Chapter 5

Phenetic and cladistic analyses of Australian *Bulbostylis* Kunth

Introduction

This chapter focuses on the limits of Australian taxa within the genus *Bulbostylis* Kunth nom. cons.

Bulbostylis is a large and mostly pantropical genus comprising around c. 200 species, with the centre of diversity in the African continent (Haines and Lye 1983; Goetghebeur and Coudijzer 1985); the generic rank is now widely accepted (see Chapter 1 for historical perspective). Currently, there are six species of *Bulbostylis* recognised that occur in Australia; *B. burbidgeae* K.L.Wilson, *B. turbinata* S.T.Blake, and *B. pyriformis* S.T.Blake are endemic, while *B. barbata* (Rottb.) C.B.Clarke and *B. densa* (Wall.) Hand.-Mazz. have a widespread distribution. *Bulbostylis humilis* (Kunth) C.B.Clarke (syn *B. striatella* C.B.Clarke; see World Checklist of Mononcotyledons) is a relatively recent introduction to Australia, and known in the Armidale – Glenn Innes area of New South Wales.

Intermediate morphology due to clinal variation or hybridisation is common for some species within the genus e.g. *B. schoeinoides* complex (Gordon-Gray 1988), *B. hispidula* complex (Haines and Lye 1983; Lye 1995), *B. densa* complex (Haines and Lye 1983; Gordon-Gray 1995; Lye 1996), creating uncertainties in species limits and confusion for the identification of specimens.

Bulbostylis densa (as *Bulbostylis capillaris* var. *trifida* (Kunth) C.B.Clarke) was separated from *B. capillaris* (L.) Kunth ex C.B.Clarke due to morphological differences between the American and Asian/Pacific specimens. Blake (1941), however, commented that the Australian material that Clarke assigned with the Indian *B. capillaris* var. *trifida*, was indistinguishable from the American *B. capillaris* var. *capillaris*. Since then, other species and subspecies have been separated from and within *B. densa* (Haines and Lye 1983), e.g. *B. pusilla* (Hochst. ex A.Rich) C.B.Clarke and *B. densa* subsp. *afromontana* (Lye) R.W.Haines were split to delimit the African variation. Collections from Kwazulu-Natal, South Africa, which have nuts at the plant base that are distinctly larger than the aerial counterparts (i.e. the plants are amphicarpic), do not fit the current description of *B. densa* or similar species (Haines and Lye 1983; Gordon-Gray 1995). In addition, two collections, one from China and the other from Queensland, Australia (*B.* sp. aff. *densa* 1), have morphology similar to *B. densa* s.s., but with different nut characteristics; the Queensland collection does not fit descriptions of any accepted Australian species. It is necessary to compare Australian (including Pacific), African, and Asian material of *B. densa*, with the American material of *B. capillaris*, to assess species limits of *B. densa* in Australia.

Bulbostylis barbata is another cosmopolitan species where the morphological variation needs to be compared globally. *Bulbostylis barbata* subsp. *pulchella* (Thwaites) T.Koyama was separated to demarcate the variation in plants from southern India and Indo-China generally.

A putative new species of *Bulbostylis* (*B.* sp. aff. *barbata*), with distinctly piliferous glume margins, and hairy sheaths and leaf blades, was collected from the Kakadu National Park in the Northern Territory. These plants grow interspersed with plants of *B. barbata* and have a similar growth habit and inflorescence--synflorescence structure. Although the nuts of the putative new species are similar to those seen in *B. barbata* there are apparent differences between the collections of both taxa. The species limits for *B.* sp. aff. *barbata* required testing before a new species can be defined.

Blake (1941) described *B. pyriformis* S.T.Blake and commented on the style base that may or may not persist on the nut. This feature of the style base has been a cause of great confusion in the placement of *B. hispidula* (Vahl) R.W.Haines, as is evident from the many nomenclatural synonyms (World Checklist of Monocotyledons 2004); the persistence of the style base on the nut was a key character in assigning taxa to *Bulbostylis*, with non-persistence characteristic for *Fimbristylis*. Embryo morphology provided the evidence that united specimens of *B. hispidula* with *Bulbostylis* through sharing the Bulbostylis-type embryo (Van der Veken 1965). Some specimens of *Bulbostylis turbinata* also show variability in the persistence of the style base on the nut. The Australian *B. pyriformis* shares similar characteristics in general plant morphology and nut micromorphology with taxa of the *B. hispidula* complex. It was necessary to compare the Australian material with some of the African *B. hispidula* subspecies to test the species limits.

Wilson (1980) described *Bulbostylis burbidgeae* as a new species endemic to Australia. Two separate collections, *P.K. Latz 11364* (NSW 452329) (*B.* sp. aff. *puberula*) and *C.R. Dunlop* (DNA 14302, NSW) (*B.* sp. aff. *burbidgeae*) superficially resemble *B. burbidgeae*, but have nuts that are quite distinct from each other and from those typical of *B. burbidgeae*. Both collections are from the Northern Territory and therefore outside the known Western Australian distribution range for *B. burbidgeae*. The collections of *B.* sp. aff. *puberula* and *B.* sp. aff. *burbidgeae* need to be compared to the other Australian species and to *B. puberula* (Poir.) C.B.Clarke, to assess the species boundaries.

As a recent introduction to Australia (Wilson 1993), the African species *Bulbostylis humilis*, needs to be included to assess the extended range of distribution.

The limits of all species and putative species of Australian *Bulbostylis* were tested using phenetic analysis. The relationships of those species and of the genus as sampled here were then assessed for monophyly in the cladistic analysis.

Materials and methods

Taxa

All Australian taxa currently recognised as *Bulbostylis*, i.e. *B. barbata*, *B.densa*, *B.turbinata*, *B. pyriformis* and *B. burbidgeae* (Wilson 1980, 1993), formed the basis of the phenetic study. Putative new species, i.e. *B.* sp. aff. *barbata*, *B.* sp. aff. *burbidgeae*, *B.* sp. aff. p*uberula* and *B.* sp. aff. *densa* 1, were included for species level assessment (Table 5.1). Overseas specimens for the widespread *Bulbostylis barbata* and *B. densa* were included with Australian material in the phenetic analyses to define the species on a global level. Representative specimens of *B. capillaris* (TYPE species for the genus) *B. humilis*, *B. puberula*, and samples from the *B. hispidula* complex (*B. hispidula* (Vahl) R.W.Haines subsp. *pyriformis*

Table 5.1 Specimens sampled as the focus group in the phenetic assessment of Australian *Bulbostylis*. The 'OTU' corresponds to the label used in phenetic analyses. States are given for Australian collections and the Country of origin for all other samples collected overseas. N.T. = Northern Territory, W.A. = Western Australia, S.A. = South Australia, Qld = Queensland, N.S.W. = New South Wales, P.N.G = Papua New Guinea. See Appendix 1 for specimen details.

Species	OTU	State or Country	Collector
Bulbostylis sp. aff. *barbata*	baffba1	N.T.	Clarke K.L 184, Bruhl J.J., Wilson K.L., Cowie I.D.
	baffba2	N.T.	Rice B.L.
	baffba3	N.T.	Clarke K.L 245, Bruhl J.J., Wilson K.L., Cowie I.D.
	baffba4	N.T.	Clarke K.L 241, Bruhl J.J., Wilson K.L., Cowie I.D.
	baffba5	N.T.	Bruhl J.J. 369A
	baffba6	N.T.	Clarke K.L 251, Bruhl J.J, Wilson K.L., Cowie I.D.
	baffba7	N.T.	Clarke K.L 239, Bruhl J.J, Wilson K.L., Cowie I.D.
Bulbostylis barbata	bba1	Qld	Wilson K.L. 5442
	bba2	N.T.	Beauglehole A.C. 26084
	bba3	W.A.	Mitchell A.S. 1150
	bba4	N.S.W.	Tindale M.D. 2058
	bba5	N.T.	Bruhl J.J., Hunter J.T., Egan J. 1269B
	bba6	N.S.W.	Bell D.B.
	bba7	N.T.	Latz P.K. 8263
	bba8	W.A.	Clarke K.L 160, Bruhl J.J, Wilson K.L.
	bba9	N.T.	Knight F. 14185
	bba10	N.T.	Clarke K.L 221, Bruhl J.J, Wilson K.L., Cowie I.D.
	bba11	W.A.	Clarke K.L 113, Bruhl J.J, Wilson K.L.
	bba12	Qld	Clarke K.L 100, Bruhl J.J.
	bba13	Singapore	Burkill H.M., Shah M. HMB235
	bba14	USA	Hill S.R. 24361
	bba15	Kenya	Napper D.M., Kanuri 2079
	bba16	India	Raizada M.B.
	bba17	America	Correll D.S. 52337
	bba18	India	Rajn R.R.V.
	bba19	South Africa	Polhill R. 847, Paulo S.
	bba20	Thailand	Larsen K. 1299, Smitinand T., Warncke E.
Bulbostylis turbinata	bt1	S.A.	Cleland J.B.
	bt2	W.A.	Mitchell A.A. 479
	bt3	N.T.	Latz P.K.7126
	bt4	N.T.	Latz P.K. 6339
	bt5	W.A.	Royce R.D. 1491
	bt6	N.T.	Latz P.K. 7087
	bt7	W.A.	George A.S. 820
	bt8	W.A.	Payne A.L. PRP 1854
	bt9	Qld	Harris P.L. 342
	bt10	N.T.	Beauglehole A.C. 26568
Bulbostylis densa	bde1	N.S.W.	Bruhl J.J., Quinn F.C. 1197
	bde2	N.S.W.	Hunter J.T., Hunter V. 2737
	bde3	Qld	Forster P.I. PIF8482
	bde4	Qld	Blake S.T. 21453
	bde5	Qld	Bean A.R. 1570

Table 5.1 cont'd

	bde7	Qld	Hubbard C.E. 3128
	bde8	Qld	McKee H.S. 9317
	bde9	N.S.W.	Williams J.B.
	bde10	N.S.W.	Gray M. 3255
	bde11	P.N.G.	Croft 34706, Lelean
	bde12	P.N.G.	Robbins R.G. 2660
	bde13	Philippines	Ramos M., Edaro G.
	bde15	Sri Lanka	Davidse G. 7614
Bulbostylis sp. aff. *densa* 1	baffd1	Qld	Bean A.R. 3236
	baffd2	China	Field survey team 820
Bulbostylis sp. aff. *densa* 2	bde16	South Africa	Meeuse A.D.J. 10158
	bde17	South Africa	Scheepers J.C. 1141
	bde18	Swaziland	Haines R.W. 7048
Bulbostylis burbidgeae	bbu1	W.A.	Hart R.P. 2092
	bbu2	W.A.	Carolin R.7640
	bbu3	W.A.	Mitchell A.A. 1929
	bbu4	W.A.	Burbidge N. 1102
	bbu5	N.S.W.	Payne A.L. PRP976
Bulbostylis sp. aff. *burbidgeae*	baffbu	N.T.	Dunlop C.R. 4725
Bulbostylis sp. aff. *puberula*	baffpu	N.T.	Latz P.K. 11364
Bulbostylis pyriformis	bpy1	N.S.W.	Johnson L.A.S.
	bpy2	N.T.	Latz P.K. 10622
	bpy3	N.S.W.	Hunter J.T., Bell D.B.
	bpy4	N.T.	Latz P.K. 488?
	bpy5	N.S.W.	Wilson K.L. 1479A
	bpy6	N.T.	Latz P.K. 9852
	bpy7	Qld	Sharpe P.R. 232
	bpy8	Qld	Bean A.R. 4227

(Lye) R.W.Haines and *B. hispidula* subsp. *senegalensis* (Cherm.) Vanden Berghen) were restricted to use in cladistic analysis.

