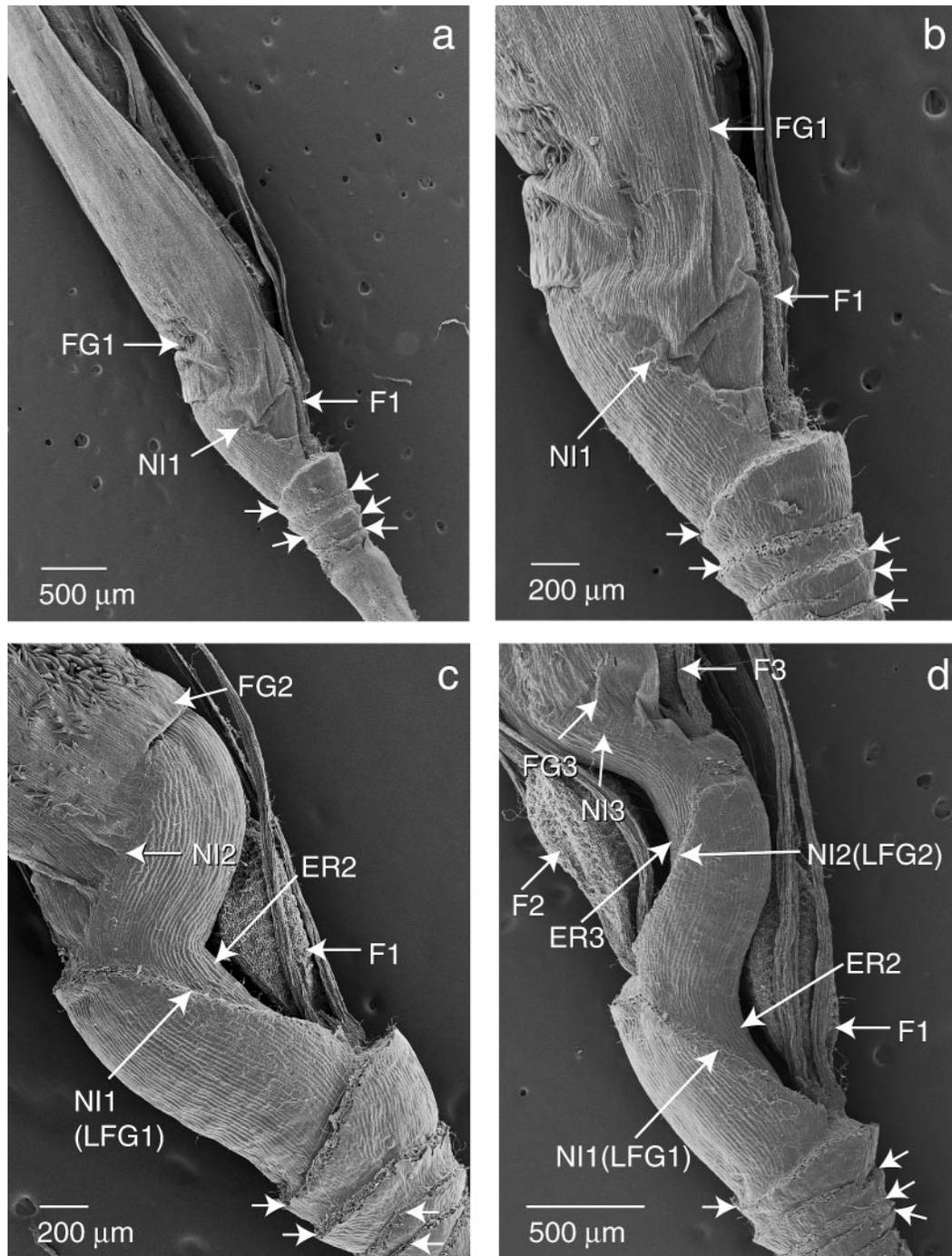
Fig. 6.   Scanning electron micrographs of spikelet structure in Schoeneae. a–d. *Schoenus brevifolius* (K. L. Wilson 9912). a. Spikelet with proximal sterile glumes (lines of attachment indicated by short arrows) removed. The lowest flower (F1) terminates the main axis of the spikelet and is partly enclosed by the lowest fertile glume (FG1). The lowest inclined node (NI1) makes the arch-shaped base of FG1 (half of the arch-shaped base of FG1 is visible here). b. Close-up of Fig. 6a; the lowest point of the line of attachment of FG1 is at the same level as F1 (arrow points to edge of immature nut and anther filaments of F1). c. The proximal fertile glume (FG1; LFG1, line of attachment) was removed from a spikelet similar to that in Fig. 6a. The next (second) "rachilla" internode (ER2) grows between FG1 and F1. The next higher (i.e., second) flower (here hidden by the second fertile glume, FG2) terminates ER2 and is enclosed by FG2. The next higher (second) inclined node (NI2) makes the arch-shaped base of FG2 (half of the arch-shaped base of FG2 is visible here). The lowest point of the line of attachment of FG2 is lower than the second flower. d. The second fertile glume (FG2; LFG2, line of attachment) removed from a spikelet similar to that in Fig. 6c. The next (third) "rachilla" internode (ER3) arises between FG2 and the second flower (F2). The third flower (F3) terminates ER3 and is partly enclosed by the third fertile glume (FG3). The lowest point of the line of attachment of FG3 is at the same level as F3. The third inclined node (NI3) makes the arch-shaped base of FG3 (half of the arch-shaped base of FG3 is visible here). The next (fourth) "rachilla" internode arises between FG3 and F3 (not visible here), i.e., the same branching pattern continues and usually ends with an empty glume after the fifth flower (see Fig. 7v).
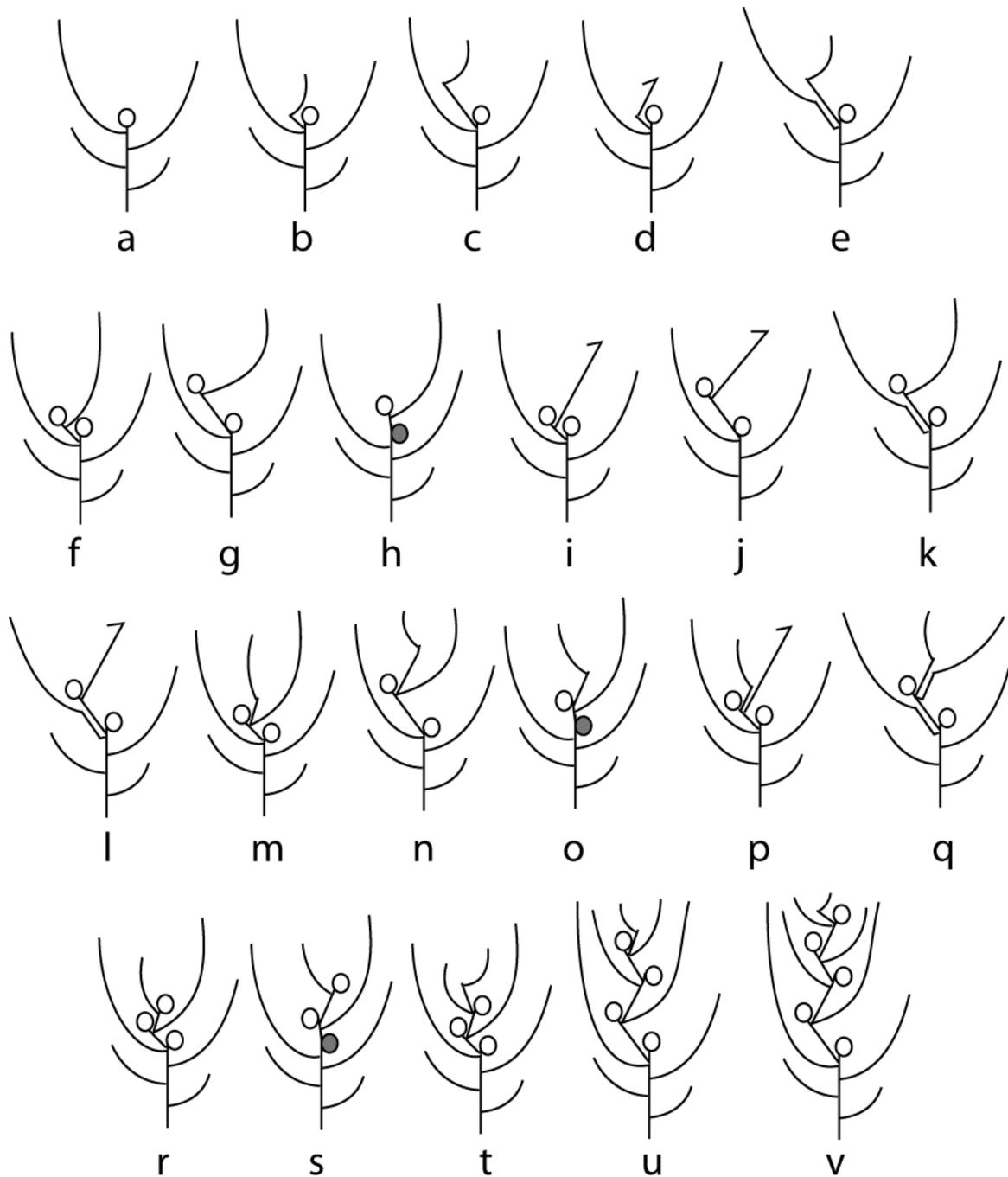
