

Chapter 2 Sympodial Structure of Spikelets in the Tribe Schoeneae (Cyperaceae)

2.1 Introduction

The branching pattern of spikelets, an important character in determining systematic arrangements within Cyperaceae, has received considerable attention. The spikelets, however, are extremely contracted and the internodes very slightly developed, leading to different interpretations of spikelet morphology in Cyperaceae, especially in the tribe Rhynchosporeae (or Schoeneae) (Pax 1886, 1887; Celakovský 1887; Holttum 1948; Hamlin 1956; Koyama 1961; Kern 1962, 1974; Schultze-Motel 1964; Haines 1967; Raynal 1971; Eiten 1976; Haines and Lye 1977, 1983; Kukkonen 1986; Browning and Guthrie 1994), and consequently different classificatory solutions. For example, Rhynchosporeae was placed in the same subfamily as Scirpeae by Bentham (1883), but Pax (1887) removed it to the different subfamily Caricoideae on account of the sympodial structure of the spikelet. Later, Schultze-Motel (1964) considered the spikelets of the tribe 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 Hofmeister (1868, after Weberling 1989), it has been customary to classify inflorescences as racemes (racemose inflorescences) or as cymes (cymose inflorescences) based on a distinction between monopodial or sympodial construction (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 divided into 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.

2.1 a–c). This type of inflorescence is also called a scorpioid cyme (Radford et al. 1974; Eiten 1976).

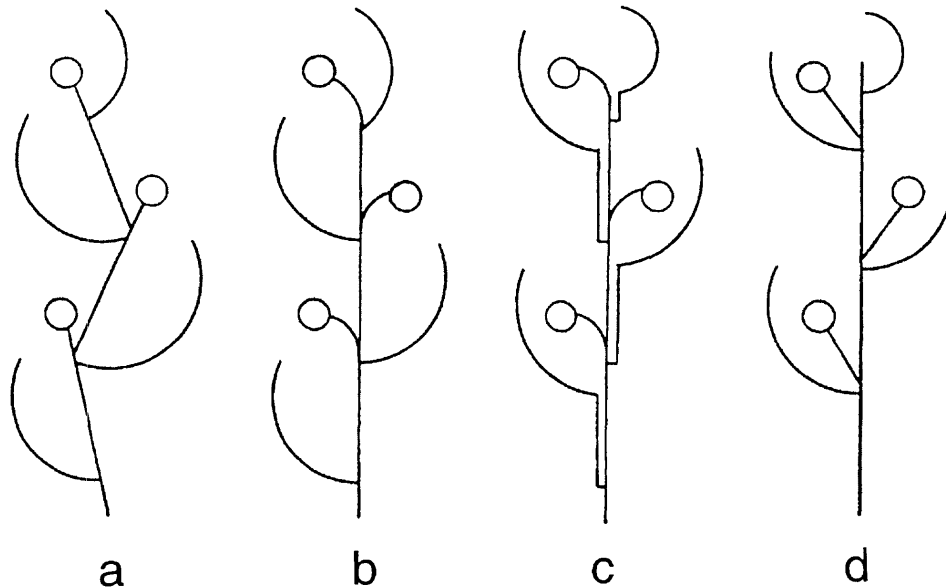


Fig. 2.1. Sympodial and monopodial spikelet structure. **a**, Sympodial structure (rhipidium). **b**, Sympodial structure with straight ‘rachilla’. **c**, Sympodial structure with ‘rachilla’ internodes adnate to basal part of each subtending glume. **d**, Monopodial structure. (Adapted from Eiten 1976, p. 87).

That the spikelet structure in tribe Schoeneae (or Rhynchosporeae) is cymose and its rachilla is sympodial was first proposed by Pax (1886, 1887) and supported by some later authors (Celakovský 1887; Hamlin 1956; Kern 1962; Schultze-Motel 1964). They interpreted the spikelet structure of Schoeneae (or Rhynchosporeae) 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. 2.1. a–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 by Blaser (1941) for *Rhynchospora macrostachya*, by Mora (1960) for *Cladium* and *Schoenus*, by Schönland (1922) for the Schoeneae of Clarke (1908), by Levyns (1943) and Phillips (1951) for *Trianoptiles*, by Leighton et al. (1947) and Levyns (1959) for *Epischoenus*, and by Browning (1994) for

Costularia. In this view, Pax (1886, 1887), Celakovský (1887) and Mora (1960) identified the more distal bracts as prophylls subtending the inflorescence axis with flowers on the opposite side, 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 other authors (Holtum 1948; Koyama 1961; Haines 1967; Raynal 1971; Eiten 1976; Haines and Lye 1977; Kukkonen 1986; Browning and Guthrie 1994). They considered the spikelet structure of Rhynchosporeae (including Schoeneae) as follows: the flowers do not terminate the rachilla and the rachilla continues growing to produce further glumes and flowers, and each flower is situated in the axil of the subtending glume, that is, between the glume and the rachilla (Fig. 2.1 d). They used different evidence to support this view. Holtum (1948, p. 535) stated that the two-keeled prophyll 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, and the arrangement of the glumes in the Scirpoid spikelet supported the interpretation of a racemose spikelet structure. The explanation of Haines (1967) was not based on non-prophyll bracts. He explained that each flower was enwrapped by the wing-like 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 interpretation of the spikelet structure as racemose by her 'preliminary observation that there is no anatomical evidence for recaulescence and therefore sympodality', i.e. 'the glumes are really on the same side of the rachilla as their flowers, appearing 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) could not accept the cymose spikelet structure in *Carpha* and interpreted 'the floret as occupying considerable space and appearing pseudo-terminal, making further rachilla growth possible only as a slightly elongated

extension that must curve to accommodate the expanding floret with its maturing fruit', although they found that spikelets in *Carpha* showed the same picture as the description by Levyns for the sympodial spikelet structure of *Trianoptiles* and *Epischoenus*.

How to judge the two inflorescence types? Mora (1960) stated that the decisive indication for cymose structure (the rachilla is sympodial) or racemose structure (the rachilla is monopodial) is that the rachilla has a terminal flower at its apex in the former but not in the latter. Eiten (1976, p 87) pointed out the weakness of Mora's criterion and stated that '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.'

Besides the two main views above, a third interpretation was proposed by Meeuse (1975) on the basis of his Anthocorm theory. He considered that occurrence of both cymose and racemose part-inflorescences in the Scirpoideae (he adopted the classification of Schultze-Motel 1964, in which the subfamily Scirpoideae includes all the genera in the tribes Rhynchosporae and Schoeneae) as reported by some workers to be highly improbable. This was the philosophical framework adopted by Goetghebeur (1986; see also Bruhl 1991).

Browning and Gordon-Gray (1995a, 1995b) also suggested that a more convincing explanation should be sought because they considered that the flowers are not axillary to the glumes, and an interpretation of sympodial construction for the spikelet is not acceptable based on their observations on *Epischoenus*, *Schoenus* and *Rhynchospora gracillima* ssp. *subquadrata*. However, they did not pursue this issue further.

In this study, I seek to address these controversial issues to understand the spikelet structure in the tribe Schoeneae. The aims are to:

- reveal and understand spikelet structure in Schoeneae; and
- clarify differing interpretations and some relevant concepts of spikelet structure in Schoeneae.

2.2 Materials and Methods

2.2.1 Materials

I examined spikelets of 250 herbarium and fresh specimens (Table 2.1) of 47 species in 15 genera of Schoeneae of Bruhl (1995). The herbarium specimens were from the following herbaria: 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 (Kosciuszko National Park, the South Coast of NSW, 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.

2.2.2 Dissection

Glumes were carefully removed from the proximal to the distal end under a Stemi 2000 Zeiss or a Leica MZ75 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.

2.2.3 Scanning Electron Microscopy

Spikelets from herbarium specimens, after removal of selected glumes and fruit(s), were mounted on stubs using double-sided tape, sputter-coated with gold using a coating unit E5100, and viewed under a JEOL JSM-5800LV scanning electron microscope (SEM) at 15 kV. For some species whose rachillas are easily broken 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 (each step for 5 to 10 minutes: 70% → 70% → 80% → 80% → 80% → 90% → 90% → 90% → 95% → 95% → 95% → 100% → 100% → 100%) and then mounted on stubs. Pickled material, after removal of selected glumes and fruit(s), was dehydrated using the same alcohol dehydration series, and then mounted on stubs.

Table 2.1. Spikelet structure and voucher information for the 250 specimens of Schoeneae studied. Herbarium abbreviation and sheet number, the first collector and collection number are given; type specimens are in bold; “or” indicates some uncertainty; and “—” indicates the absence of information. See Fig. 2.2 for explanation of spikelet structure.