Phenetic study

As *Bulbostylis* was recovered as a distinct group in the main phenetic analysis performed in Chapter 3, only taxa from *Bulbostylis* were included in the phenetic analyses for this chapter.

Pattern analyses

Additional OTUs were added to the *Bulbostylis* OTUs in the main data set (in Chapter 3). A total of 70 specimens (OTUs) of *Bulbostylis* formed the basis for the phenetic study (Table 5.1 see also Appendix 1 for full species list), where 20 quantitative and 89 qualitative morphological characters (Table 5.2) were analysed in PATN (Belbin 1993).

Data were subjected to ordination, cluster and network analyses as detailed in Chapter 2, and the combined data set, analysed using the Gower Metric similarity-coefficient, is presented here.

Groups that were clear-cut in the first analysis for the genus were removed and the data re-analysed as subsets to assess the remaining taxa. Two-dimensional scatter plots were used to present the ordination results. Boundaries of the 3-dimensional ordinations were outlined in the corresponding 2-dimensional scatter if the 2-dimensional groupings were indistinct.

Table 5.2 Attribute codes and definitions used in the main phenetic analyses for the Australian *Bulbostylis*, including corresponding initial weight values. Weight values changed in subset analyses.

Attribute	Description	Weight
char1	Mean aerial spikelet width in mm (spikelets with mature fruit) at the widest point	1
char2	Mean aerial nut length in mm from base of stipe to nut apex (excluding persistent style base)	1
char3	Mean aerial nut width in mm at widest point	1
char4	Aerial nut length:width (ratio 1:W/L(x) (to decimal 1/x), ratio coefficient	1
char5	Mean aerial nut 'stipe' length in mm	1
char6	Stipe length/nut length (proportion)	1
char7	Mean aerial anther length in mm (including appendages)	1
char8	Mean aerial style length in mm (including style base to base of style arm junction)	1
char9	Mean aerial style width in mm (at mid third)	1
char10	Style length:width (1:W/L(x) to decimal 1/x), ratio coefficient	1
char11	Mean aerial stylebase length in mm (from base to constriction at style junction)	1
char12	Mean aerial stylebase width in mm (at widest point)	1
char13	Style base length:width (1:W/L(x) to decimal 1/x); ratio coefficient	1
char14	Mean aerial glume length in mm (from base of nerve to apical point)	1
char15	Mean aerial glume width in mm (at widest point)	1
char16	Glume length:width (1:W/L(x) to decimal 1/x); ratio coefficient	1
char17	Mean leaf width in mm (at mid third)	1
char18	Mean culm width in mm (at mid third)	1
char19	Mean root width in mm (one cm below plant base)	1
char20	Mean inflorescence–synflorescence length in mm (from base of main bract to furthermost point of spikelets)	1
char21	Basal spikelets 0–absent: always only aerial; 1–present: basal spikelets (morphologically distinct) as well as aerial spikelets	0.5
char22	Sub-radical spikelets (Wilson 1980), spikelets that are aggregated near the plant base that are morphologically similar to the aerial spikelets: the nuts are indistinct from aerial nuts	0.5
char23	Nut shape in transverse section is plano-convex; dorsal/ventral sides of a 3-angled fruit with the adaxial face distinct from the rest, being broader than the abaxial faces, often +/- rounded	0.2
char24	Nut shape in transverse section is strongly triqetrous with deeply concave faces	0.2
char25	Nut shape in transverse section is triquetrous, having 3-angles, with faces being concave	0.2
char26	Nut shape in transverse section is trigonous, 3-angles with faces somewhat flattened	0.2
char27	Nut shape in transverse section is rounded trigonously, with 3 equal sides but well rounded edges and faces (convex)	0.2
char28	Nut outline obovate (2:1 or 3:2)	0.125
char29	Nut outline widely obovate (6:5)	0.125
char30	Nut outline very widely obovate (1:1)	0.125
char31	Nut outline pyriform (pear-shaped)	0.125
char32	Nut outline obtrullate	0.125
char33	Nut outline widely obtrullate (6:5)	0.125
char34	Nut outline very widely obtrullate 1:1)	0.125

Table 5.2 (cont'd)

char35	Nut outline napiform	0.125
char36	Nut epidermis without protuberances (apparent at 50x magnification under a dissecting microscope	0.125
char37	Nut epidermis rugulose (minutely rugose)	0.125
char38	Nut epidermis rugose with rounded waves	0.125
char39	Nut epidermis rugose with acute waves (apex acute from a central raised silica body	0.125
char40	Nut epidermis sub-puncticulate, from single raised cells that are not prominent and are scattered over the surface	0.125
char41	Nut epidermis puncticulate, from prominent single cells raised evenly over surface	0.125
char42	Nut epidermis with rows of warts on face, usually 2 vertical rows on each face	0.125
char43	Nut epidermis reticulate, from distinct and raised cell walls	0.125
char44	Nut epidermis finely hexagonal, giving a honeycomb appearance, obvious at 10x magnification under a dissecting microscope	0.2
char46	Nut epidermal cells isodiametric; almost square to just rectangular	0.2
char47	Nut epidermal cells oblong longitudinally (2:1)	0.2
char48	Nut epidermal cells narrowly oblong longitudinally (6;1;3;1)	0.2
char49	Stamen number: 1	0.33
char50	Stamen number: 2	0.33
char51	Stamen number: 3	0.33
char52	Sheath glabrous (hairs absent)	0.33
char53	Sheath with short to medium hairs (60-100 μm)	0.33
char54	Sheath with bristly hairs almost erect from surface (> 100-1000 μm)	0.33
char55	Glume margins entire	0.25
char56	Glume margins ciliolate; small fine hair-like projections from the margins, sometimes only distally (5 div @ 50x - sometimes only distally)	0.25
char57	Glume margins fimbriolate; small, flattened projections from margins, sometimes only distally (100 μm)	0.25
char58	Glume margins piliferous; fine, long, loose hairs arising from the margins (1000 μm)	0. 25
char59	Glume apex rounded	0.143
char60	Glume apex acute (muticous)	0.143
char61	Glume apex sub-mucronulate	0.143
char62	Glume apex mucronulate	0.143
char63	Glume apex mucronate	0.143
char64	Glume apex acuminate	0.143
char65	Glume apex aristate	0.143
char66	Glume outline ovate	0.25
char67	Glume outline trullate (kite-shaped)	0.25
char68	Glume outline narrowly triangular	0.25
char69	Glume outline linearly triangular	0.25
char70	Glume apex reflexed at maturity	0.5
char71	Glume apex not reflexed at maturity	0.5
char72	Glume nerve muticous	0.33
char73	Glume nerve to a mucro point	0.33
char74	Glume nerve excurrent (greater than 0.5 mm)	0.33
char75	Glume abaxial surface glabrous	0.167

Table 5.2 (cont'd)

char76	Glume abaxial surface with nerve only scabrid	0.167
char77	Glume abaxial surface scabrid over lower half of glume (even - isolated, sparse, dense toothed hairs)	0.167
char78	Glume abaxial surface scabrid over most of the glume back (20-40 μm)	0.167
char79	Glume abaxial surface with short hairs (100 μm)	0.167
char80	Glume abaxial surface bristly, with erect hairs (> 1000 μm)	0.167
char81	Glume arrangement on the rachilla distichously spiral (glumes opposite each other and glume pairs ascending arranged spirally)	0.5
char82	Glume arrangement on the rachilla tristichous	0.5
char83	Non fertile glume number at the base of each spikelet: 0	0.5
char84	Non fertile glume number at the base of each spikelet: 1	0.5
char85	Leaf to culm ratio: 1to1	0.2
char86	Leaf to culm ratio: 2to3	0.2
char87	Leaf to culm ratio: 1to2	0.2
char88	Leaf to culm ratio: 1to3	0.2
char89	Leaf to culm ratio: 1 to 4	0.2
char90	Culm surface glabrous	0.25
char91	Culm surface scabrid (includes distally)	0.25
char92	Culm surface with short hairs that are almost erect (c. 100 μm)	0.25
char93	Culm surface bristly with stiff erect hairs (includes distally)	0.25
char94	Leaf abaxial surface glabrous	0.2
char95	Leaf abaxial surface with scabrid margins	0.2
char96	Leaf abaxial surface scabrid over the abaxial surface	0.2
char97	Leaf abaxial surface with erect to ascending hairs (c. 100 μm)	0.2
char98	Leaf abaxial surface bristly/hispid (1000 μm – erect to outwardly ascending)	0.2
char99	Inflorescence–synflorescence mostly solitary (HF1), or 1–2 coflorescences (Cofl)	0.2
char100	Inflorescence–synflorescence as anthelodia, main florescence (HF1) plus multiple primary coflorescences (Cofl) on lengthened epipodia (rays); some coflorescences may be sessile, but not all	0.2
char101	Inflorescence–synflorescence as ramified (compound) anthelodia	0.2
char102	Inflorescence–synflorescence as 'heads' of 3-7 sessile spikelets	0.2
char103	Inflorescence–synflorescence hemispherical 'head' of > 7 sessile spikelets	0.2
char104	Inflorescence–synflorescence bracts present and glume-like	0.5
char105	Inflorescence–synflorescence bracts present and leaf-like	0.5
char106	Inflorescence–synflorescence bracts shorter than inflorescence–synflorescence length	0.33
char107	Inflorescence–synflorescence bracts equals the inflorescence–synflorescence length	0.33
char108	Inflorescence–synflorescence bracts longer than the inflorescence–synflorescence length	0.33
char109	Inflorescence–synflorescence prophyllar buds or spikelets present	0.5
char110	Inflorescence–synflorescence prophyllar buds or spikelets absent	0.5

Cladistic analysis

Ingroup

Species of *Crosslandia* and *Abildgaardia* that were defined in Chapters 3 and 4 were combined with the terminal taxa of *Bulbostylis* as determined in the phenetic analyses of this chapter. Samples of *Bulbostylis humilis*, *B. puberula*, *B. hispidula* subsp. *pyriformis* and *B. hispidula* subsp. *senegalensis* were added to the ingroup data. Terminal taxa of *Fimbristylis* used in previous analyses were maintained in this cladistic analysis (Table 5.3).

Outgroup

The outgroup in the cladistic analysis for this chapter comprised *Arthrostylis* aphylla, provisional *Actinoschoenus compositus*, *Trachystylis stradbrokensis* (Domin.) Kük., *Schoenoplectus tabernaemontani* (C.C.Gmel.) Palla (= S. *validus* Vahl), *Schoenoplectiella lateriflora* (J.F.Gmel.) Lye (= *Schoenoplectus lateriflorus*), and *Schoenoplectiella laevis* (S.T.Blake) Lye (= *Schoenoplectus laevis*) (Appendix 1).