Fig. 7. Spikelet structure in Schoeneae. Open circle = a bisexual flower; filled circle = a male flower; hooked line = a prophyll; curved line = bract; curved line with straight base = bract with base adnate to internode (also see Fig. 1). a. Spikelet with one flower without an empty uppermost glume. b–e. Spikelet with one flower and an empty uppermost glume (or prophyll). b. "Rachilla" above the fertile glume not elongated. c. "Rachilla" above the fertile glume elongated. d. "Rachilla" above the fertile glume not elongated; spikelet with a prophyll at the apex. e. "Rachilla" above the fertile glume elongated and adnate to the base of the glume. f–l. Spikelet with two flowers and without an empty uppermost glume. f. "Rachilla" above the fertile glume not elongated. g. "Rachilla" above the fertile glume elongated. h. "Rachilla" straight and not elongated above proximal male flower. i. Spikelet with a prophyll subtending distal flower; "rachilla" not elongated above the fertile glume. j. Spikelet with a prophyll subtending distal flower; "rachilla" elongated above the fertile glume. k. "Rachilla" above the fertile glume elongated and adnate to the base of the glume. l. Spikelet with prophyll subtending distal flower; "rachilla" above the fertile glume elongated and adnate to the base of the glume. m–q. Spikelet with two flowers and an empty uppermost glume. m. "Rachilla" above the fertile glumes not elongated. n. "Rachilla" above the fertile glumes elongated. o. The "rachilla" straight and not elongated above the proximal male flower, but elongated above distal bisexual flower. p. Spikelet with a prophyll (partly) enclosing the distal flower. q. "Rachilla" above the fertile glumes elongated and adnate to the base of the glumes. r–s. Spikelet with three flowers and without an empty uppermost glume. r. "Rachilla" above the fertile glumes not elongated. s. "Rachilla" above the male flower (the lowest) is straight and not elongated, but elongated above the bisexual (second) flower. t. Spikelet with three flowers and an empty uppermost glume; "rachilla" above the fertile glumes not elongated. u–v. Spikelets with four and five flowers and an empty uppermost glume; "rachilla" above the fertile glumes elongated.