Species	Herbarium abbreviation & number	Collector & number	Spikelet structure
<i>Capeobolus brevicaulis</i>	NE 80079	J. J. Bruhl 1720	h
<i>Capeobolus brevicaulis</i>	NE 80081	J. J. Bruhl 1736	h
<i>Carpha alpina</i>	BM 000092170	R. Brown 6020	b
<i>Carpha alpina</i>	BM 000092173	J. D. Lovis 1077	b
<i>Carpha alpina</i>	BM 000092174	J. D. Lovis 931	b
<i>Carpha alpina</i>	CANB 107745	R. Schodde 1827	b
<i>Carpha alpina</i>	CANB 147508	T. G. Hartley 12996	b
<i>Carpha alpina</i>	CANB 183330	M. M. J. v. Balgooy 88	b
<i>Carpha alpina</i>	CANB 241321	G. Hope ANU10766	b
<i>Carpha alpina</i>	HO 125977	A. Moscal 1376	b
<i>Carpha alpina</i>	HO 143800	A. Moscal 10336	b
<i>Carpha alpina</i>	HO 24161	W. M. Curtis <i>s.n.</i>	b
<i>Carpha alpina</i>	HO 24169	E. Rodway <i>s.n.</i>	b
<i>Carpha alpina</i>	HO 328073	A. M. Gray 676	b
<i>Carpha alpina</i>	HO 409964	A. M. Buchanan 13611	b
<i>Carpha alpina</i>	HO 411185	S. J. Jarman <i>s.n.</i>	b
<i>Carpha alpina</i>	K <i>s.n.</i>	T. G. Hartley 12996	b
<i>Carpha alpina</i>	MEL 2066107	T. Kirk <i>s.n.</i>	b
<i>Carpha alpina</i>	MEL 252110	J. Goodger J63	b, f
<i>Carpha alpina</i>	MEL 49294	R. Brown <i>s.n.</i>	b
<i>Carpha alpina</i>	MEL 522763	J. H. Willis <i>s.n.</i>	b
<i>Carpha alpina</i>	MEL 658311	S. J. Forbes 1399	b
<i>Carpha alpina</i>	MEL 693734	R. J. Adair 1620	b
<i>Carpha alpina</i>	NE 70799	K. L. Wilson 6643	b
<i>Carpha alpina</i>	NE 70800	K. L. Wilson 6312	b
<i>Carpha alpina</i>	NE 71803	J. J. Bruhl 1878A	b
<i>Carpha alpina</i>	NE 71826	J. J. Bruhl 1886	b
<i>Carpha alpina</i>	NE 71849	J. J. Bruhl 1897B	b
<i>Carpha alpina</i>	NSW 462089	E. H. Norris 356	b
<i>Carpha alpina</i>	NSW 462091	J. Thompson 2947	b
<i>Carpha alpina</i>	NSW 462093	L. A. S. Johnson 7566	b
<i>Carpha alpina</i>	NSW 462094	C. B. Trevarthen <i>s.n.</i>	b
<i>Carpha alpina</i>	NSW 462095	R. Melville 6372	b
<i>Carpha alpina</i>	NSW 462097	J. Croft LAE62353	b
<i>Carpha alpina</i>	NSW 462100	P. Goetghebeur 3544	b
<i>Carpha angustissima</i>	B 100000959	H. Humbert 8586	k
<i>Carpha angustissima</i>	B 100000961	H. Humbert 7722	k
<i>Carpha angustissima</i>	EA <i>s.n.</i>	J. W. Purseglove 2199	k
<i>Carpha angustissima</i>	EA <i>s.n.</i>	K. A. Lye 5289	k
<i>Carpha angustissima</i>	K <i>s.n.</i>	A. B. Katende K207B	k
<i>Carpha angustissima</i>	K <i>s.n.</i>	H. U. Stauffer 793	k
<i>Carpha angustissima</i>	K <i>s.n.</i>	J. W. Purseglove P2199	k
<i>Carpha angustissima</i>	K <i>s.n.</i>	K. A. Lye 5289	k
<i>Carpha angustissima</i>	P 00199386	G. Troupin 14282	e, k

Table 2.1. (Continued)

Species	Herbarium abbreviation & number	Collector & number	Spikelet structure
<i>Carpha borbonica</i>	K <i>s.n.</i>	I. B. Balfour <i>s.n.</i>	e, k
<i>Carpha bracteosa</i>	K <i>s.n.</i>	H. Bolus 2867	k
<i>Carpha bracteosa</i>	K <i>s.n.</i>	P. N. Parker <i>s.n.</i>	k
<i>Carpha bracteosa</i>	K <i>s.n.</i>	R. Schlechter 8970	k
<i>Carpha bracteosa</i>	NU <i>s.n.</i>	H. C. Taylor 5988	k
<i>Carpha bracteosa</i>	PRE <i>s.n.</i>	E. E. Esterhuysen 10611	k
<i>Carpha bracteosa</i>	PRE <i>s.n.</i>	H. C. Taylor 5220	k
<i>Carpha bracteosa</i>	PRE <i>s.n.</i>	P. v. d. Merwe 1199	k
<i>Carpha capitellata</i> (syntype of <i>Asterochaete tenuis</i>)	K <i>s.n.</i>	Drège 1840.	e, k
<i>Carpha capitellata</i> (syntype of <i>Asterochaete tenuis</i>)	K <i>s.n.</i>	Drège 1840	e, k
<i>Carpha capitellata</i>	K <i>s.n.</i>	H. G. Flanagan 920	k
<i>Carpha capitellata</i>	K <i>s.n.</i>	H. G. Fourcade 4476	k
<i>Carpha capitellata</i>	K <i>s.n.</i>	Levyns 8391	k
<i>Carpha capitellata</i>	MEL 1543862	L. MacOwan 351	k
<i>Carpha capitellata</i>	NU <i>s.n.</i>	E. A. Robinson 1976	k
<i>Carpha capitellata</i>	NU <i>s.n.</i>	H. Getliffe 56	k
<i>Carpha capitellata</i>	PRE <i>s.n.</i>	C. Reid 1807	k
<i>Carpha capitellata</i>	PRE <i>s.n.</i>	J. P. H. Acocks 23507	k
<i>Carpha capitellata</i>	PRE <i>s.n.</i>	M. F. Thompson 2282	k
<i>Carpha cf. bracteosa</i> (syntype of <i>Carpha bracteosa</i>)	K <i>s.n.</i>	L. MacOwan 1616	k
<i>Carpha cf. bracteosa</i> (syntype of <i>Carpha bracteosa</i>)	K <i>s.n.</i>	L. MacOwan 2187	k
<i>Carpha cf. bracteosa</i>	K <i>s.n.</i>	R. Storey 36820	k
<i>Carpha cf. bracteosa</i>	NE 66170	B. Sonnenberg 301	k
<i>Carpha cf. bracteosa</i>	NU <i>s.n.</i>	B. Sonnenberg 301	k
<i>Carpha cf. bracteosa</i>	NU <i>s.n.</i>	B. Sonnenberg 336	k
<i>Carpha cf. nitens</i>	K <i>s.n.</i>	C. Barclay 1251	e
<i>Carpha cf. nitens</i>	K <i>s.n.</i>	C. Barclay 501	e
<i>Carpha cf. nitens</i>	K <i>s.n.</i>	I. B. Balfour <i>s.n.</i>	e, k
<i>Carpha cf. nitens</i>	PRE <i>s.n.</i>	H-J. Schlieben 10904	k
<i>Carpha curvata</i>	HO 122194	A. M. Buchanan 9948	b
<i>Carpha curvata</i>	HO 411849	S. J. Jarman <i>s.n.</i>	b
<i>Carpha curvata</i>	HO 412117	S. J. Jarman <i>s.n.</i>	b
<i>Carpha curvata</i>	HO 443230	S. J. Jarman <i>s.n.</i>	b
<i>Carpha curvata</i>	HO 53801	A. V. Ratkowsky <i>s.n.</i>	b
<i>Carpha curvata</i>	HO 91835	J. Kirkpatrick <i>s.n.</i>	b
<i>Carpha curvata</i>	NE 71839	J. J. Bruhl 1892i	b
<i>Carpha curvata</i>	NE 71843	J. J. Bruhl 1894	b
<i>Carpha curvata</i>	NE 71844	J. J. Bruhl 1895	b
<i>Carpha curvata</i>	NE 71845	J. J. Bruhl 1896A	b
<i>Carpha eminii</i>	EA <i>s.n.</i>	K. A. Lye 1249	a
<i>Carpha eminii</i>	K <i>s.n.</i>	F. Utacock 109	a
<i>Carpha eminii</i>	K <i>s.n.</i>	G. F. Roveridge 120	a
<i>Carpha eminii</i>	K <i>s.n.</i>	H. O. Osmaston 3210	a
<i>Carpha eminii</i>	K <i>s.n.</i>	J. W. Purseglove P270	a

Table 2.1. (Continued)

Species	Herbarium abbreviation & number	Collector & number	Spikelet structure
<i>Carpha eminii</i>	K <i>s.n.</i>	L. O. Hedberg <i>s.n.</i>	b
<i>Carpha eminii</i>	K <i>s.n.</i>	O. Hedberg 435	a
<i>Carpha eminii</i>	K <i>s.n.</i>	R. W. Haines 277	a
<i>Carpha filifolia</i>	K <i>s.n.</i>	N. J. Devenish 1067	k
<i>Carpha filifolia</i>	K <i>s.n.</i>	N. J. Devenish 1821	k
<i>Carpha filifolia</i>	NU 3500279	O. M. Hilliard 16258	k
<i>Carpha filifolia</i>	NU 3500280	Hilliard & Burt 9788	k
<i>Carpha filifolia</i>	NU 3500282	O. M. Hilliard 12609	k
<i>Carpha filifolia</i>	NU 3500296	C. Schwabe 0171	k
<i>Carpha filifolia</i>	NU 3500299	J. Browning 696	k
<i>Carpha filifolia</i>	PRE <i>s.n.</i>	F. K. Hoener 2138	k
<i>Carpha filifolia</i>	PRE <i>s.n.</i>	N. J. Devenish 1067	k
<i>Carpha glomerata</i>	NU <i>s.n.</i>	B. Sonnenberg 387	q
<i>Carpha glomerata</i>	NU <i>s.n.</i>	C. J. Ward 7196	q
<i>Carpha glomerata</i>	NU <i>s.n.</i>	F. Getliffe 1142	q
<i>Carpha glomerata</i>	NU <i>s.n.</i>	J. Browning 228	q
<i>Carpha glomerata</i>	NU <i>s.n.</i>	J. Browning 803	q
<i>Carpha glomerata</i>	PRE <i>s.n.</i>	C. Boucher 911	q
<i>Carpha glomerata</i>	PRE <i>s.n.</i>	T. H. Arnold 1041	q
<i>Carpha glomerata</i>	PRE <i>s.n.</i>	T. H. Arnold 1065	q
<i>Carpha nitens</i>	K <i>s.n.</i>	C. Barclay 1920	e, k
<i>Carpha nitens</i>	K <i>s.n.</i>	C. Barclay 1966	k
<i>Carpha nitens</i>	K <i>s.n.</i>	M. J. E. Coode 4186	k, q
<i>Carpha nivicola</i>	CANB 478753	M. Gray 6201	b
<i>Carpha nivicola</i>	CBG 8001431	B. Barnsley 1287	b
<i>Carpha nivicola</i>	MEL 1578959	M. G. Corrick 10667	b
<i>Carpha nivicola</i>	MEL 2066099	J. H. Willis <i>s.n.</i>	b
<i>Carpha nivicola</i>	MEL 2066100	M. L. Cupper 08	b
<i>Carpha nivicola</i>	MEL 649163	R. J. Adair 1644	b
<i>Carpha nivicola</i>	NE 66025	J. J. Bruhl 146	b
<i>Carpha nivicola</i>	NE 70655	J. J. Bruhl 1872	b
<i>Carpha nivicola</i>	NE 70795	J. Thompson 4500	b
<i>Carpha nivicola</i>	NE 72987	X. Zhang 14	b
<i>Carpha nivicola</i>	NSW 19610	L. A. S. Johnson <i>s.n.</i>	b
<i>Carpha nivicola</i>	NSW 248289	A. N. Rodd 1613	b
<i>Carpha nivicola</i>	NSW 462102	A. C. Gray 5035	b
<i>Carpha perrieri</i>	B 100000970	H. Humbert 3878	k
<i>Carpha perrieri</i>	K <i>s.n.</i>	H. Humbert 6146	e, k
<i>Carpha perrieri</i>	K <i>s.n.</i>	Perrier de la Bâthie 14555	k
<i>Carpha perrieri</i>	P 00199383	Perrier de la Bâthie 14555	k
<i>Carpha perrieri</i>	P 00199389	P. Morat 2307	k
<i>Carpha perrieri</i>	P 00199390	H. Humbert 6146	e, k
<i>Carpha rodwayi</i>	HO 100424	A. Moscal 1955	b
<i>Carpha rodwayi</i>	HO 100425	A. Moscal 2108	b
<i>Carpha rodwayi</i>	HO 121972	P. Collier 4562	b
<i>Carpha rodwayi</i>	HO 24187	W. D. Jackson <i>s.n.</i>	b
<i>Carpha rodwayi</i>	HO 30509	A. T. Dobson 77245	b
<i>Carpha rodwayi</i>	HO 326461	S. J. Jarman 244	b
<i>Carpha rodwayi</i>	HO 91834	J. Kirkpatrick <i>s.n.</i>	b