Characters and homology

Guaglianone (1970) observed intraprophyllar buds within the inflorescence prophylls of species in *Bulbostylis*, and proposed the presence of intraprophyllar buds as a generic separator between *Bulbostylis* and *Fimbristylis*; intraprophyllar buds are absent in *Fimbristylis*. All specimens of *Bulbostylis* used in this study were examined for the presence of intraprophyllar buds or spikelets.

Table 5.3 Taxa included in the cladistic analyses to assess the relationships of Australian species of *Bulbostylis*. Species from *Crosslandia* and *Abildgaardia* included here were defined in Chapter 3 and 4 respectively. See Table 5.1 for *Bulbostylis* specimen list and Appendix 1 for specimen details.

Taxa	**No. specimens sampled**
Ingroup	
Abildgaardia macrantha (provisional)	10
Abildgaardia mexicana	5
Abildgaardia odontocarpa (provisional)	2
Abildgaardia ovata	13
Abildgaardia oxystachya (provisional)	13
Abildgaardia pachyptera (provisional)	11
Abildgaardia schoenoides	12
Abildgaardia triflora	4
Bulbostylis barbata	20
Bulbostylis burbidgeae	5
Bulbostylis capillaris	4
Bulbostylis densa	15
Bulbostylis hispidula subsp. *pyriformis*	3
Bulbostylis hispidula subsp. *senegalensis*	2
Bulbostylis puberula	7
Bulbostylis pyriformis	8
Bulbostylis humilis	3
Bulbostylis turbinata	8
Bulbostylis sp. aff. *barbata*	7
Bulbostylis sp. aff. *burbidgeae*	1
Bulbostylis sp. aff. *densa* 1	2
Bulbostylis sp. aff. *densa* 2	3
Bulbostylis sp. aff. *turbinata* 1	1
Bulbostylis sp. aff. *turbinata* 2	1
Bulbostylis sp. aff. *puberula*	1
Crosslandia anthelata (provisional)	5
Crosslandia setifolia	18
Crosslandia spiralis (provisional)	3
Crosslandia vaginata (provisional)	14
Fimbristylis bahiensis	4
Fimbristylis blakei	2
Fimbristylis cinnamometorum	5
Fimbristylis depauperata	2
Fimbristylis fimbristyloides	4
Fimbristylis furva	2
Fimbristylis hygrophila	2
Fimbristylis microcarya	2
Fimbristylis schultzii	2
Fimbristylis sp L.	2
Fimbristylis variegata	1
Outgroup	
Actinoschoenus compositus (provisional)	4
Arthrostylis aphylla	4
Schoenoplectiella laevis	5
Schoenoplectiella lateriflora	5
Schoenoplectus tabernaemontani	3
Trachystylis stradbrokensis	7

Embryo morphology

Van der Veken (1965) and Goetghebeur (1986) sampled embryos of some species of *Bulbostylis*, reporting variation in general embryo shape and size, and primordial leaf development. *Bulbostylis barbata* was the only Australian species sampled in both studies. In this study, embryos from representatives of each of the species (and subspecies) were sampled and compared (Appendix 1). Second and third (if present) primordial leaves were not scored due to difficulties in observing these structures in many of the embryos. Tissues in small embryos were much denser than in the larger embryos sampled, and I was unable to clear some small embryos sufficiently to define the inner layers (e.g. *B.* sp. aff. *barbata*, and *B.* sp. aff. *densa* 1). Alternative methods in pre-treating the embryo before clearing, or using a different clearing medium, may be necessary in future work.

Anatomy

Leaf blade and culm anatomy were sampled across the species of *Bulbostylis* studied to compare general shape and tissue arrangement. General anatomy (Metcalfe 1969, 1971) and photosynthetic pathway in *Bulbostylis* (Goetghebeur 1986; Bruhl 1995); has been reported to be the same as commonly found in *Fimbristylis*; sampling tested the uniformity in this study.

PAUP analyses*

Parsimony analysis was performed on 47 terminal taxa and 155 characters using heuristic searches (hsearch swap=TBR addseq=rand nreps=1000 hold=5 multrees=yes). Branch support was assessed using Bootstrap analysis (1000 bootstrap replications) because the computational time required to calculate the Bremer support indices past 3 extra tree length steps was too protracted, even when limiting the addition-sequence replications to 10. Characters were traced in MacClade and the most relevant characters are presented in the cladogram.

Results

Phenetic study

Representative OTUs for the genus *Bulbostylis* formed a distinct group in the initial main analysis (see Chapter 3), with some species groups of OTUs (*B.* sp. aff. *barbata*, *B. barbata*, *B. burbidgeae* and *B.* sp. aff. *puberula*) apparent in the *Bulbostylis* cluster at the broad level in 2-dimensional analysis (Figure 5.1).

When additional samples of *Bulbostylis* were added to the first main analysis and re-analysed (see Materials and methods, this chapter), distinct species groups were formed by the OTUs in the 2-dimensional ordination (stress = 0.18; Figure 5.2).

Characters that were most strongly correlated with the groups formed within the ordination were consistent with the synflorescence type, nut epidermal patterning, number of stamens, anther length, nut stipe length to nut length ratio, hairiness (or absence of) of culms and glumes, and shape of glumes (Figure 5.3). The hemispherical heads of sessile spikelets associated with *B. barbata* and *B.* sp. aff. *barbata* and the mostly primary rayed anthelodium (i.e. spikelets on lengthened epipodia) of *B. pyriformis* and *B. turbinata* were correlated with the separation of the groups.

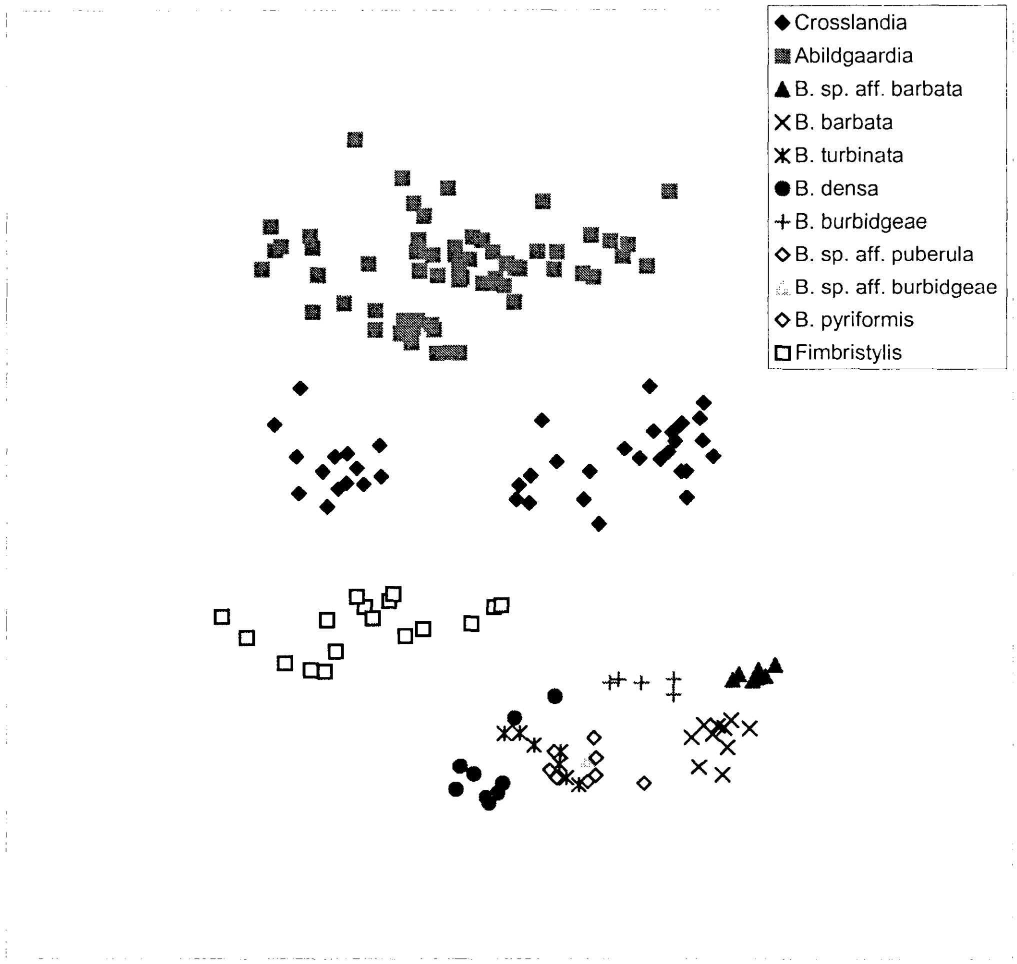


Figure 5.1. MDS ordination in 2-dimensions (stress = 0.17) from primary phenetic analysis (see Chapter 3) highlighting *Bulbostylis*. Species groups for *B*. sp. aff. *barbata*, *B. barbata* and *B. burbidgeae* are distinct in this broad level ordination. See Table 5.1 and Appendix 1 for OTU and specimen details.