laris and *Tricostularia pauciflora*) (Fig. 7; Appendix, see Supplemental Data accompanying the online version of this article), and even on the same plant: *Carpha angustissima* (P 199386), *C. borbonica* (I. B. Balfour s.n.), *C. capitellata* (Drège 1840), *C.* cf. *nitens* (I. B. Balfour s.n.), *C. nitens* (M. J. E. Coode 4186; C. Barclay 1920), *C. perrieri* (H. Humbert 6146), and *Cyathocoma hexandra* (B. Sonnenberg 477) (Fig. 7; Appendix, see Supplemental Data accompanying the online version of this article).

The proximal portion of the ''rachilla'' (the part that carries the sterile glumes) is straight and stouter than the remainder of the ''rachilla'' (Figs. 2, 3d, 4a, d, e, 5 and 6c, d). The distal portion (the part that carries fertile glumes and the empty uppermost glume) is more or less curved (zigzag) except for any node on which a male flower occurs. If a node carries a male flower, the internode above that node lies in the same direction as the internode below it (Fig. 7h, o, s), which occurs consistently in *Capeobolus brevicaulis*, *Costularia pilisepala*, *Gahnia sieberiana*, *Gymnoschoenus sphaerocephalus*, and *Schoenus paludosus*, and occasionally in some specimens of other species: *Carpha schlechteri* (R. Schlechter 10010; M. R. Levyns 8098; J. Browning 823), *Cyathochaeta avenacea* (NSW 462122), *C. clandestina* (NE 66021), *C. diandra* (NE 66023, NE 72997, NSW 462124) (Fig. 7h, o, s; Appendix, see Supplemental Data accompanying the online version of this article).