Table 2.1. (Continued)

Species	Herbarium abbreviation & number	Collector & number	Spikelet structure
<i>Carpha rodwayi</i>	NE 71815	J. J. Bruhl 1881A	b
<i>Carpha rodwayi</i>	NE 71834	J. J. Bruhl 1890	b
<i>Carpha schlechteri</i>	BOL 63205	R. Schlechter 10010	h
<i>Carpha schlechteri</i>	BOL 63206	M. R. Levyns 8098	h
<i>Carpha schlechteri</i>	K <i>s.n.</i>	R. Schlechter 10010	o
<i>Carpha schlechteri</i>	NU <i>s.n.</i>	B. Sonnenberg 458	q
<i>Carpha schlechteri</i>	NU <i>s.n.</i>	J. Browning 823	h
<i>Carpha schlechteri</i>	PRE <i>s.n.</i>	R. Levyns 8098	h
<i>Carpha schlechteri</i>	PRE <i>s.n.</i>	R. Schlechter 10010	h
<i>Carpha schoenoides</i>	BM 000092177	E. J. Godley 755a	m
<i>Carpha schoenoides</i>	BM 000092178	Banks & Solander <i>s.n.</i>	f
<i>Carpha schoenoides</i>	K <i>s.n.</i>	D. M. Moore 1835	m or p
<i>Carpha schoenoides</i>	K <i>s.n.</i>	U. S. South Pacific Exploring Expedition <i>s.n.</i>	f
<i>Carpha schoenoides</i>	K <i>s.n.</i>	W. J. Eyerdam 10586A	m or p
<i>Carpha schoenoides</i>	MO 1626156	P. Dusén <i>s.n.</i>	f or i
<i>Carpha schoenoides</i>	MO 2150322	D. M. Moore 1925	f or i
<i>Carpha schoenoides</i>	NY <i>s.n.</i>	A. Hollermayer 1334	m
<i>Carpha schoenoides</i>	NY <i>s.n.</i>	W. J. Eyerdam 10586A	m
<i>Costularia elongata</i>	K <i>s.n.</i>	I. B. Balfour <i>s.n.</i>	i
<i>Costularia elongata</i>	K <i>s.n.</i>	M. Boivin 998	i
<i>Costularia pilisepala</i>	K <i>s.n.</i>	M. S. Clemens 51062	o
<i>Costularia pilisepala</i>	K <i>s.n.</i>	W. L. Chew 4966	o
<i>Costularia pilisepala</i>	K <i>s.n.</i>	L. J. Brass 8802	o
<i>Cyathochaeta avenacea</i>	NSW 364042	K. L. Wilson 8912	a
<i>Cyathochaeta avenacea</i>	NSW 462122	M. D. Crisp 5351	h
<i>Cyathochaeta clandestina</i>	CANB 511559	B. J. Lepschi BJL3682	m
<i>Cyathochaeta clandestina</i>	NE 66021	J. J. Bruhl 707	h
<i>Cyathochaeta clandestina</i>	NSW 462121	K. L. Wilson 3038	f
<i>Cyathochaeta diandra</i>	NE 66023	J. J. Bruhl 229	h
<i>Cyathochaeta diandra</i>	NE 72997	X. Zhang 24	h
<i>Cyathochaeta diandra</i>	NSW 462124	K. L. Wilson 2300	s
<i>Cyathocoma hexandra</i>	BOL102565	E. Esterhuysen 13596	p
<i>Cyathocoma hexandra</i>	BOL102566	H. G. Fourcade 1007a	p
<i>Cyathocoma hexandra</i>	NE 66175	B. Sonnenberg 484	p
<i>Cyathocoma hexandra</i>	NU <i>s.n.</i>	B. Sonnenberg 477	b or d, i
<i>Cyathocoma hexandra</i>	NU <i>s.n.</i>	C. J. Ward 1060	f or i
<i>Cyathocoma hexandra</i>	PRE <i>s.n.</i>	R. Schlechter 10280	b or d
<i>Gahnia aspera</i>	NE 51153	J. B. Williams <i>s.n.</i>	a
<i>Gahnia aspera</i>	NE 70161	K. L. Wilson 9386	a
<i>Gahnia aspera</i>	NE 72072	J. H. Hosking 1734	a
<i>Gahnia sieberiana</i>	NE 51150	J. B. Williams <i>s.n.</i>	h
<i>Gahnia sieberiana</i>	NE 62751	J. T. Hunter 1554	h
<i>Gymnoschoenus sphaerocephalus</i>	NE 65497	P. R. Williams 213	h
<i>Gymnoschoenus sphaerocephalus</i>	NE 72981	X. Zhang 8	h
<i>Gymnoschoenus sphaerocephalus</i>	NSW 262708	K. L. Wilson 8408	h

Table 2.1. (Continued)

Species	Herbarium abbreviation & number	Collector & number	Spikelet structure
<i>Mesomelaena graciliceps</i>	NSW 364509	K. L. Wilson 9193	r
<i>Mesomelaena graciliceps</i>	NSW 462119	K. L. Wilson 2942	f
<i>Mesomelaena graciliceps</i>	NSW 462120	K. L. Wilson 3056	f
<i>Oreobolus distichus</i>	NE 50965	J. B. Williams <i>s.n.</i>	a
<i>Oreobolus distichus</i>	NE 70653	J. J. Bruhl 1870	a
<i>Oreobolus distichus</i>	NE 72990	X. Zhang 17	a
<i>Oreobolus distichus</i>	NE 72992	X. Zhang 19	a
<i>Oreobolus distichus</i>	NSW 462112	R. Melville 3102	a
<i>Oreobolus oxycarpus</i>	NSW 462114	K. L. Wilson 974	a
<i>Oreobolus oxycarpus</i>	NSW 462115	A. C. Beauglehole 41161	a
<i>Oreobolus oxycarpus</i>	NSW 462117	A. Moscal 9623	a
<i>Oreobolus pumilio</i>	NE 70651	J. J. Bruhl 1869b	a
<i>Oreobolus pumilio</i>	NE 71809	J. J. Bruhl 1879	a
<i>Oreobolus pumilio</i>	NE 72985	X. Zhang 12	a
<i>Oreobolus pumilio</i>	NSW 462116	J. Thompson 2680	a
<i>Ptilothrix deusta</i>	NE 56828	S. M. Capararo 3	n
<i>Ptilothrix deusta</i>	NE 65013	J. B. Williams <i>s.n.</i>	c
<i>Ptilothrix deusta</i>	NE 70548	X. Zhang 1	n
<i>Ptilothrix deusta</i>	NE 70663	L. M. Copeland 2037	c
<i>Schoenoides oligocephalus</i>	HO 102690	A. Moscal 977	i
<i>Schoenoides oligocephalus</i>	HO 144781	A. M. Buchanan 11305	b
<i>Schoenoides oligocephalus</i>	HO 47874	J. B. Davies <i>s.n.</i>	i
<i>Schoenoides oligocephalus</i>	HO 60127	A. V. Ratkowsky <i>s.n.</i>	i
<i>Schoenoides oligocephalus</i>	NE 71832	J. J. Bruhl 1889A	b
<i>Schoenus andinus</i>	BM 000092164	U.S. South Pacific Exploring Expedition <i>s.n.</i>	c
<i>Schoenus andinus</i>	BM 000092165	P. Dusén 612	c
<i>Schoenus andinus</i>	K <i>s.n.</i>	S. Laegaard 12532	c
<i>Schoenus andinus</i>	NY <i>s.n.</i>	G. Ljungner 887	c
<i>Schoenus antarcticus</i>	BM 000092162	E. J. Godley 487b	c
<i>Schoenus antarcticus</i>	BM 000092163	E. J. Godley 651a	c
<i>Schoenus brevifolius</i>	NSW 472134	K. L. Wilson 9912	v
<i>Schoenus calostachyus</i>	NE 60026	J. J. Bruhl 1097B	v
<i>Schoenus calostachyus</i>	NE 68916	J. J. Bruhl 570	u
<i>Schoenus maschalinus</i>	NE 37917	A. G. Floyd 773	a
<i>Schoenus maschalinus</i>	NSW 247917	K. L. Wilson 6363	g
<i>Schoenus maschalinus</i>	NSW 422022	S. J. Griffith Kattang 7a	n
<i>Schoenus paludosus</i>	NE 42442	S. J. Griffiths <i>s.n.</i>	o
<i>Schoenus paludosus</i>	NE 52083	S. J. Griffiths <i>s.n.</i>	o
<i>Schoenus rhynchosporoides</i>	BM 000092179	H. Gunckel 3017	m
<i>Schoenus rhynchosporoides</i>	BM 000092180	A. Guagardo <i>s.n.</i>	f
<i>Schoenus rhynchosporoides</i>	MO 1211234	—	f
<i>Schoenus rhynchosporoides</i>	NY <i>s.n.</i>	A. Hollermayer 1323	m
<i>Schoenus rhynchosporoides</i>	NY <i>s.n.</i>	R. Santesson 1224	m, t
<i>Schoenus turbinatus</i>	NE 21695	K. G. Griffiths <i>s.n.</i>	b
<i>Schoenus turbinatus</i>	NE 42453	S. J. Griffiths <i>s.n.</i>	b
<i>Schoenus turbinatus</i>	NE 63101	J. T. Hunter 2357	m
<i>Schoenus turbinatus</i>	NE 71936	K. L. Wilson 9772	b
<i>Tetralia capillaris</i>	NSW 279525	V. Klaphake 643	a