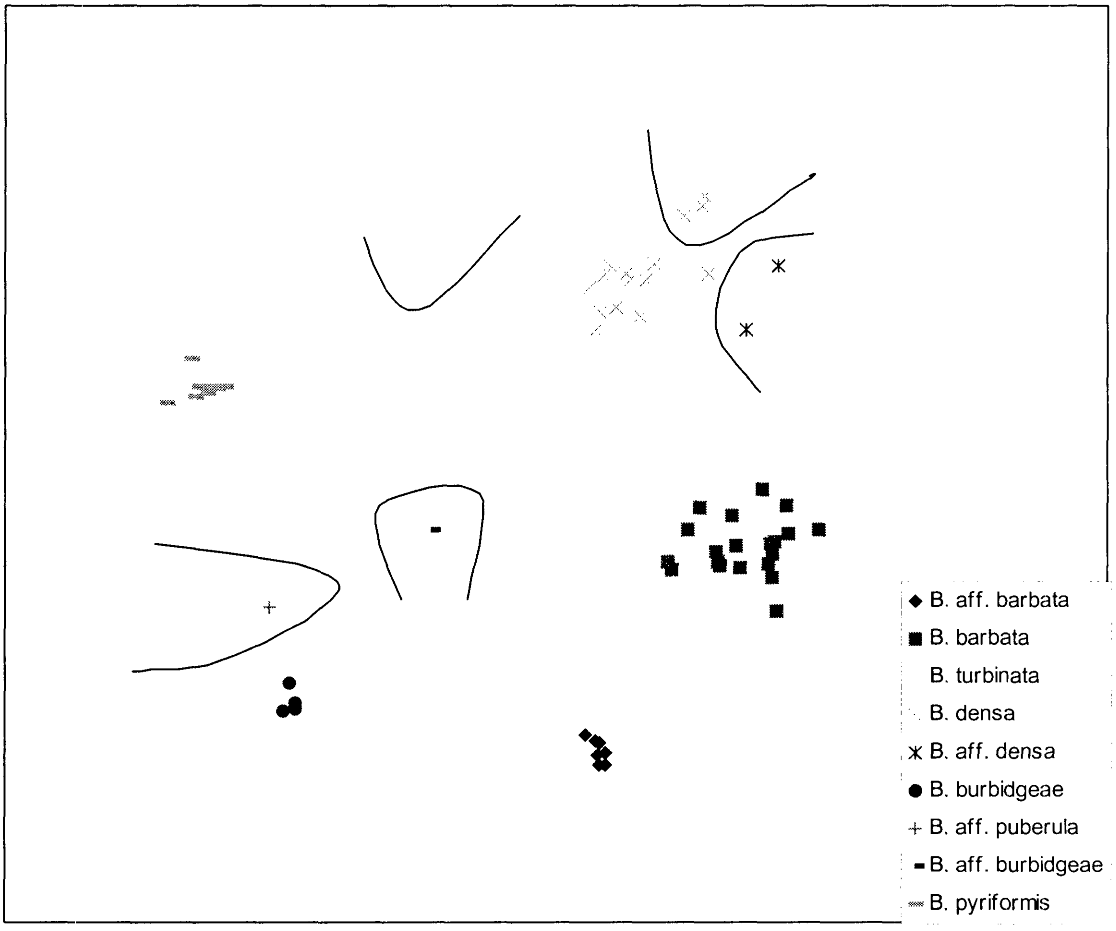


Figure 5.2. MDS ordination for OTUs of *Bulbostylis* (stress = 0.18). Lines separating OTUs in *B. densa* (amphicarpic specimens) and *B.* sp. aff. *densa* indicate the clear-cut groups observed in 3-dimensions (stress = 0.12). See Table 5.1 and Appendix 1 for OTU and specimens details.

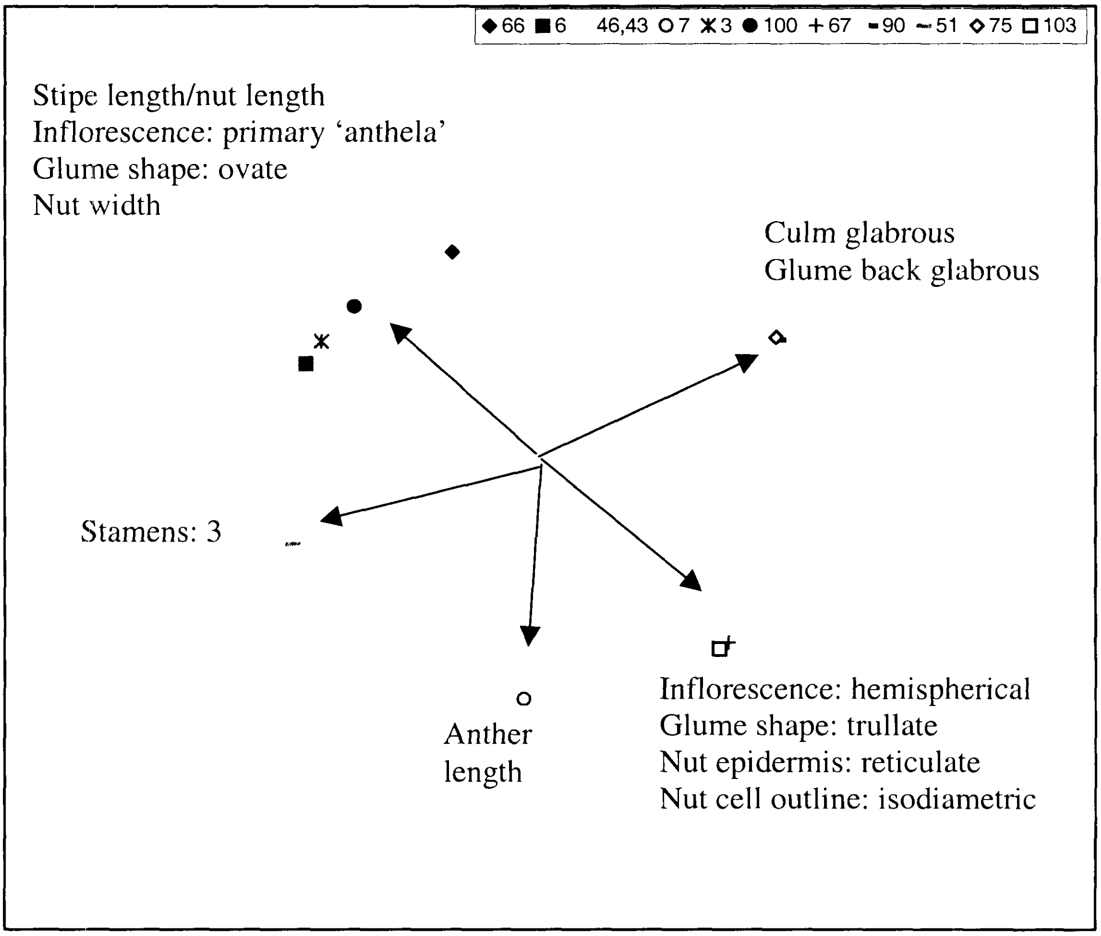


Figure 5.3 Characters that correlate (>80%) to group formation in the ordination shown in Figure 5.1. Inflorescence-synflorescence of many sessile spikelets forming a hemispherical 'head', glume shape: trullate, nut epidermis being reticulate with isodiametric cells, plus anther length separated *Bulbostylis barbata* and *B.* sp aff. *barbata* from the other OTU groups. Culm and glume backs glabrous contributed to separating the *B. densa* group and stamens numbering 3 correlated strongest with the *B. burbidgeae* OTUs. The group containing OTUs for *B. turbinata* and *B. pyriformis* were consistent with the correlated characters of inflorescence–synflorescence: primary 'anthela', highest stipe length-nut length ratio; *B. pyriformis* has the greatest nut widths. See Table 5.2 for attribute definitions.

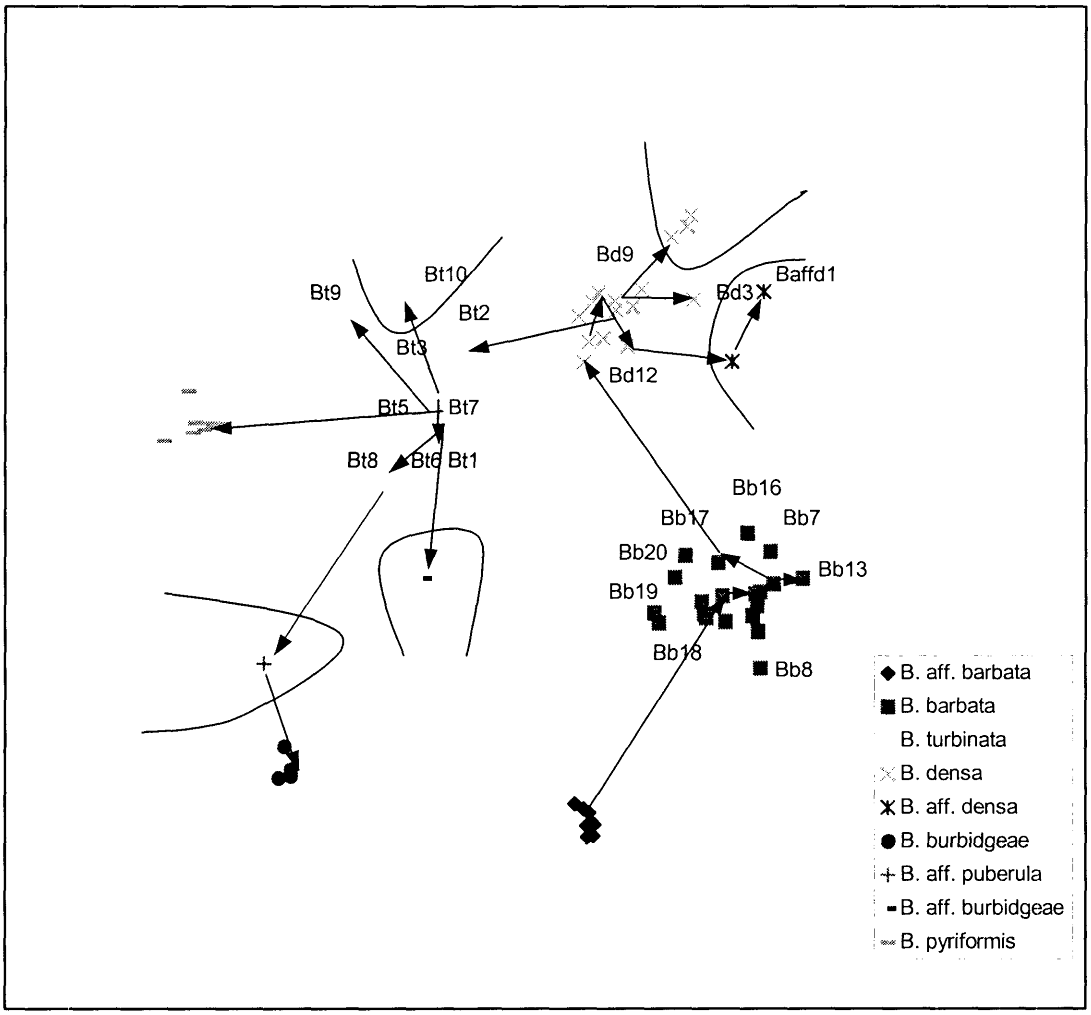


Figure 5.4. Minimum spanning tree (MST) for OTUs of *Bulbostylis* corresponding to ordination in Figure 5.2. Borders indicate greater separation seen in 3-dimensions (stress = 0.12). See Appendix 1 for specimen details.