In some species, the ''rachilla'' elongates above the nodes on which the bisexual flowers occur (Fig. 7c, e, g, j, k, l, n, o, q, s, u, v; Appendix, see Supplemental Data accompanying the online version of this article). These internodes are much longer than the lower internodes associated with the proximal sterile glumes. Such elongated ''rachilla'' internodes exist in *Carpha angustissima*, *C. borbonica*, *C. bracteosa* (Fig. 4d, e), *C. capitellata* (Fig. 5a), *C. filifolia*, *C. glomerata*, *C. nitens*, *C. perrieri*, *C. schlechteri* (B. Sonnenberg 458), *Ptilothrix deusta* (Figs. 3d, 4a), *Schoenus andinus* (Fig. 2d), *S. antarcticus*, some specimens of *S. maschalinus* (NSW 422022, NSW 247917), *S. calostachyus*, *S. brevifolius* (Fig. 6c, d), *Trianoptiles capensis*, *T. stipitata*, and *T. solitaria*. In other species, the ''rachilla'' does not elongate at all; internodes above the fertile glume(s) have almost the same length as internodes above the proximal sterile glume(s) (Figs. 2a, 5b–d, 7a, b, d, f, h, i, m, p, r, t; Appendix, see Supplemental Data accompanying the online version of this article).

Spikelet structures of some species of *Schoenus* (*Schoenus andinus*, *S. antarcticus*, *S. brevifolius*, *S. calostachyus*, and some specimens of *S. maschalinus*) and of *Ptilothrix deusta* are special. The proximal part of the ''rachilla'' (which carries sterile glumes), as in other species of Schoeneae examined here, is straight, and the glumes on it have a curved, more or less truncate base (Figs. 3a, b, 4b). However, the distal parts (which carry fertile glumes) elongate to produce a strongly zigzag ''rachilla,'' and result in inclined nodes and irregular shaped internodes. In turn, each inclined node results in the arch-shaped base of the glume that initiates at that node and subtends the next axillary internode and surrounds its flower on the opposite side of that internode (Figs. 2b–d, 3c, d, 4a, c, 6).

In spikelets of some species, the base of each fertile glume is adnate to the ''rachilla'' above it (Fig. 7e, k, l, q; Appendix, see Supplemental Data accompanying the online version of this article). This occurs in *Carpha angustissima*, *C. borbonica*, *C. bracteosa* (Fig. 4d, e), *C. capitellata* (Fig. 5a), *C. fil-*

ifolia, *C. glomerata*, *C. nitens*, *C. perrieri*, *C. schlechteri* (B. Sonnenberg 458), *Trianoptiles capensis* (BOL 63222), and *T. solitaria*.

A prophyll was seen in only a few of the spikelets observed. Only *Costularia elongata*, *Cyathocoma hexandra* (except R. Schlechter 10280, and C. J. Ward 1060; both have a bract with two obscure veins that seems like a prophyll), and *Schoenoides oligocephalus* (HO 47874, HO 60127 and HO 102690) have an obvious two-veined prophyll distal to the proximal fertile glume in the spikelet (Fig. 7d, i, p; Appendix, see Supplemental Data accompanying the online version of this article). The glume distal to the proximal fertile glume in the spikelet in *Carpha schoenoides* (MO 2150322; MO 1626156; D. M. Moore 1835; W. J. Eyerdam 10586A), *Tricostularia pauciflora*, *Trianoptiles capensis*, *T. stipitata*, and *T. solitaria* has two keels and two obscure veins, which we interpret as possibly a prophyll. We list two possible kinds of spikelet structure for these specimens in the Appendix (see Supplemental Data accompanying the online version of this article). If the distal organ is not interpreted as a prophyll, the first spikelet structure listed in each case would be the appropriate one; otherwise, the second structure is appropriate (Fig. 7d, i, j, l, p; Appendix, see Supplemental Data accompanying the online version of this article). All other species have no trace of a two-veined prophyll in the spikelets, in which all the glume(s) distal to the proximal fertile glume have only one keel (one vein) or are not keeled (no vein) at all. Moreover, no prophylls were found in any part of the inflorescences in most species of Schoeneae examined, such as in species of *Schoenus* and *Carpha* (except *C. schoenoides*).