Table 2.1. (Continued)

Species	Herbarium abbreviation & number	Collector & number	Spikelet structure
<i>Tetraria capillaris</i>	NSW 462110	D. E. Albrecht 5079	b
<i>Trianoptiles capensis</i>	BOL 63221	E. Esterhuysen 34668	g or j
<i>Trianoptiles capensis</i>	BOL 63222	E. Esterhuysen 34749	k or l
<i>Trianoptiles capensis</i>	BOL 63225	M. R. Levyns 9775	g or j
<i>Trianoptiles capensis</i>	BOL 63226	M. R. Levyns 9994	g or j
<i>Trianoptiles capensis</i>	K <i>s.n.</i>	U. J. Ecklon 854	g or j
<i>Trianoptiles solitaria</i>	BOL 102568	E. Esterhuysen 29741	k or l
<i>Trianoptiles solitaria</i>	BOL 63233	E. Esterhuysen 33995	k or l
<i>Trianoptiles solitaria</i>	BOL 63234	J. P. H. Acock 4746	k or l
<i>Trianoptiles solitaria</i>	K <i>s.n.</i>	W. Dod 3348	k or l
<i>Trianoptiles solitaria</i>	NSW 462123	V. Stajsic 706	k or l
<i>Trianoptiles stipitata</i>	BOL 102569	J. P. H. Acock 4745	g or j
<i>Trianoptiles stipitata</i>	BOL 63228	M. R. Levyns 7678	g or j
<i>Trianoptiles stipitata</i>	BOL 63229	M. R. Levyns 7641	g or j
<i>Trianoptiles stipitata</i>	BOL 63230	M. R. Levyns 7663	g or j
<i>Trianoptiles stipitata</i>	BOL 63231	N. S. Pillans 4874	g or j
<i>Tricostularia pauciflora</i>	NSW 404649	R. G. Coveny 17484	o or p
<i>Tricostularia pauciflora</i>	NSW 462108	V. Stajsic 110	h or i
<i>Tricostularia undulata</i>	NSW 462105	P. K. Latz 112885	a
<i>Tricostularia undulata</i>	NSW 462106	G. J. Leach 4179	a

2.3 Terminology

Spikelet: A spikelet is usually defined as a small spike (typically the smallest repeated unit of an inflorescence, unless the inflorescence is reduced to a single spikelet), i.e. a racemously branched structure consisting of an axis (Lawrence 1951; Eiten 1976; Harris and Harris 1994; Kukkonen 1994). The spikelet of Schoeneae has been interpreted to be monopodial by some authors (Holttum 1948; Koyama 1961; Haines 1967; Raynal 1971; Eiten 1976; Haines and Lye 1977; Kukkonen 1986), and to be sympodial by some others (Pax 1886, 1887; Celakovský 1887; Hamlin 1956; Kern 1962; Schultze-Motel 1964). When the spikelet is interpreted as a monopodial structure, it is a spikelet according to the above definition. When the spikelet is interpreted as a sympodial structure, it is not a true spikelet in the light of the above definition. However, most authors who interpreted the 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 others used ‘partial inflorescence’, ‘Scheinährchen’ (pseudospikelet) or ‘spikelet’ (in quotes) for it (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 a sympodial branching pattern are called sympodial spikelets, and spikelets with a monopodial branching pattern 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 rachilla (Fig. 2.1 d); sympodial spikelets have successive axes which are composed of nodes and internodes, resulting in a ‘rachilla’ consisting of a number of single rachillas or axes (Fig. 2.1 a–c).

Glume: Most authors have used the term glume in describing the parts of the spikelet in Cyperaceae, but Haines and Lye (1983) used both ‘glume’ and ‘scale’ in describing the spikelets of *Carpha* and its relatives. Since ‘scale’ has been used for one kind of perianth in Cyperaceae, it should not be used as a synonym of ‘glume’. Bruhl et al. (1992) and Bruhl (1995) used ‘floral bracts’ (‘sterile bracts’, ‘fertile floral bracts’) in describing the spikelet in Cyperaceae. Bruhl (1995, p. 132) explained that the reason for using ‘floral bracts’ (‘sterile bracts’, ‘fertile floral bracts’) was to ‘accept the idea of homology’. In Poaceae, ‘glume’ refers to one of the two bracts at the base of the spikelet, and the flower is subtended by a lemma and palea, while in Cyperaceae, ‘glume’ refers to the small bracts in the spikelet, whether each of these subtends a flower or not. No detailed study has been conducted to decide whether the uses of ‘glume’ in Poaceae and Cyperaceae are homologous or not. Thus, in this study ‘glume’ is still used. 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 partially encloses an adjacent male, female or bisexual flower.

Sterile glume: A glume that does not directly enclose a flower.

Basal shape of glumes: Most species observed have the glumes with a typically slightly curved, more or less truncate base (see Fig. 2.5 b). However, the fertile glumes in some species of *Schoenus* and in *Ptilothrix deusta* have an arch-shaped cavity at their base (Figs 2.3 b, c, 2.4 c, 2.5 c, 2.7; also see Browning and Gordon-Gray 1995a, Fig. 5).

Line of attachment: This refers to a line on the node of rachilla/‘rachilla’ on which a glume grows.

Prophyll: A prophyll is defined as having 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, and it is, when present, the first foliar organ on a lateral axis, i.e. proximal on the lateral shoot (Haines 1967; Kern 1974; Haines and Lye 1983; Bruhl et al. 1992; Kukkonen 1994).

Bisexual flower: This refers to a flower with both pistil and stamens although sometimes both are not functional together.

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

2.4 Results

The spikelet structure of the individual spikelets in the specimens examined can be classed as one of the 22 types illustrated in Fig. 2.2. For each specimen, spikelet structure is listed in Table 2.1. The spikelets of Schoeneae are bisexual, having 3–7(–12) distichous to subdistichous glumes, with a few (1–8) of the proximal glumes empty, then 1–3(–5) bisexual flowers, and occasionally a proximal male flower. They develop acropetally. Some spikelets have an empty uppermost glume while others do not have this. The flowers of Schoeneae have a very contracted stalk or are sessile (Figs 2.2, 2.3 c, d, 2.4 d, 2.5 e, 2.6 a–d and 2.7 c–d). Each fertile glume is on the opposite side of the ‘rachilla’ from its flower and subtends a new branch forming the next ‘rachilla’ internode regardless of whether the ‘rachilla’ is elongated or not and whether a prophyll exists or not, i.e. the spikelet structure is consistently sympodial.

Fig. 2.2. Spikelet structure in Schoeneae. Open circle = a bisexual flower; closed circle = a male flower; hooked line = a prophyll (also see Fig. 2.1). **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 (partially) 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.