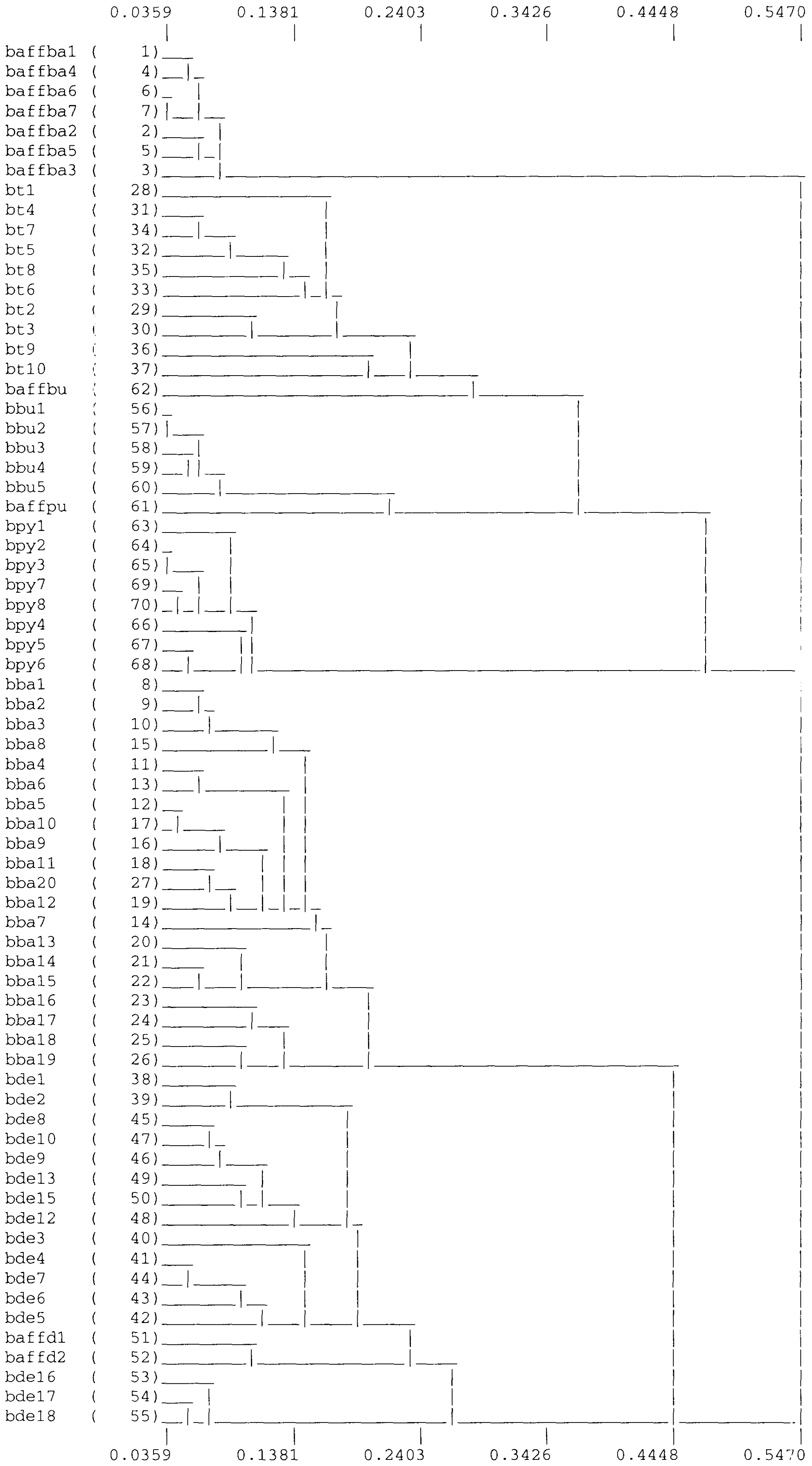


Figure 5.5. WPGMA ($\beta = -0.1$) phenogram that corresponds with the ordination in Figure 5.2, for all OTUs of *Bulbostylis*. OTUs form six groups, the putative species *B.* sp. aff. *barbata* is clearly separated from *B. barbata*. See Table 5.1 and Appendix 1 for OTU and specimen details.

Species groups in the ordination were generally supported by network (Figure 5.4) and cluster analyses (Figure 5.5). Stronger grouping was obtained in the ordination for 3-dimensions (stress = 0.12) as indicated in the 2-dimensional scatter plot (Figure 5.2).

Individual OTUs, baffbu (*B*. sp. aff *burbidgeae*), baffpu (*B*. sp. aff. *puberula*), bt9 and bt10 (*B. turbinata*), were separated from other groups, and from each other, in the 3-dimensional ordination. Although the separation is evident in 2-dimensions for baffbu and baffpu, this is not the case for OTUs bt9 and bt10, which appear as if distinctly clustered with the other *B. turbinata* OTUs. Within the phenogram (Figure 5.5), baffbu is clustered with OTUs of *B. turbinata* and baffpu is broadly included with the *B. burbidgeae* OTU group. However, the dissimilarity of baffpu to OTUs of *B. burbidgeae* is present in the phenogram.

Discrete groups of OTUs were retrieved as the species groups *B*. sp. aff. *barbata*, *B. barbata*, *B. pyriformis*, *B. burbidgeae* and *B. turbinata* (excluding bt9, bt10) within 3- and 2-dimensional ordinations (Figure 5.2), and generally in the phenogram (Figure 5.5). The remaining OTUs formed the *B. densa* group that included baffd1, 2 (*B*. sp. aff. *densa*) and bde16, 17, 18 (African amphicarpic samples of *B. densa*).

Bulbostylis densa *group*

In the subset analyses of the *B. densa* group, OTUs for the amphicarpic specimens collected from Africa formed a group separate to the main *B. densa* OTUs, and to the OTUs of *B*. sp. aff. *densa*. The three groups are more robust in 3-dimensions (stress = 0.12), indicated by the drawn boundaries around the specific groups in the 2-dimensional scatter plot (Figure 5.6). There were 16 characters with greater than

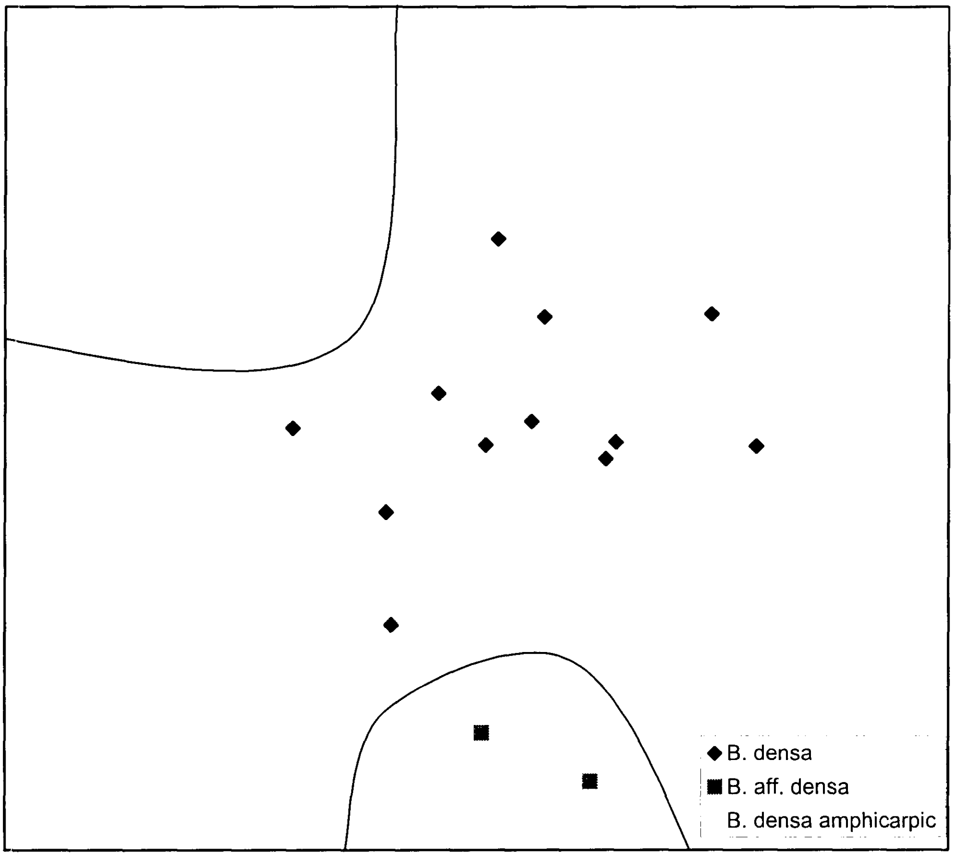


Figure 5.6 MDS ordination in 2 dimensions (stress = 0.18) for the *Bulbostylis densa* group from the primary *Bulbostylis* analysis (see Figure 5.2). OTUs for the amphicarpic material from Africa form a group separate to the main *B. densa* group and the separate OTUs of *B.* sp. aff. *densa*. The boundaries shown indicate the distinct OTU groups in the 3-dimensional ordination (stress = 0.12). See Table 5.1 and Appendix 1 for OTU and specimen details.

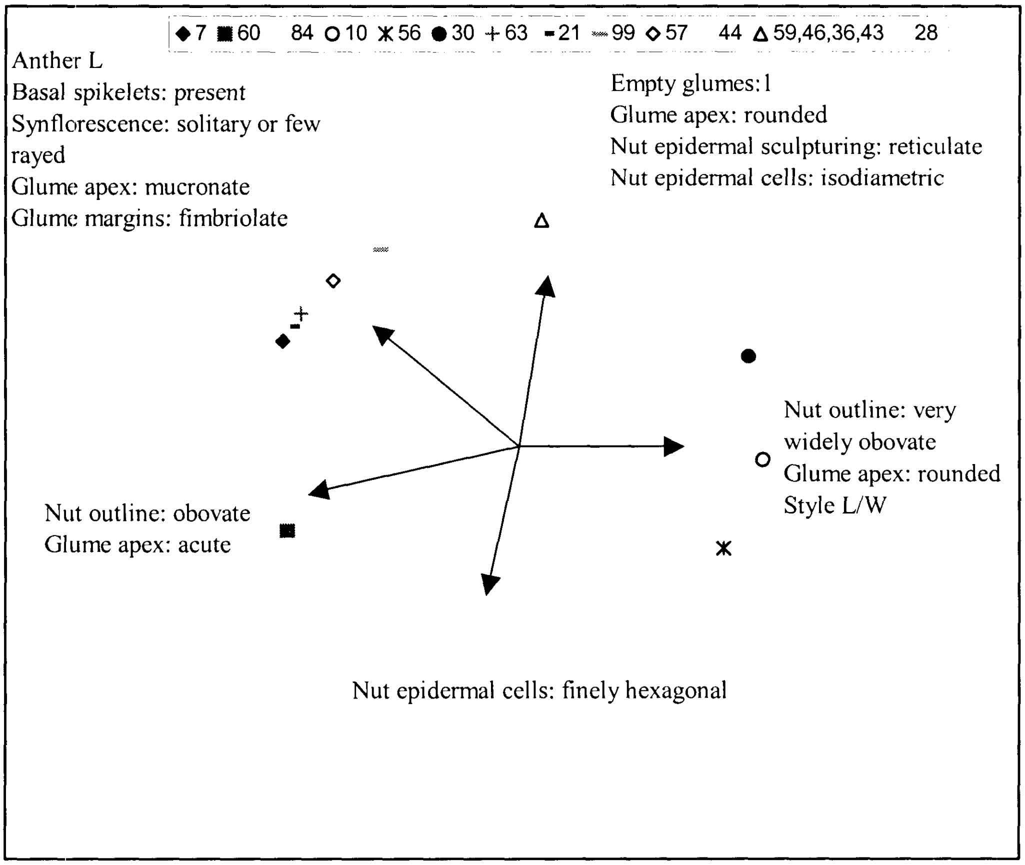


Figure 5.7 Characters correlated (> 70 %) with the ordination in Figure 5.6 for OTUs of the *Bulbostylis densa* group. Characters with >80 % correlation to the ordination were anther length, glume apex: acute, empty glume: 1, style length to width ratio, glume margins: ciliolate, and nut shape: obovate. L=length. See Table 5.2 for attribute definitions.