In summary, the spikelets of Schoeneae develop acropetally. The ''rachilla'' is formed sympodially, that is, each flower is terminal on a ''rachilla'' internode and surrounded by its subtending glume. The next ''rachilla'' internode is axillary to the proximal fertile glume and is produced between that glume and its flower. The ''rachilla'' may then produce another terminal flower and the process may be repeated. The flower does not appear axillary to its glume but opposite it, with the ''rachilla'' internode between the two. Spikelets in Schoeneae can vary in the following ways:

- spikelets of some species vary in flower number within and between plants;
- the empty uppermost glume of some species may be present or absent within and between plants;
- a proximal male flower may be present or absent (when present, the internode above this male flower lies in the same direction as the internode below it);
- ''rachilla'' internodes above fertile glumes can be markedly elongated and/or adnate to the base of subtending fertile glumes; and
- a two-veined prophyll can be present or absent in spikelets.

DISCUSSION

Spikelets in Schoeneae are constructed sympodially, and flowers are terminal on each ''rachilla'' internode. In other words, the spikelet structure of Schoeneae is cymose, or more precisely, a rhipidium (scorpioid cyme), according to the inflorescence definition of, for example, Radford et al. (1974), Eiten (1976), Guédès (1979), and Bell (1991). The flowers in the spikelets have a very contracted stalk or are sessile (Figs. 2–6). All types of spikelet structures in Schoeneae (Fig. 7) can be derived simply by changing the flower stalks to short or

very short from a standard rhipidium (Fig. 1a–c). Monopodial spikelets in Schoeneae, as described by most of the current literature, including floras, were not found in this study.

Spikelet structures in Schoeneae are consistently sympodial rather than monopodial. Because they have strongly zigzag, elongated "rachillas" in the fertile distal part of their spikelets, species of *Schoenus* have often been chosen as an example to illustrate spikelet structure for Schoeneae (or Rhynchosporeae) in previous studies. Haines (1967) illustrated how each flower was enclosed by the winglike margins of the glume above in *Schoenus* and other genera. Kukkonen (1986, p. 118) also argued that "in the inflorescence of *Schoenus ferrugineus* the glume extends to the opposite side of the inflorescence axis, between the glume and flower, and embraces the flower as well as the axis." The arch-shaped base of fertile glumes in some species of *Schoenus* has also been described as decurrent on the rachilla (Holttum, 1948; Kern, 1974). These descriptions are contradicted by the fact that the fertile glume is on the opposite side of the "rachilla" from the point of attachment of its flower and subtends a new branch forming the next "rachilla" internode. The actual line of glume attachment to the "rachilla" is below, or at least at the same level as, the point of attachment of its flower on the opposite side of the "rachilla" (Figs. 2, 3, 4a, d, e, 5, 6 and 7). In species of *Schoenus*, there are two types of "rachilla." In one type, the "rachilla" above the fertile glumes does not elongate (Figs. 7a, b, f, m, o, t; Appendix, see Supplemental Data accompanying the online version of this article), for example in *S. rhynchosporoides* (Fig. 5b–d). Here the "rachilla" internode above a fertile glume is between the fertile glume and its flower, and the lines of attachment of the two fertile glumes are lower than the point of attachment of the flowers subtended by them respectively. The other type is where the "rachilla" internode above a fertile glume elongates strongly (Fig. 7c, g, n, u, v; Appendix, see Supplemental Data accompanying the online version of this article) and fertile nodes are inclined, such as in *S. andinus* (Fig. 2b–d) and *S. brevifolius* (Fig. 6). The shape of the inclined nodes leads to the glumes initiated on them having an arch-shaped base. The lowest point of the line of glume attachment to the "rachilla" is below, or at least at the same level as, the point of attachment of its flower on the opposite side of the "rachilla." Another genus that has fertile glumes with an arch-shaped base is the monotypic genus *Ptilothrix*. In *P. deusta*, the "rachilla" is elongated above the fertile glume, the fertile nodes are inclined, and the glumes that are attached to these inclined nodes have an arch-shaped base (Figs. 3c, 4c). The lowest point of the line of glume attachment to the "rachilla" is below the point of attachment of its flower on the opposite side of the "rachilla" (Figs. 3c, d, 4a). All the other genera had the line of glume attachment to the "rachilla" below the point of attachment of its flower on the opposite side of the "rachilla" (Figs. 2a, 4d, e, 5a, 7). These results are supported by the independently derived illustrations of Celakovský (1887) for *Schoenus*, Blaser (1941) for *Rhynchospora macrostachya*, Levyns (1943) for *Trianoptiles*, Leighton et al. (1947) and Levyns (1959) for *Epischoenus*, Browning (1994) for *Costularia*, Browning and Guthrie (1994) for *Carpha*, and Browning and Gordon-Gray (1995a, b) for *Epischoenus*, *Schoenus*, and *Rhynchospora gracillima* subsp. *subquadrata*, and by the developmental work of Mora (1960) for *Cladium* and *Schoenus*, and Richards (2002) for *Cladium*.