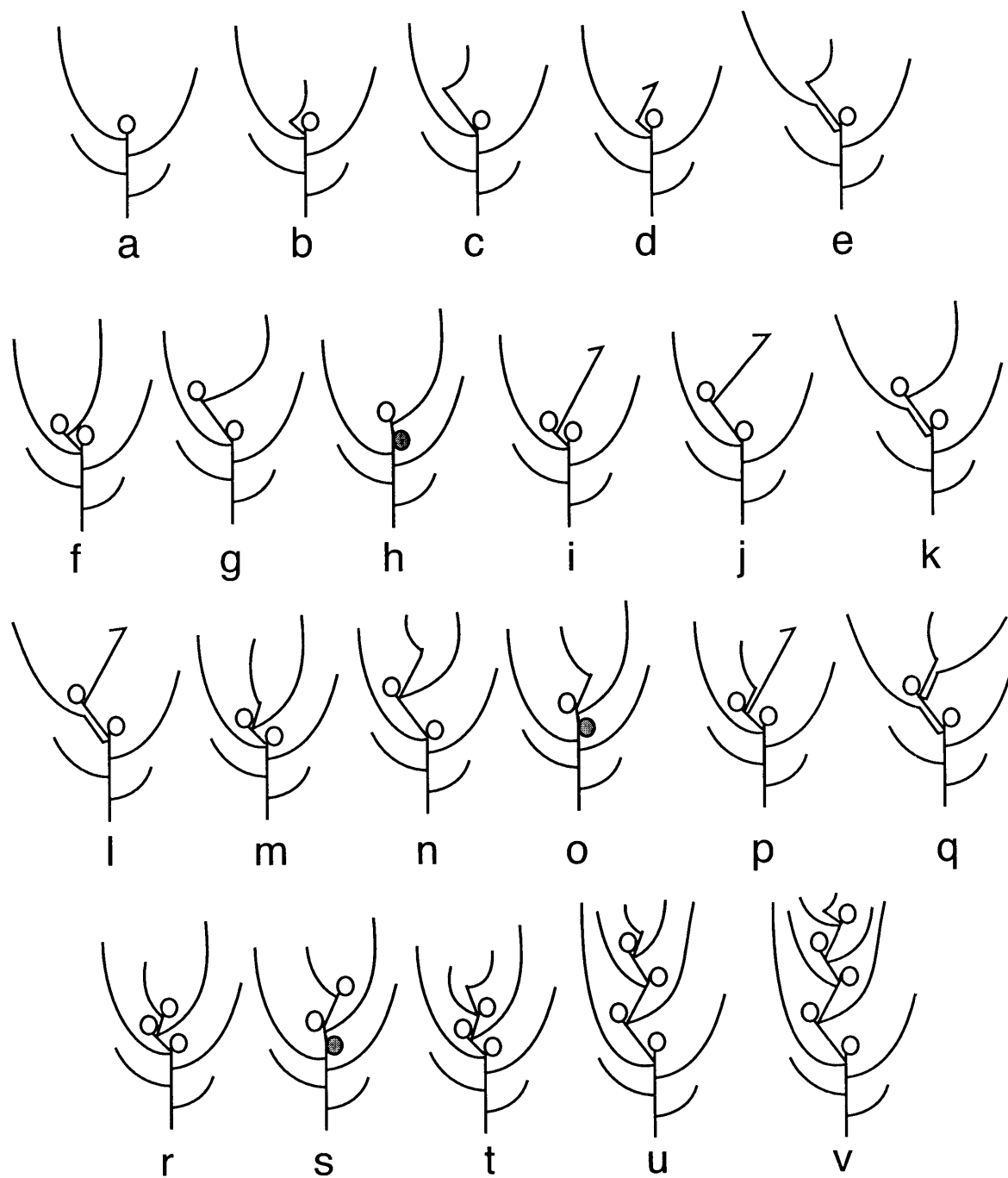


Fig. 2.3. SEM micrographs of spikelet structure in Schoeneae. **a**, *Carpha curvata* (A. V. Ratkovsky s.n., HO 53801). Spikelet with four proximal sterile glumes (lines of attachment of three of these indicated by short arrows) and terminal flower removed (PF, point of attachment). Fertile glume (FG) subtends the contracted axis (indicated by asterisk) that bears the empty uppermost glume (UEG). Line of attachment of FG is lower than the flower attachment point. **b–d**, *Schoenus andinus* (S. Laegaard 12532, K s.n.). **b**, Spikelet with four proximal sterile glumes removed (lines of attachment indicated by short arrows). A flower (F) with mature nut present terminates the main axis of the spikelet and is partially enclosed by the fertile glume (FG). A new ‘rachilla’ internode arises between FG and F (hidden in Fig. 2.3 b, but visible in Fig. 2.3 d). The fertile node is inclined (NI). **c**, A magnification of Fig. 2.3 b; 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 an arch-shaped cavity at base of FG (only one side is visible here). **d**, FG removed (LFG, line of attachment) from a spikelet similar to that in Fig. 2.3 b, 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.

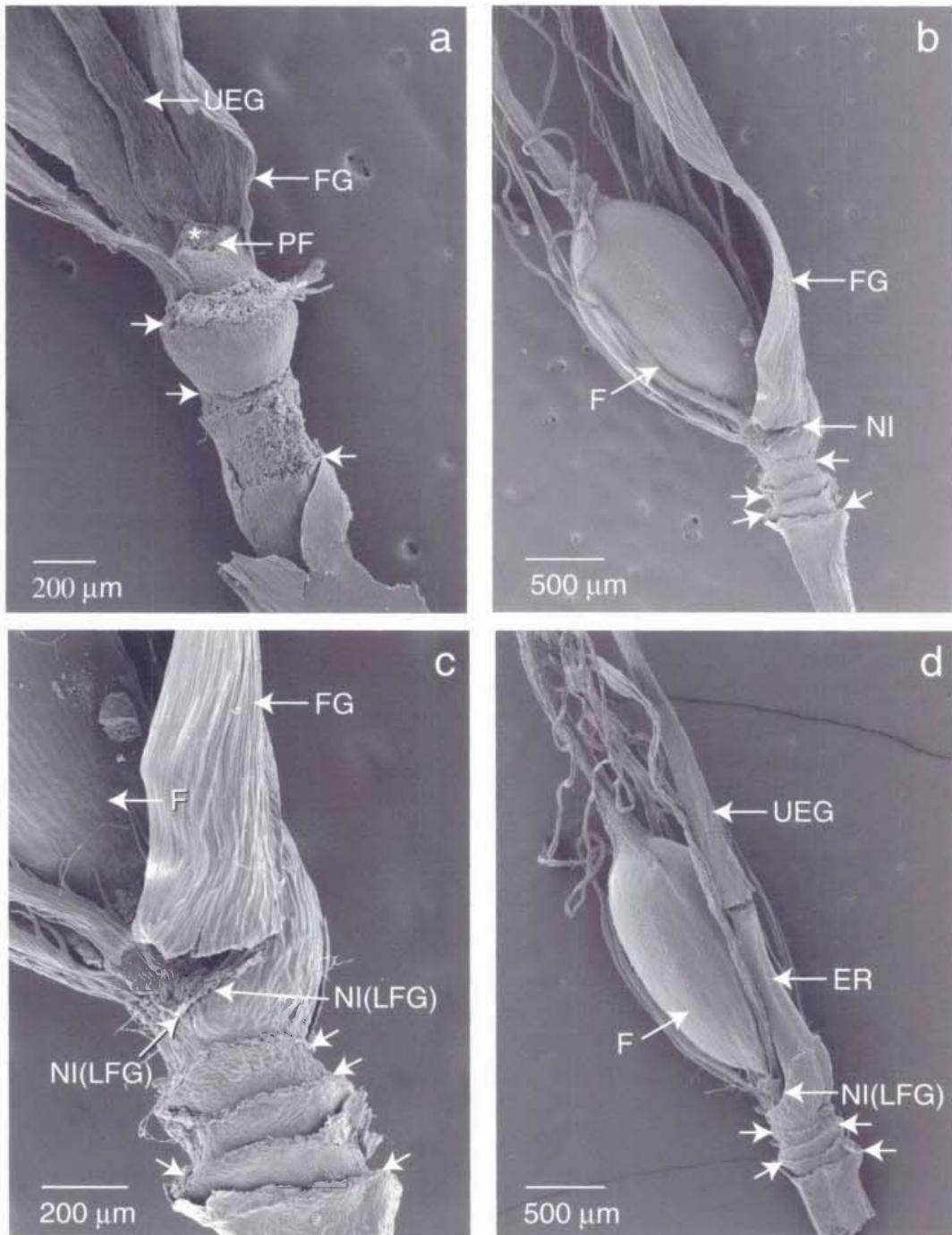


Fig. 2.4. SEM micrographs of spikelet structure in Schoeneae. **a–d**, *Ptilothrix deusta* (X. Zhang 1, NE 70548). **a**, lower half of a spikelet. SN1 indicates the first sterile node, attached to which is the proximal sterile glume (SG1) with curved, more or less truncate base (also see Fig. 2.5 b). **b**, SG1 removed from a spikelet similar to that in Fig. 2.4 a, 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. 2.5 b). **c**, SG2 removed from a spikelet similar to that in Fig. 2.4 b. NI1 indicates the inclined node, i.e, the proximal fertile node. FG1 is the proximal fertile glume with an arch-shaped cavity at base (seen more clearly in Fig 2.5 c). **d**, FG1 removed from a spikelet similar to that in Fig. 2.4 c. Proximal flower (F1) terminates the main axis of the spikelet and is surrounded by FG1 (removed). A new elongated ‘rachilla’ internode (ER) arises between FG1 and F1, and bears FG2, the distal fertile glume, at its apex.

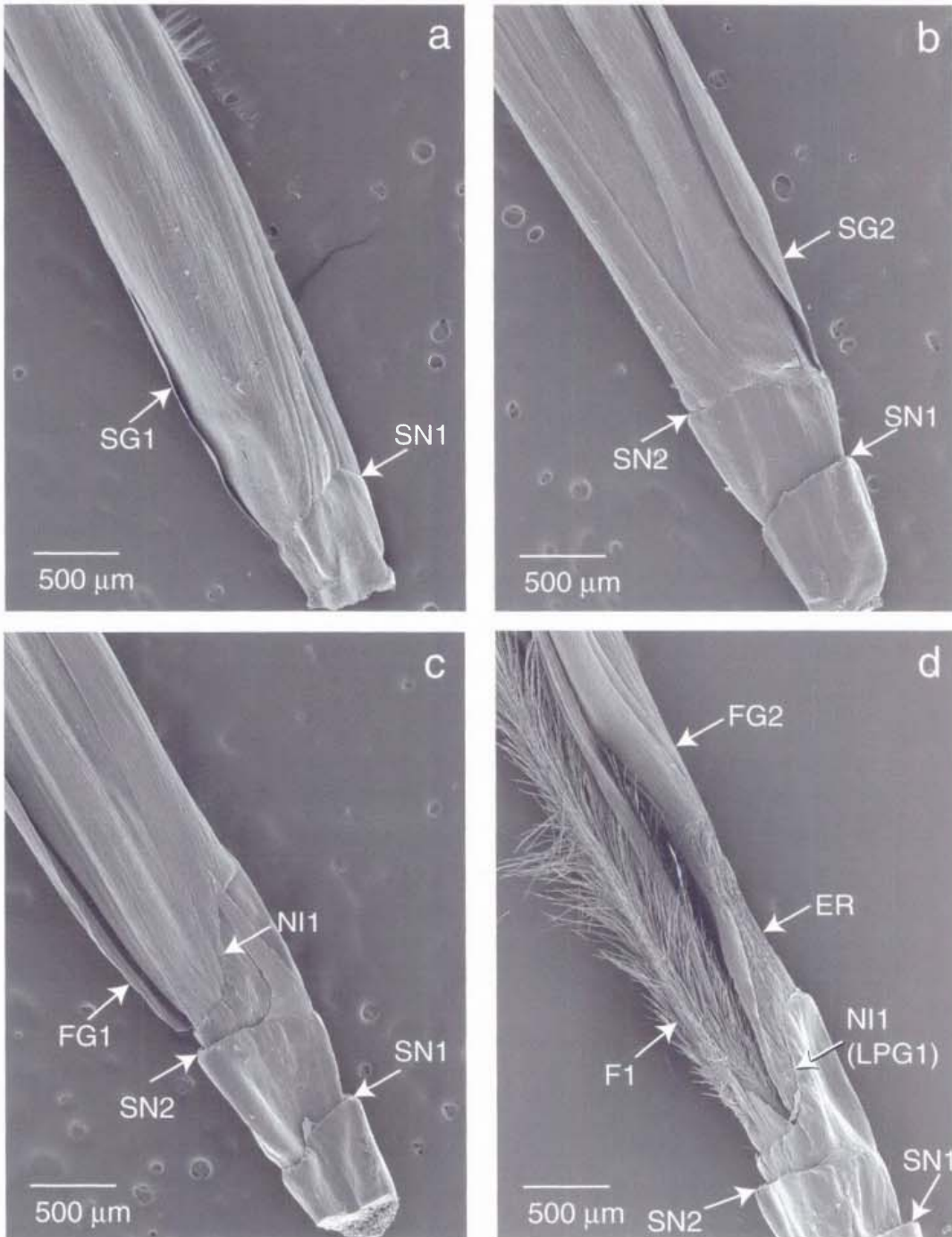


Fig. 2.5. SEM micrographs of spikelet structure in Schoeneae. **a–c**, *Ptilothrix deusta* (X. Zhang 1, NE 70548). **a**, The distal fertile glume FG2 (LFG2, line of attachment) and distal flower (PF2, point of attachment) removed from a spikelet similar to, but much older than, that in Fig. 2.4 d. The 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 cavity at base. **d, e**, *Carpha bracteosa* (H. Bolus 2867, K s.n). **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 partially enclosed by the proximal fertile glume (FG1). A new elongated ‘rachilla’ internode (ER) arises between FG1 and the proximal flower. The base of FG1 partially adnate to ER. Line of attachment of FG1 is lower than the proximal flower. FG2 is the distal fertile glume. **e**, FG2 (LFG2, line of attachment) was removed from a spikelet similar to that in Fig. 2.5 d to show the distal flower (F2) terminal on ER.