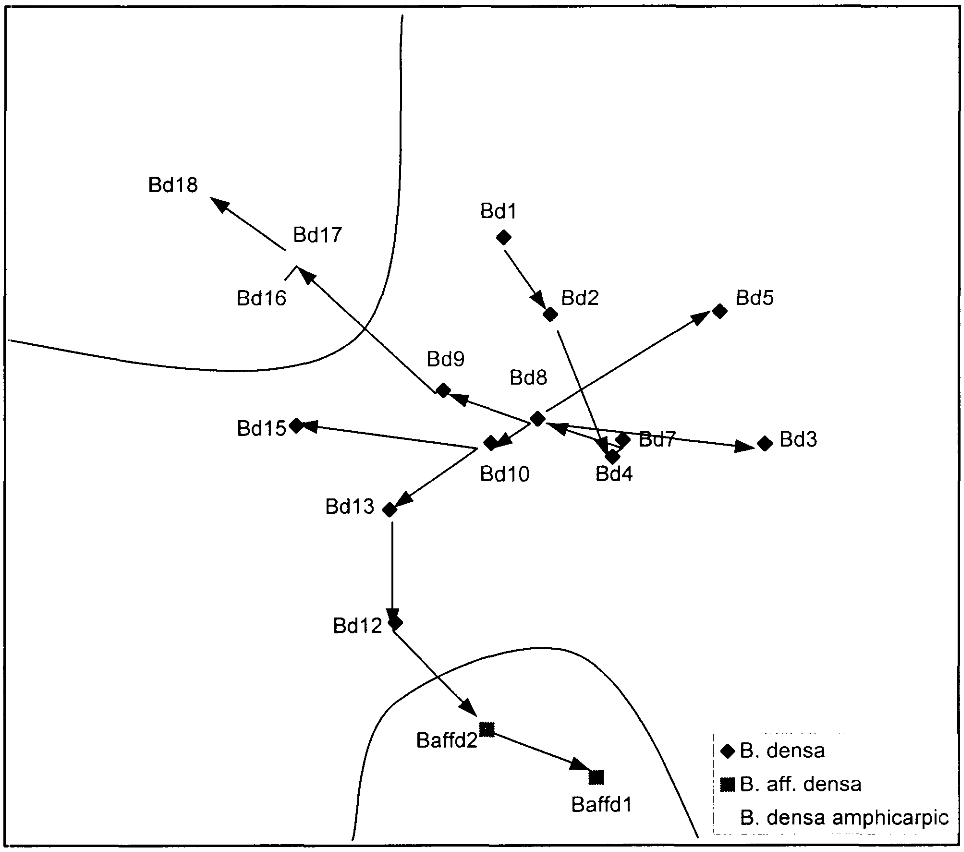


Figure 5.8 Minimum spanning tree (MST) with linkages for the *Bulbostylis densa* group plotted onto the 2-dimensional ordination in Figure 5.6. See Appendix 1 for specimen details.

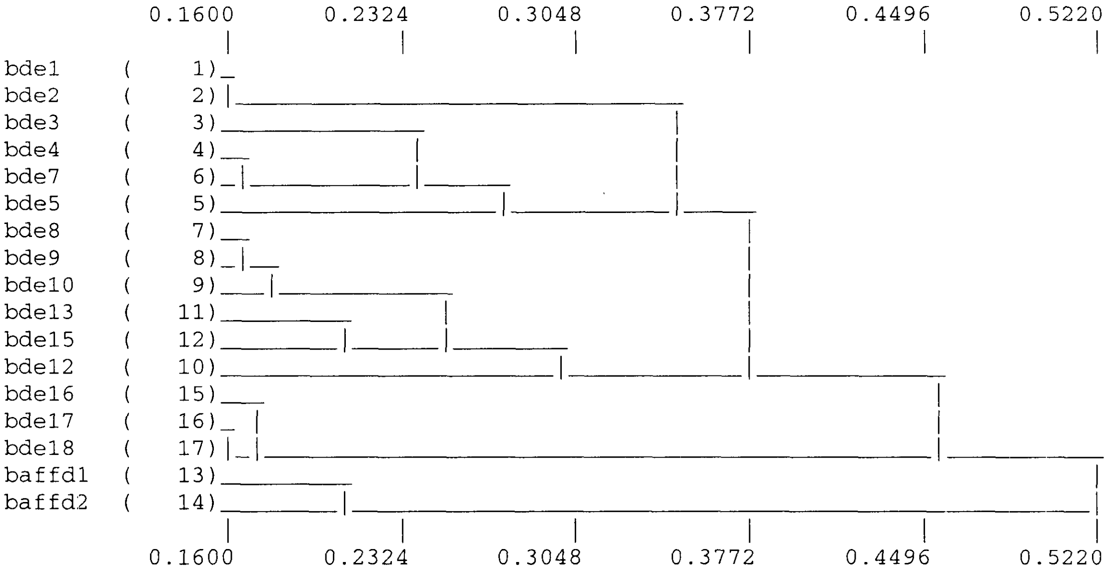


Figure 5.9 WPGMA (β = -0.1) phenogram for the *Bulbostylis densa* subset (see Figure 5.2 for all species of *Bulbostylis*) that best correlates with the ordination (Figure 5.6) and Minimum Spanning Tree (MST) (Figure 5.8). Operative Taxonomic Units (OTUs) for *B. densa* with amphicarpic nuts (bde16-18) are grouped together separate to the remaining OTUs for *B. densa*. Similarly, OTUs for *B.* sp. aff. *densa* (baffd1, baffd2) group separately. See Table 5.1 and Appendix 1 for OTU and specimen details.

70% correlation to the three groups seen in the ordination scatter plot (Figure 5.7). Characters with >80% correlation to the ordination were anther length, glume apex: acute, empty glume number: 1, style length to width ratio, glume margins: ciliolate, and nut shape: obovate. Linkages between OTUs in the minimum spanning tree (Figure 5.8) support the major groups (*B. densa* s.s., *B. densa* 'amphicarpic', *B.* sp. aff. *densa*) and the minor groups (within *B. densa* s.s.) observed in the phenogram (Figure 5.9).

Bulbostylis turbinata–B. *sp. aff.* burbidgeae *group*

Subset analysis of the *B. turbinata–B.* sp. aff. *burbidgeae* group of OTUs indicates that *B.* sp. aff. *burbidgeae* bt9 and bt10 are discrete units from the main OTU group of *B. turbinata* in the 3-dimensional ordination (stress = 0.1), and to a lesser extent in 2-dimensions (Figure 5.10). There were 24 characters with >70% correlation to the ordination; characters with >80% correlation were inflorescence prophyllar branching: present, inflorescence prophyllar branching: absent, culm width, style length, glume width and style base width (Figure 5.11). The minimum spanning tree OTU linkages (Figure 5.12) correspond to the groups from the ordination and cluster analysis (Figure 5.13).

Terminal taxa as recognised in the phenetic analyses, i.e. *Bulbostylis* sp. aff. *barbata*, *B. barbata*, *B. turbinata*, *B.* sp. aff. *turbinata* 1, (bt9), *B.* sp. aff. *turbinata* 2 (bt10), *B. pyriformis*, *B. burbidgeae*, *B. densa*, *B.* sp. aff. *densa* 1, *B.* sp. aff. *densa* 2 (African amphicarpic), *B.* sp. aff. *burbidgeae*, and *B.* sp. aff. *puberula*, were combined with samples from *B. humilis*, *B. capillaris*, *B. hispidula* subsp. *senegalensis*, and *B. hispidula* subsp. *pyriformis* for use in cladistic analysis.

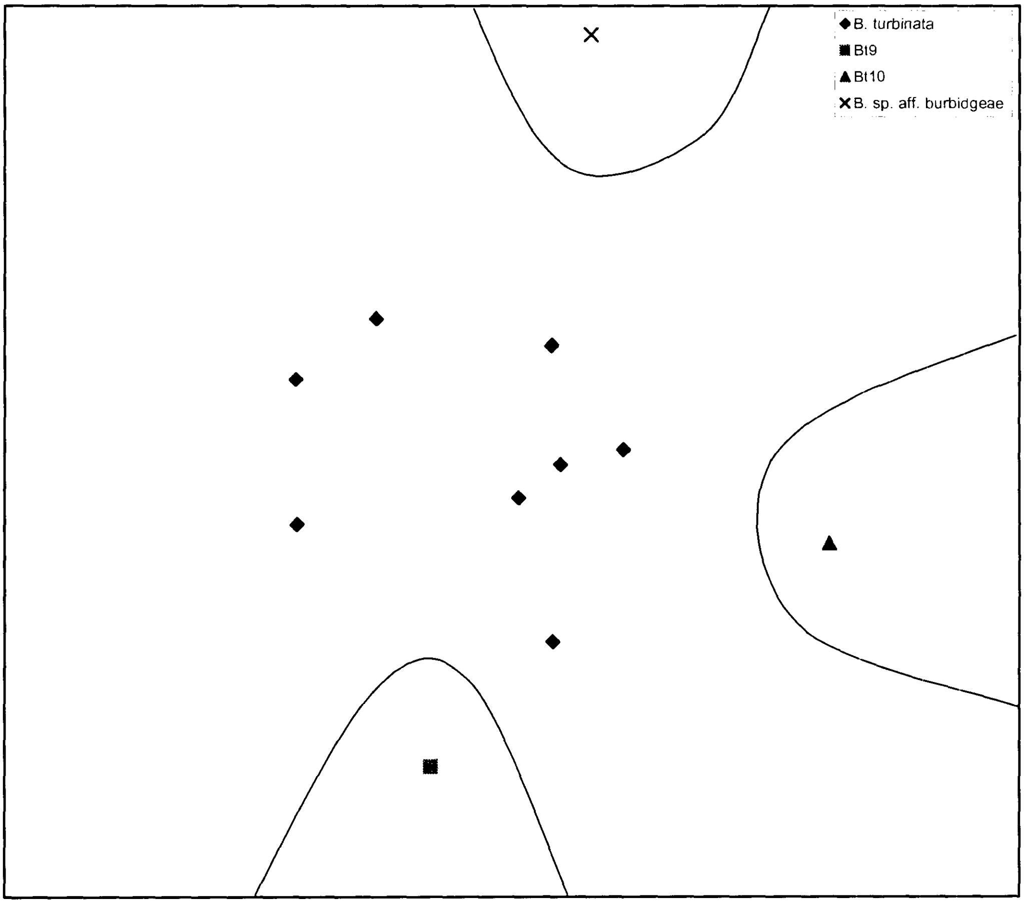


Figure 5.10 MDS ordination in 2-dimensions (stress= 0.18) for OTUs of the *B. turbinata* group from Figure 5.2 The OTUs bt9, bt10 and *B.* sp. aff *burbidgeae* (baffbu) are separated from the main group of *B. turbinata* OTUs. The boundaries indicate the stronger group resolution seen in the 3-dimensional ordination (stress = 0.11). See Table 5.1 and Appendix 1 for OTU and specimen details.