Browning and Guthrie (1994) and Browning and Gordon-

Gray (1995a, b), however, could not accept the spikelet structure as cymose, although their diagram (1994, fig. 1A, E) clearly shows that the spikelet structure is cymose and its "rachilla" is best interpreted as sympodial. Browning and Gordon-Gray (1995a, p. 150) also concluded that flowers in *Epischoenus* and *Schoenus* are nonaxillary, and wondered "if the bisexual floret does indeed terminate the spikelet rachilla, why should the functionally male florets in *Epischoenus* appear so markedly laterally placed in relation to the rachilla, and why should the rachilla appear to continue growth directly, without evidence of growth of a branch of succeeding order?" Later Browning and Gordon-Gray (1995b) suggested that a more convincing explanation should be sought because they considered the flowers not to be axillary to the glumes, but that an interpretation of sympodial construction for the spikelet was not acceptable for *Rhynchospora gracillima* subsp. *subquadrata*.

If each glume is positioned on the opposite side of the "rachilla" from the point of attachment of its flower (Fig. 1a–c), the spikelet structure is best interpreted as sympodial. In a monopodial structure, the glumes are on the same side of the rachilla as the points of attachment of their flowers (Fig. 1d) (Eiten, 1976). If the flower is not axillary to the glume, it must be terminal to the "rachilla," and the "rachilla" develops sympodially. The illustrations of Browning (1994, p. 654, figs. B, C, D) for *Costularia*, Browning and Guthrie (1994, p. 150, fig. 1) for *Carpha*, and Browning and Gordon-Gray (1995a, p. 151, fig. 6; 1995b, p. 321, figs. 2, 3) for *Epischoenus*, *Schoenus*, and *Rhynchospora* clearly show that each flower is not axillary to its glume; each fertile glume is on the opposite side of the "rachilla" from the point of attachment of its flower and subtends a new branch forming the next "rachilla" internode. Thus, the spikelets have a sympodial structure, and the bisexual flowers and the male flowers terminate the spikelet "rachilla" internodes. If the spikelets were racemose, flowers should be in the axils of glumes and between the glume and axis, i.e., the flowers should be on the same side of the rachilla as the glumes subtending them (Fig. 1d). However, they are not. A spikelet must be constructed in one of two ways, i.e., either monopodial or sympodial, depending on whether the position of each new distal shoot unit is apical or axillary (Bell, 1991).

In Schoeneae, when a proximal male flower is present, the internode above this male flower lies in the same direction as the internode below it (Fig. 7h, o, s). It is not difficult to understand why sympodial structure can have some flowers appearing so markedly laterally placed in relation to the "rachilla." In some sympodial inflorescences, the consecutive branches are constructed more or less in the direction of the main axis, and their respective terminal flowers are pushed to the side, creating a superficial impression of a monopodial axis with flowers developing from an axillary position (Weberling, 1989). Bell (1991) gave *Fremontodendron californica* as an example of this phenomenon.

Browning and Gordon-Gray (1995a, p. 150) explained the arch-shaped base of fertile glumes in some species of *Schoenus* as resulting from "drying of the rachilla following fruit maturation [so that] there is tearing away from the main body of the glume, of the portion that was adnate to the rachilla, causing the arch-shaped hole and leaving the two lateral strips attached to the node from which the glume developed." However, no evidence of glumes being adnate to the "rachilla" from which they originate and subsequently causing their arch-

shaped bases was found in species of *Schoenus* observed in the present study. The nodes associated with the flowers that are functionally bisexual incline in some species of *Schoenus*, and the glumes growing on them have an obvious demarcation line from the "rachilla" (Figs. 2c, 6). That these glumes have an arch-shaped base is only because they grow on the inclined nodes and match the shape of the node. This is also seen in *Ptilothrix* (Figs. 3c, d, 4a, c).