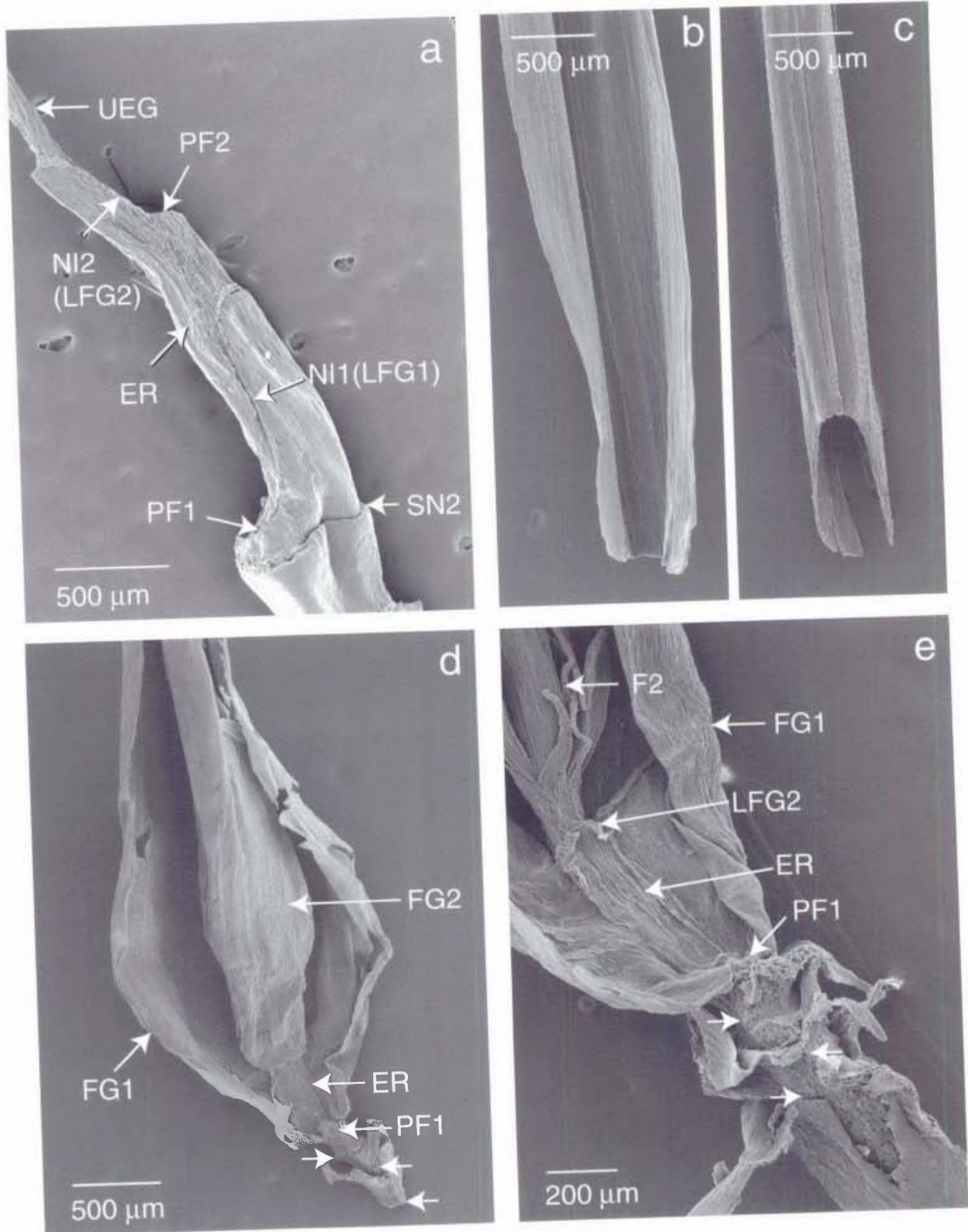


Fig. 2.6. SEM micrographs of spikelet structure in Schoeneae. **a**, *Carpha capitellata* (Levyns 8391, K *s.n.*). Spikelet with proximal sterile glumes (lines of attachment indicated by short arrows), proximal flower (PF1, point of attachment) and distal fertile glume (LFG2, line of attachment) removed. 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) terminates ER and was enclosed by the distal fertile glume. **b–d**, *Schoenus rhynchosporoides* (A. Hollermayer 1323, NY *s.n.*). **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 partially enclosed by proximal fertile glume (FG1). Line of attachment of FG1 is lower than F1. **c**, FG1 (LFG1, line of attachment) removed from a spikelet similar to that in Fig. 2.6 b. The next ‘rachilla’ internode (R1) grows between FG1 and F1. Distal flower (F2) terminates R1 and is partially enclosed by distal fertile glume (FG2). Line of attachment of FG2 is lower than F2. **d**, FG2 (LFG2, line of attachment) and F2 (PF2, point of attachment) removed from a spikelet similar to that in Fig. 2.6 b, c. The branch forming the next ‘rachilla’ internode (R2) grows between FG2 and F2, and bears an empty uppermost glume (UEG).

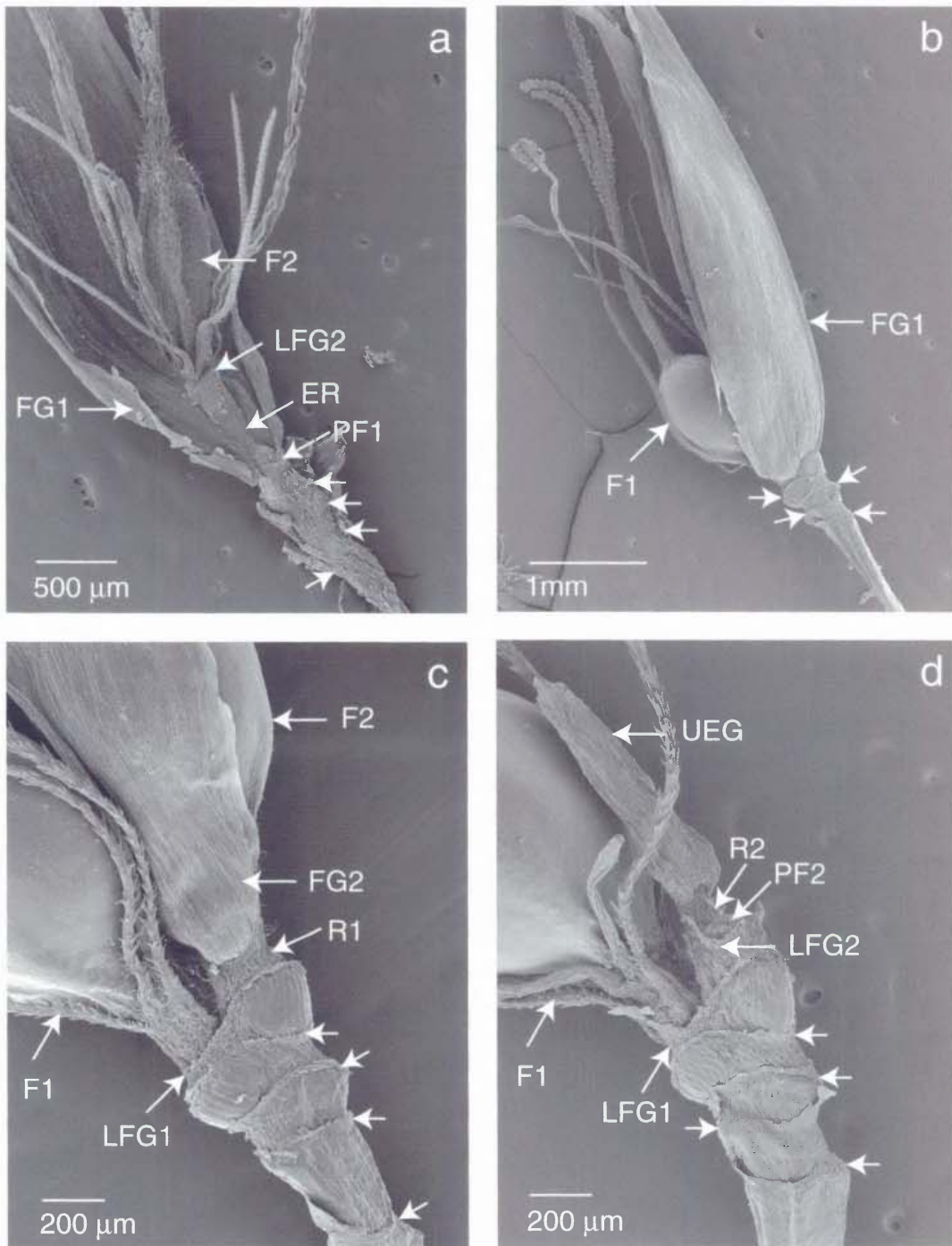
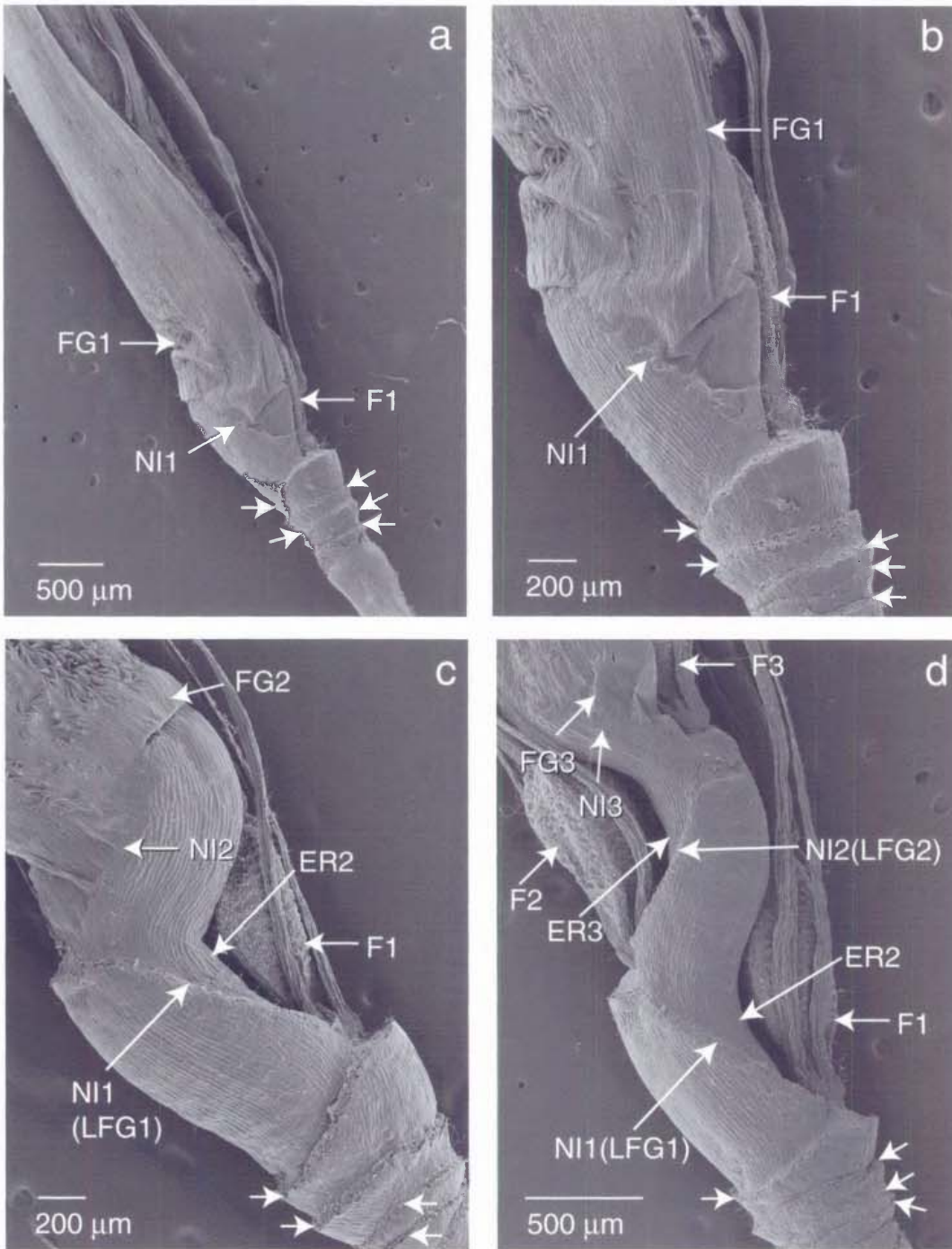