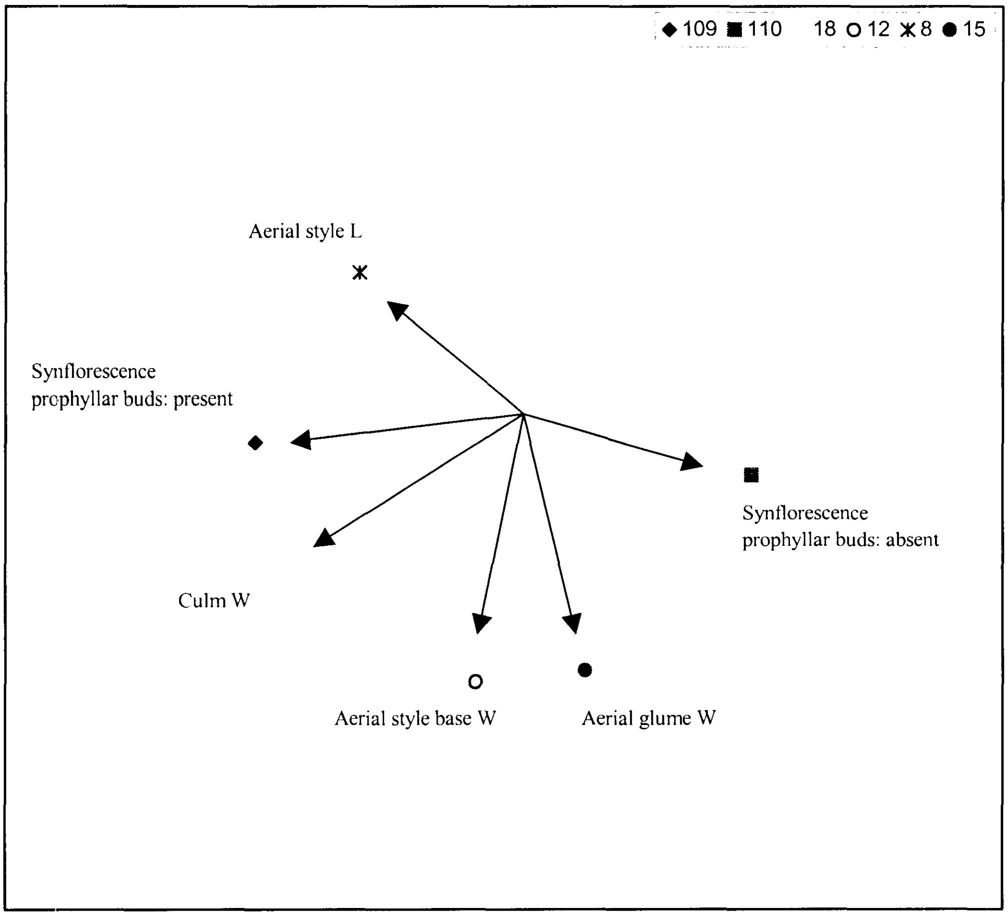


Figure 5.11 Attributes correlated (>80%) with the ordination in Figure 5.10 for OTUs of the *Bulbostylis turbinata* group. Key attributes were style length, style base width, aerial glume width, culm width, synflorescences prophyllar bud, or growth, absent/present (polymorphic). L=length, W=width. See Table 5.2 for attribute definitions.

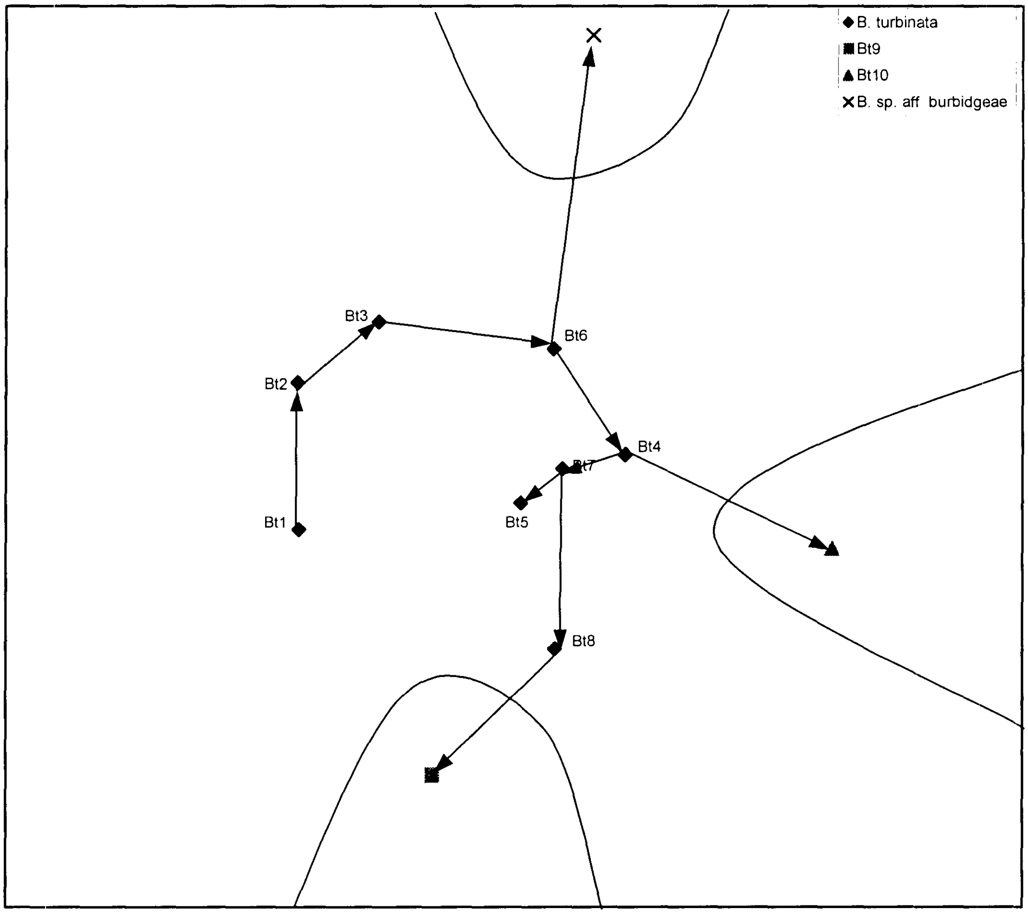


Figure 5.12 Minimum spanning tree (MST) with linkages for the *Bulbostylis turbinata* group plotted onto the 2-dimensional ordination of Figure 5.10. See Appendix 1 for specimen details.

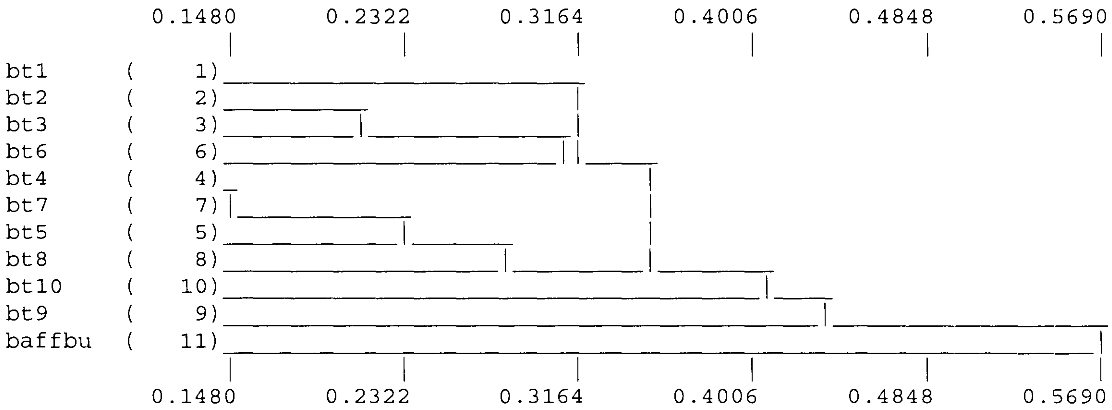


Figure 5.13 WPGMA ($\beta = -0.1$) phenogram for the *Bulbostylis turbinata* subset (see Figure 5.2 for all OTUs of *Bulbostylis*) that fits the ordination (Figure 5.10) and MST (Figure 5.12). *Bulbostylis* OTUs group together and the OTUs bt9, bt10, and *B*. sp. aff. *burbidgeae* (baffbu) remain separate. See Table 5.1 and Appendix 1 for OTU and specimen details.

Cladistic analysis

One hundred and twelve most parsimonious trees were retrieved (Tree length=1210, CI=0.4455, HI=0.5545, RI=0.5984, RC=0.2666) from a heuristic search. Tree 1 had similar topology to the tree obtained from strict consensus, and was selected to show branch support and character/branch associations (Figure 5.14).

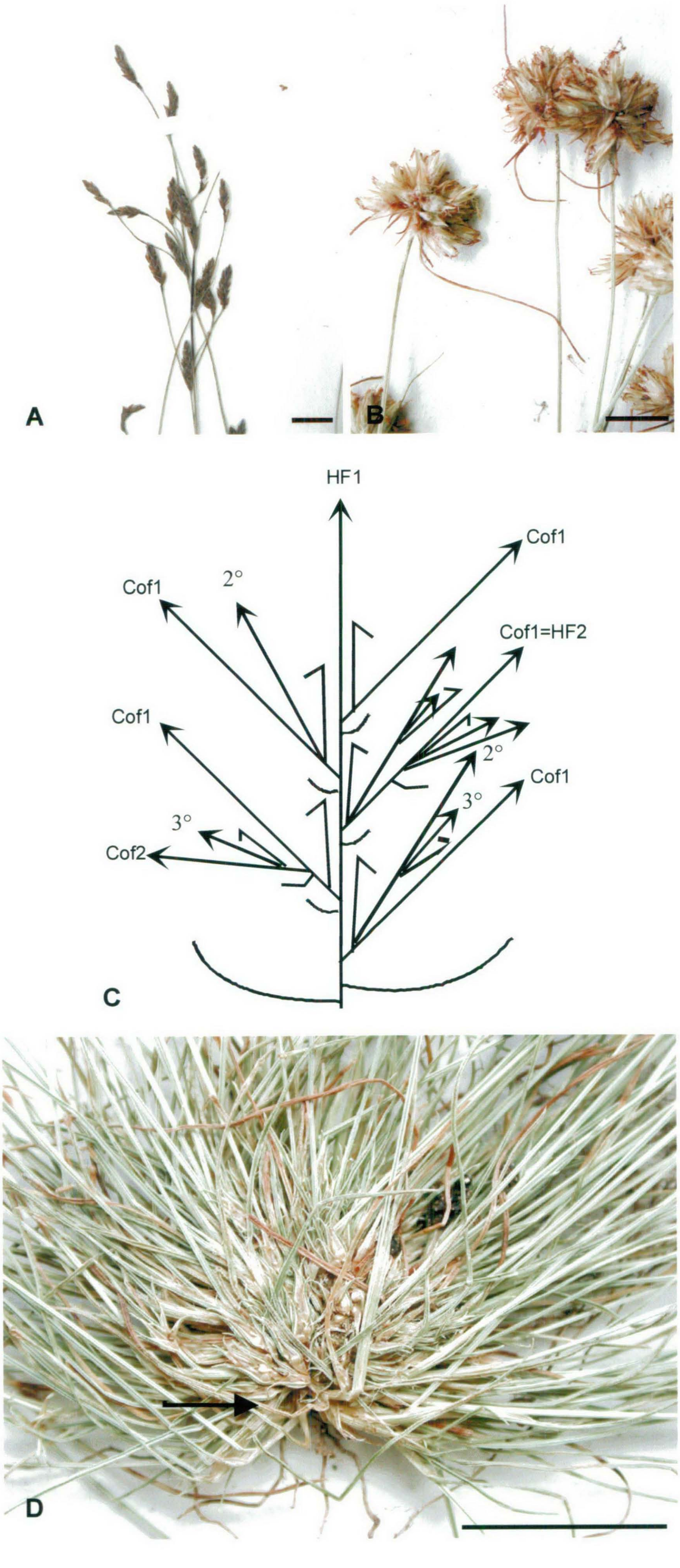
Two broad sister clades, the *Bulbostylis–Fimbristylis* clade (A) and the *Abildgaardia–Crosslandia* clade (B), form an internal clade sister to *Fimbristylis bahiensis*, which is, in turn, sister to *Fimbristylis variegata* (Figure 5.14).