In some species in tribe Schoeneae, the basal part of the fertile glumes is adnate to the next internode (Figs. 4d, e, 5a, 7e, k, l, q). This was previously observed by Levyns (1943) in *Trianoptiles solitaria*. That the basal part of the fertile glumes is adnate to the next internode is evidence that the new branch (or next "rachilla" internode) arises in the axil of the glume (i.e., it is sympodial in structure).

Using prophyll presence or absence to determine inflorescence type is not reliable. Spikelets of some species have a prophyll and/or prophyll-like structures distal to the proximal fertile glume (Fig. 7d, i, j, l, p; Appendix, see Supplemental Data accompanying the online version of this article). This result is supported by previous findings of Pax (1886) in *Elynanthus*, Mora (1960) in *Cladium*, and Browning (1994) in *Costularia*. Such a prophyll was also reported in *Asterochaete* (Pax, 1886), *Gahnia* (Pax, 1886), and *Schoenus* (Celakovský, 1887; Pax, 1887; Mora, 1960), but it was not found in our sample of *Asterochaete* (= *Carpha p.p.*), *Gahnia* or *Schoenus* in this study. No prophylls were found in spikelets of many species of Schoeneae (Fig. 7; Appendix, see Supplemental Data accompanying the online version of this article) in this study. Sometimes prophylls do not exist anywhere in the whole inflorescence. This has been previously reported by Haines (1967) and Bruhl (1995). Holttum (1948) considered the existence of a prophyll as a criterion to judge whether branching occurred. This opinion cannot be accepted due to the following points. Firstly, the prophyll is highly reduced in spikelets and inflorescences of some genera in Cyperaceae. Many species in Schoeneae do not have prophylls in the spikelets (Fig. 7; Appendix, see Supplemental Data accompanying the online version of this article) although their spikelets are sympodial in structure. Secondly, Blaser (1944) indicated that "prophyll" is only a leaf with various modifications and occasionally distinguished by its apparent position, and the extreme reduction and specialization of all organs of leaf-rank in inflorescences makes the distinction of prophylls and bracts difficult or impossible. In fact, it is obvious that to distinguish a two-veined prophyll from a glume does not help to determine spikelet structure at all in Schoeneae.

Mora (1960) stated that the decisive indication for cymose structure (sympodial) or racemose structure (monopodial) is whether the spikelet has a terminal flower at its apex or not, respectively. This was applied by Browning (1994). However, the results of this study show that this criterion is not reliable for deciding spikelet types and flower position (lateral or terminal) on the rachilla/"rachilla." From Figs. 2a, d, 4a, d, e, 5a, d, and 7, it is apparent that these "rachillas" are sympodial and flowers are terminal, regardless of whether the "rachilla" has a terminal flower at its apex or not. In Schoeneae the spikelets develop acropetally. Sometimes in a species and even in the same plant, some spikelets have an empty uppermost glume while others do not (Fig. 7; Appendix, see Supplemental Data accompanying the online version of this article). So whether an apical flower is present or not cannot be used to decide whether the spikelet is sympodial or monopodial.

For the inflorescence whose monopodial or sympodial nature is not obvious, careful scrutiny of the relative position of flowers, bracts, and axis is necessary to judge inflorescence type (Bell, 1991). This is the case in the Cyperaceae where the inflorescence units (spikelets) are extremely contracted. If each glume is on the opposite side of the axis from the point of attachment of its flower (Fig. 1a–c), the spikelet structure is best interpreted as sympodial. If the glumes are on the same side of the axis as the points of attachment of their flowers, the spikelet structure is monopodial (Fig. 1d) (Eiten, 1976).

Because of the extremely contracted spikelet rachilla/"rachilla" in Cyperaceae, the same controversial issues regarding spikelet structure also exist in other tribes. For example, Eiten (1976) considered the spikelet of tribes Cypereae and Scirpeae had a racemose structure, while Schultze-Motel (1964) thought their spikelets were cymose. Kern (1974, p. 446) once wrote "the structure of the spikelets is in all Cyperaceae probably sympodial," while other authors (Raynal, 1971; Eiten, 1976; Haines and Lye, 1983; Goetghebeur, 1998) held different views. Therefore, spikelet structure in other tribes of Cyperaceae needs to be reinvestigated before any definitive statement can be made about spikelet structure in the whole family.

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