Fig. 2.7. SEM micrographs of spikelet structure in Schoeneae. **a–d**, *Schoenus brevifolius* (K. L. Wilson 9912, NSW 472134). **a**, Spikelet with proximal sterile glumes (lines of attachment indicated by short arrows) removed. The lowest flower (F1) terminates the main axis of the spikelet and is partially enclosed by the lowest fertile glume (FG1). The lowest inclined node (NI1) makes an arch-shaped cavity at base of FG1 (half of the arch-shaped base of FG1 is visible here). **b**, A magnification of Fig. 2.7 a; the lowest point of the line of attachment of FG1 is at the same level as F1. **c**, FG1 (LFG1, line of attachment) was removed from a spikelet similar to that in Fig. 2.7 a. 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 an arch-shaped cavity at 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**, FG2 (LFG2, line of attachment) was removed from a spikelet similar to that in Fig. 2.7 c. The next (third) ‘rachilla’ internode (ER3) arises between FG2 and the second flower (F2). The third flower (F3) terminates ER3 and is partially enclosed by the third fertile glume (FG3). The lowest point of the line of attachment of FG3 is at the same level as F3. NI3 is the third inclined node and makes an arch-shaped cavity at 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 by an empty glume after the fifth flower (see Fig 2.2 v).



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, and this variation sometimes occurs on the same plant, such as in *Carpha alpina* (MEL 252110), *C. angustissima* (P 00199386), *C. borbonica* (*I. B. Balfour s.n.*, K *s.n.*), *C. capitellata* (*Drège 1840*, K *s.n.*), *C. cf. nitens* (*I. B. Balfour s.n.*, K *s.n.*), *C. nitens* (*C. Barclay 1920*, K *s.n.*), *C. perrieri* (*Humbert 6146*, K *s.n.*; P 00199390), *Cyathocoma hexandra* (*B. Sonnenberg 477*, NU *s.n.*) and *Schoenus rhynchosporoides* (*R. Santesson 1224*, NY *s.n.*) (Table 2.1; Fig. 2.2). 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*, *Tetralaria capillaris* and *Tricostularia pauciflora*), and even on the same plant: *Carpha angustissima* (P 00199386), *C. borbonica* (*I. B. Balfour s.n.*, K *s.n.*), *C. capitellata* (*Drège 1840*, K *s.n.*), *C. cf. nitens* (*I. B. Balfour s.n.*, K *s.n.*), *C. nitens* (*M. J. E. Coode 4186*, K *s.n.*; *C. Barclay 1920*, K *s.n.*), *C. perrieri* (*Humbert 6146*, K *s.n.*; P 00199390), *Cyathocoma hexandra* (*B. Sonnenberg 477*, NU *s.n.*) (Table 2.1; Fig. 2.2).

The proximal portion of the ‘rachilla’ (the part which carries the sterile glumes) is straight and more stout than the remainder of the ‘rachilla’ (Figs 2.3, 2.4 d, 2.5 a, d, e, 2.6 and 2.7 c, d). The distal portion (the part which carries fertile glumes and the empty uppermost glume) is more or less curved (zigzag) except the node on which a male flower occurs. If the node carries a male flower, the internode above that node lies in the same direction as the internode below it (Fig. 2.2 h, o, s), which occur consistently in *Capeobolus brevicaulis*, *Costularia pilisepala*, *Gahnia sieberiana*, *Gymnoschoenus sphaerocephalus* and *Schoenus paludosus*, and some specimens of other species: *Carpha schlechteri* (*R. Schlechter 10010*, K *s.n.*; *R. Levyns 8098*, PRE *s.n.*; *R. Schlechter 10010*, PRE *s.n.*; *J. Browning 823*, NU *s.n.*; BOL 63205; BOL 63206), *Cyathochaeta avenacea* (NSW 462122), *C. clandestina* (NE 66021), *C. diandra* (NE 66023, NE 72997, NSW 462124) (Table 2.1; Fig. 2.2).

In some species, the ‘rachilla’ elongates above the nodes on which the bisexual flowers occur (Fig. 2.2 c, e, g, j, k, l, n, o, q, s, u, v; Table 2.1). 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. 2.5 d, e), *C. capitellata* (Fig. 2.6 a), *C. filifolia*, *C. glomerata*, *C. nitens*, *C. perrieri*, *C. schlechteri* (B. Sonnenberg 458, NU s.n.), *Ptilothrix deusta* (Figs 2.4 d, 2.5 a), *Schoenus andinus* (Fig. 2.3 d), *S. antarcticus*, some specimens of *S. maschalinus* (NSW 422022, NSW 247917), *S. calostachyus*, *S. brevifolius* (Fig. 2.7 c, d), *Trianoptiles capensis*, *T. stipitata*, and *T. solitaria*. In other species, the ‘rachilla’ does not elongate at all, i.e. internodes above the fertile glume(s) have almost the same length as internodes above the proximal sterile glume(s) (Figs 2.2 a, b, d, f, h, i, m, p, r, t, 2.3 a, 2.6 b–d; Table 2.1).

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 observed here, is straight, and the glumes on it have a curved, more or less truncate base (Figs 2.4 a, b, 2.5 b). However, the distal parts (which carry fertile glumes) elongate to produce a strongly zigzag ‘rachilla’, and result in the inclined nodes and internodes being irregular shapes. In turn, each inclined node results in an arch-shaped cavity at the base of the glume that initiates at that node and subtends the next axillary internode and surrounds its flower on the opposite side (Figs 2.3 b–d, 2.4 c, d, 2.5 a, c, 2.7).

In spikelets of some species, the base of each fertile glume is adnate to the ‘rachilla’ above it (Fig. 2.2 e, k, l, q; Table 2.1). This occurs in *Carpha angustissima*, *C. borbonica*, *C. bracteosa* (Fig. 2.5 d, e), *C. capitellata* (Fig. 2.6 a), *C. filifolia*, *C. glomerata*, *C. nitens*, *C. perrieri*, *C. schlechteri* (B. Sonnenberg 458, NU s.n.), *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, PRE s.n., and C. J. Ward 1060, NU s.n.; both have a bract with two obscure veins that seems like a prophyll) and *Schoenoides oligocephalus* (HO 47874, HO 60127 and HO 102690) have a prophyll distal to the proximal fertile glume on the spikelet (Fig. 2.2 d, i, p; Table 2.1). The glume distal to the

proximal fertile glume in the spikelet in *Carpha schoenoides* (MO 2150322; MO 1626156; D. M. Moore 1835, K s.n.; W. J. Eyerdam 10586A, K s.n.), *Tricostularia pauciflora*, *Trianoptiles capensis*, *T. stipitata*, and *T. solitaria* has two keels and two obscure veins which I interpret as possibly a prophyll, so I list two possible kinds of structure for these specimens in Table 2.1 with “or” in the middle. If this kind of structure is not interpreted as a prophyll, the spikelet structure before “or” would be the appropriate one, otherwise the one after “or” is appropriate. 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 of many species of Schoeneae, such as in species of *Schoenus* and *Carpha* (except *C. schoenoides*).

In summary, the spikelets of Schoeneae develop acropetally. The ‘rachilla’ is formed sympodially, i.e. 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, i.e. 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;
- ‘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.

2.5 Discussion

Spikelets in Schoeneae are constructed sympodially and flowers are terminal on each ‘rachilla’ internode, i.e. the spikelet structure of Schoeneae is cymose, 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. Spikelet structure in Schoeneae (Fig. 2.2) can be derived simply by changing the flower stalks to short or very short from a

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

Due to having strongly zigzag elongated ‘rachillas’, species of *Schoenus* have often been chosen as an example to illustrate spikelet structure for Rhynchosporae (or Schoeneae) in previous studies. Haines (1967) illustrated how each flower was enclosed by the wing-like 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 cavity at the base of the fertile glume 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 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, its flower on the opposite side of the ‘rachilla’ (Figs 2.2, 2.3, 2.4, 2.5 a, d, e, 2.6 and 2.7). In species of *Schoenus*, there are two types of ‘rachilla’. In one type, the ‘rachilla’ above the fertile glumes does not elongate (Figs 2.2 a, b, f, m, o, t; Table 2.1), for example in *S. rhynchosporoides* (Fig. 2.6 b–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 flowers subtended by them respectively. The other type is where the ‘rachilla’ internode above a fertile glume elongates strongly (Fig. 2.2 c, g, n, u, v; Table 2.1) and fertile nodes are inclined, such as in *S. andinus* (Fig. 2.3 b–d) and *S. brevifolius* (Fig. 2.7). The shape of the inclined nodes leads to the glumes initiated on them having a similar shape at their base, i.e. an arched-shaped cavity at their base. The lowest point of the line of glume attachment to the ‘rachilla’ is below, or at least at the same level as, its flower on the opposite side of the ‘rachilla’. Another genus that has fertile glumes with an arch-shaped cavity at the 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 cavity at the base (Figs 2.4c, 2.5 c). The lowest point of the line of glume attachment to the ‘rachilla’ is below its flower on the opposite side of the ‘rachilla’ (Figs 2.4 c, d, 2.5 a). The results from all the other genera showed that the line of the glume attachment to the ‘rachilla’ is below its flower on the opposite side of the ‘rachilla’ (Figs 2.2, 2.3 a, 2.5 d, e, 2.6 a). These results are supported by the independently derived illustrations of Celakovský (1887) for

Schoenus, Blaser (1941) for *Rhynchospora macrostachya*, Mora (1960) for *Cladium* and *Schoenus*, Levyns (1943) for *Trianoptiles*, Leighton et al. (1947) and Levyns (1959) for *Epischoenus*, Browning (1994) for *Costularia*, Browning and Guthrie (1994) for *Carpha*, and especially by the studies of Browning and Gordon-Gray (1995a, 1995b) for *Epischoenus*, *Schoenus* and *Rhynchospora gracillima* ssp. *subquadrata*.

Browning and Guthrie (1994) and Browning and Gordon-Gray (1995a, 1995b), however, could not accept the spikelet structure as cymose. Browning and Guthrie (1994, p. 151) interpreted the spikelet of *Carpha* as follows: ‘the floret as occupying considerable space and appearing pseudo-terminal, making further rachilla growth possible only as a slightly elongated extension that must curve to accommodate the expanding floret with its maturing fruit’. However, their diagram (1994, Fig 1 A, E) clearly shows that the spikelet structure is cymose and its ‘rachilla’ is sympodial. Browning and Gordon-Gray (1995a, p. 150) also concluded that flowers in *Epischoenus* and *Schoenus* are non-axillary, 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, and that an interpretation of sympodial construction for the spikelet was not acceptable for *Rhynchospora gracillima* ssp. *subquadrata*.

The illustrations of Browning (1994, p. 654, Figs B, C, D) for *Costularia*, Browning and Guthrie (1994, p. 150, Fig. 2.1) 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 its flower and subtends a new branch forming the next ‘rachilla’ internode. This means 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. 2.1 d). However, they are not. ‘A single branch, regardless of age or size, must be constructed in one of two ways. It can be developed by the vegetative extension of one apical meristem

(which may rest from time to time as a terminal bud giving rhythmic growth) to form a single shoot or shoot unit. The axis thus formed is a monopodium and its structure monopodial. Alternatively the axis is built up by a linear series of shoot units, each new distal shoot unit developing from an axillary bud sited on the previous shoot unit. The whole axis then constitutes a sympodium, formed by sympodial growth, and each member of the series derived from one apical meristem is termed a sympodial unit' (Bell 1991, p. 250). If each glume is positioned on the opposite side of its flower (Fig. 2.1 a–c), the spikelet structure is sympodial. For monopodial structure, the glumes are on the same side of the rachilla as their flowers (Fig. 2.1 d) (Eiten 1976). Therefore, if the flower is not axillary to the glume, it must be terminal to the 'rachilla', and the 'rachilla' develops sympodially.

Why should some flowers (the functionally male flowers in Schoeneae) appear so markedly laterally placed in relation to the 'rachilla'? It is because 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 cavity at the base of fertile glumes in some species of *Schoenus* as resulting from 'drying of the rachilla following fruit maturation 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 the arch-shaped cavity at their 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 2.3 c, 2.6 b, c, 2.7). That these glumes have an arch-shaped cavity at their base is only because they grow on the inclined nodes and match the shape of the node. This is also seen in *Ptilothrix* (Figs 2.4 c, d, 2.5 a, c).

In some species in tribe Schoeneae, the basal part of the fertile glumes is adnate to the next internode (Figs 2.2 e, k, l, q, 2.5 d, e, 2.6 a). This was previously observed by Levyns (1943) in *Trianoptiles solitaria*. That the basal part of the fertile glumes is adnate to the next internode provides powerful evidence that the new branch (or next ‘rachilla’ internode) arises in the axil of the glume, i.e. it is sympodial in structure.

Spikelets of some species have a prophyll and/or prophyll-like structures distal to the proximal fertile glume (Fig. 2.2 d, i, p; Table 2.1). This result is supported by previous findings of Pax (1886) in *Elynanthus*, Mora (1960) and Richard (2002) in *Cladium*, and Browning (1994) in *Costularia*. Such a prophyll was also reported in *Asterochaete* (Pax 1886), *Gahnia* (Pax 1886) and *Schoenus* (Pax 1887; Celakovský 1887; Mora 1960), but it was not found in *Asterochaete*, *Gahnia* and *Schoenus* in this study. No prophylls were found in spikelets of many species of Schoeneae (Fig. 2.2, Table 2.1) in this study. In so reduced a structure as a spikelet in Schoeneae, it is not surprising if no prophyll develops (Browning and Gordon-Gray 1995a).

Holttum (1948, p. 535) emphasised that ‘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.’ This opinion cannot be accepted. The prophyll of Cyperaceae cannot be used in distinguishing different types of spikelets (Raynal 1971). Firstly, the prophyll is highly reduced in spikelets and inflorescences of some genera in Cyperaceae. Many species in Schoeneae do not have prophylls in spikelets (Fig. 2.2, Table 2.1) although spikelets branch sympodially. Sometimes prophylls do not exist even in whole inflorescences. This has been previously reported by Haines (1967) and Bruhl (1995). Secondly, ‘the “prophyll” is merely a leaf, occasionally distinguished by its apparent position and sometimes modified in one of a variety of ways’ (Blaser 1944, p.62). The extreme reduction and specialization of all organs of leaf-rank in inflorescences makes the distinction of prophylls, bracts and bracteoles impossible (Blaser 1944). 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. Thus, using prophyll presence or absence to determine inflorescence type is not reliable.

Mora (1960) pointed out 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 on the rachilla/‘rachilla’ (terminal or lateral). From Figs 2.2, 2.3 a, d, 2.5 a, d, e, 2.6 a, d, 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. 2.2, Table 2.1). 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), and 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 its flower (Fig. 2.1 a–c), the spikelet structure is sympodial. If the glumes are on the same side of the axis as their flowers, the spikelet structure is monopodial (Fig. 2.1 d) (Eiten 1976).

Due to 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 to be of racemose structure, while Schultze-Motel (1964) thought their spikelets to be 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) hold different views. Therefore it is necessary to reinvestigate spikelet structure in other tribes of Cyperaceae before any definitive statement can be made about spikelet structure in the whole family.

2.6 Conclusions

1. The spikelet of Schoeneae has a sympodial structure and the flower(s) within spikelets is/are terminal to the ‘rachilla’ or to each ‘rachilla’ internode. The spikelet bears a few proximal empty glumes, the axis ends in a terminal flower, and from the axil of the proximal fertile glume a second axis may develop with the second flower terminal on

it, the axis bearing only one glume from which further branching may proceed. Monopodial spikelets were not found in this study.

2. Spikelets of many species in tribe Schoeneae have no prophylls although they are sympodial. The presence or absence of prophylls cannot be used to distinguish different branching patterns in the spikelets.
3. The spikelets of Schoeneae develop acropetally and the uppermost glume may or may not produce a flower. This last feature may be variable within species and within individual plants, so the presence or absence of this flower is not an indication of sympodial or monopodial spikelet structure in Schoeneae.
4. A branch must be constructed in a sympodial or monopodial manner (Bell 1991). If flowers are not axillary to the glumes in a spikelet, they must be terminal to the 'rachilla' internode, i.e. the spikelet is sympodial.
5. The relative position of flower, glume and axis is a reliable criterion to judge whether spikelets are sympodial or monopodial. When a fertile glume subtends an axis rather than a flower, the spikelet is sympodial (Fig. 1 a–c). Conversely, when a fertile glume subtends a flower rather than an axis, the spikelet is monopodial (Fig. 1 d).
6. In some species of *Schoenus* and in *Ptilothrix*, the formation of an arch-shaped cavity at the base of the fertile glume is caused by the shape of the inclined nodes on which the glume grows, rather than caused by tearing away from the portion that was adnate to the 'rachilla' as claimed by Browning and Gordon-Gray (1995a). Neither is it caused by being decurrent on the 'rachilla' as described by Holttum (1948) and Kern (1974).
7. This study clarifies our understanding of spikelet structure in Schoeneae and highlights the need to reinvestigate other tribes of Cyperaceae, where there are similar conflicting interpretations of spikelets.