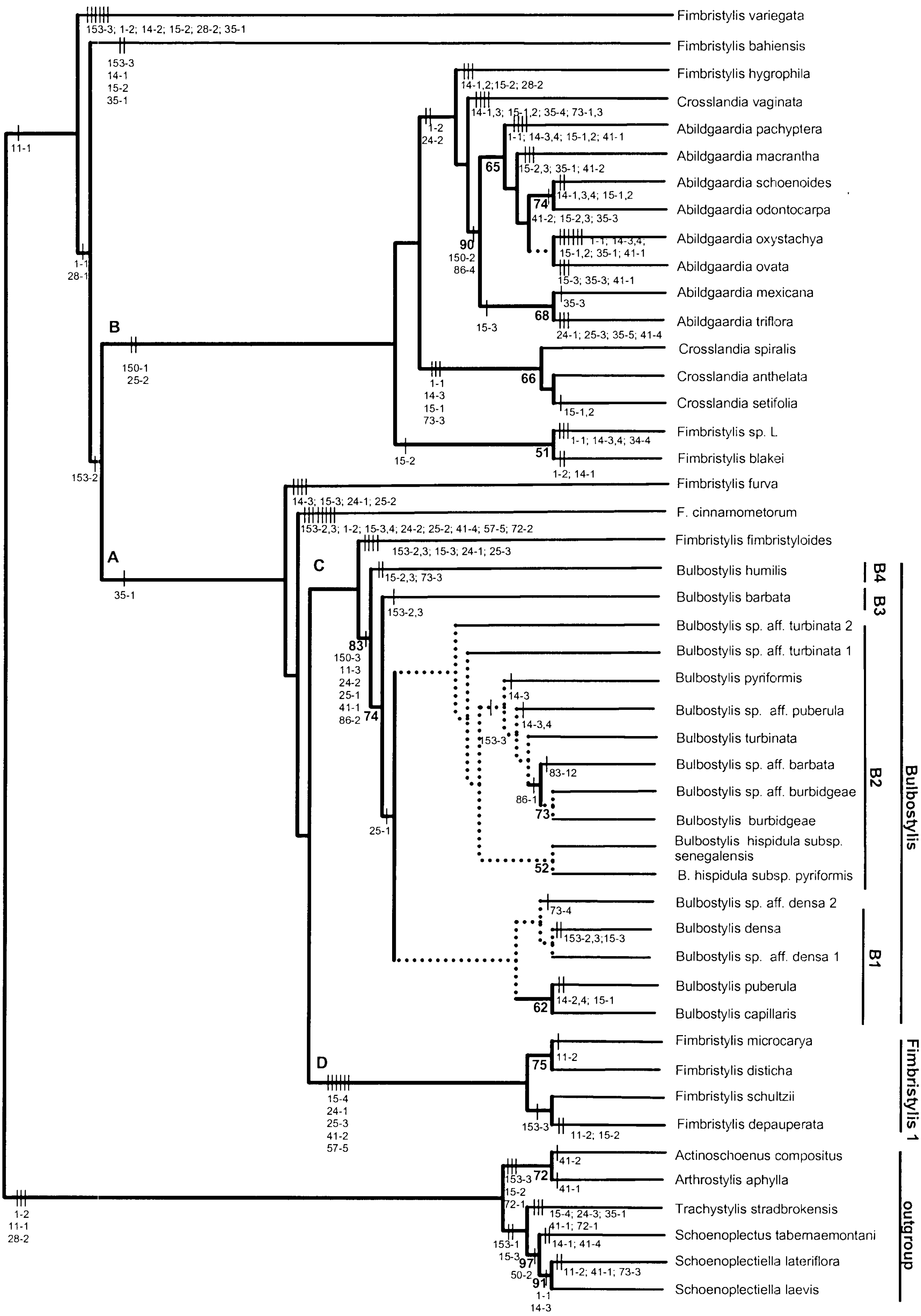
Fimbristylis continues to be retrieved as a non-monophyletic group (see also Chapters 3 and 4), seen by *F.* sp. L and *F. blakei* being placed sister to the *Crosslandia–Abildgaardia* clade. *Crosslandia* is not a monophyletic group in this analysis, as the provisional *C. vaginata* is placed sister to species of *Abildgaardia*.

Within clade A, all taxa sampled from *Bulbostylis* formed a clade (Bootstrap=83%) sister to *Fimbristylis fimbristyloides*, and combined on branch C as a group sister to the clade Fimbristylis 1 (internal branch D, contains *F. depauperata* from the TYPE section of *Fimbristylis* section *Fimbristylis*). Both clades from C and D are nested within species assigned to *Fimbristylis*.

The *Bulbostylis* clade (Bootstrap=83%) was formed by two main clades where *B. humilis* (B4) is sister to the remainder of the species (B3, B2 and B1); the latter with moderate branch support (Bootstrap=74%). *B. barbata* (B3) was sister to the terminal groups B2 (*B. pyriformis–B. turbinata–B. burbidgeae–B. hispidula* clade) and B1 (*B. capillaris–B. densa–B. puberula* clade). The strict consensus shows branch collapse for most of the terminal taxa within the *Bulbostylis* clades B1 and B2; only the terminal *B. puberula* and *B. capillaris* (with weak branch support), and *B.* sp. aff. *barbata–B. burbidgeae–B.* sp. aff. *burbidgeae* branches persist. Moderate

Figure 5.14 Cladogram for tree 1 of 112 shortest trees (tree length = 1490) in the assessment of monophyly for Australian species of *Bulbostylis*. *Bulbostylis* forms a monophyletic group sister to *Fimbristylis fimbristyloides*, forming clade C, which is sister to *Fimbristylis* 1 in clade B. *Fimbristylis depauperata* that is from the TYPE section of the genus, is placed in clade B. *Abildgaardia* and *Crosslandia* form a broad group that is sister to *Fimbristylis* sp. L and *F. blakei*; all grouped in clade D. *Crosslandia* is not monophyletic in this analysis. Within the *Bulbostylis* clade four main groups frequently occur (B1, B2, B3, B4), however, only 3 groups were retrieved from strict consensus of the 112 most parsimonious trees: B4, B3 and B1-2. Bootstrap support values are given below the branches. A, B, C, and D indicate the internal branch for the main clades. Dashed lines indicate collapsed branches in the tree from strict consensus. See Appendix 1 for specimen details and Appendix 2 for characters.


A
B
HF1
Cof1
2°
Cof1
Cof1=HF2
Cof1
2°
Cof1
3°
3°
Cof2
C
D


153-3; 1-2; 14-2; 15-2; 28-2; 35-1
Fimbristylis variegata
153-3
14-1
15-2
35-1
Fimbristylis bahiensis
11-1
1-1
28-1
14-1,2;15-2; 28-2
Fimbristylis hygrophila
14-1,3; 15-1,2; 35-4; 73-1,3
Crosslandia vaginata
1-2
24-2
1-1; 14-3,4; 15-1,2; 41-1
Abildgaardia pachyptera
65
15-2,3; 35-1; 41-2
Abildgaardia macrantha
14-1,3,4; 15-1,2
Abildgaardia schoenoides
74
41-2; 15-2,3; 35-3
Abildgaardia odontocarpa
1-1; 14-3,4;
15-1,2; 35-1; 41-1
Abildgaardia oxystachya
90
150-2
86-4
15-3; 35-3; 41-1
Abildgaardia ovata
35-3
Abildgaardia mexicana
15-3
68
24-1; 25-3; 35-5; 41-4
Abildgaardia triflora
B
150-1
25-2
Crosslandia spiralis
66
Crosslandia anthelata
1-1
14-3
15-1
73-3
15-1,2
Crosslandia setifolia
1-1; 14-3,4; 34-4
Fimbristylis sp. L
51
15-2
1-2; 14-1
Fimbristylis blakei
153-2
14-3; 15-3; 24-1; 25-2
Fimbristylis furva
153-2,3; 1-2; 15-3,4; 24-2; 25-2; 41-4; 57-5; 72-2
F. cinnamometorum
153-2,3; 15-3; 24-1; 25-3
Fimbristylis fimbristyloides
A
35-1
C
15-2,3; 73-3
Bulbostylis humilis
B4
153-2,3
Bulbostylis barbata
B3
83
150-3
11-3
24-2
25-1
41-1
86-2
74
Bulbostylis sp. aff. turbinata 2
Bulbostylis sp. aff. turbinata 1
14-3
Bulbostylis pyriformis
14-3,4
Bulbostylis sp. aff. puberula
153-3
Bulbostylis turbinata
83-12
Bulbostylis sp. aff. barbata
86-1
Bulbostylis sp. aff. burbidgeae
73
Bulbostylis burbidgeae
25-1
Bulbostylis hispidula subsp. senegalensis
52
B. hispidula subsp. pyriformis
B2
73-4
Bulbostylis sp. aff. densa 2
153-2,3;15-3
Bulbostylis densa
Bulbostylis sp. aff. densa 1
14-2,4; 15-1
Bulbostylis puberula
62
Bulbostylis capillaris
B1
Bulbostylis
11-2
Fimbristylis microcarya
75
Fimbristylis disticha
D
15-4
24-1
25-3
41-2
57-5
Fimbristylis schultzii
153-3
11-2; 15-2
Fimbristylis depauperata
Fimbristylis 1
41-2
Actinoschoenus compositus
153-3
72
15-2
72-1
41-1
Arthrostylis aphylla
1-2
11-1
28-2
15-4; 24-3; 35-1
Trachystylis stradbrokensis
41-1; 72-1
14-1; 41-4
Schoenoplectus tabernaemontani
153-1
15-3
97
50-2
11-2; 41-1; 73-3
Schoenoplectiella lateriflora
91
1-1
14-3
Schoenoplectiella laevis
outgroup

Bootstrap support (73%) for the terminal branch *B.* aff. *burbidgeae* and *B. burbidgeae* contradicts the branch collapse obtained from strict consensus (Figure 5.14).

Observations

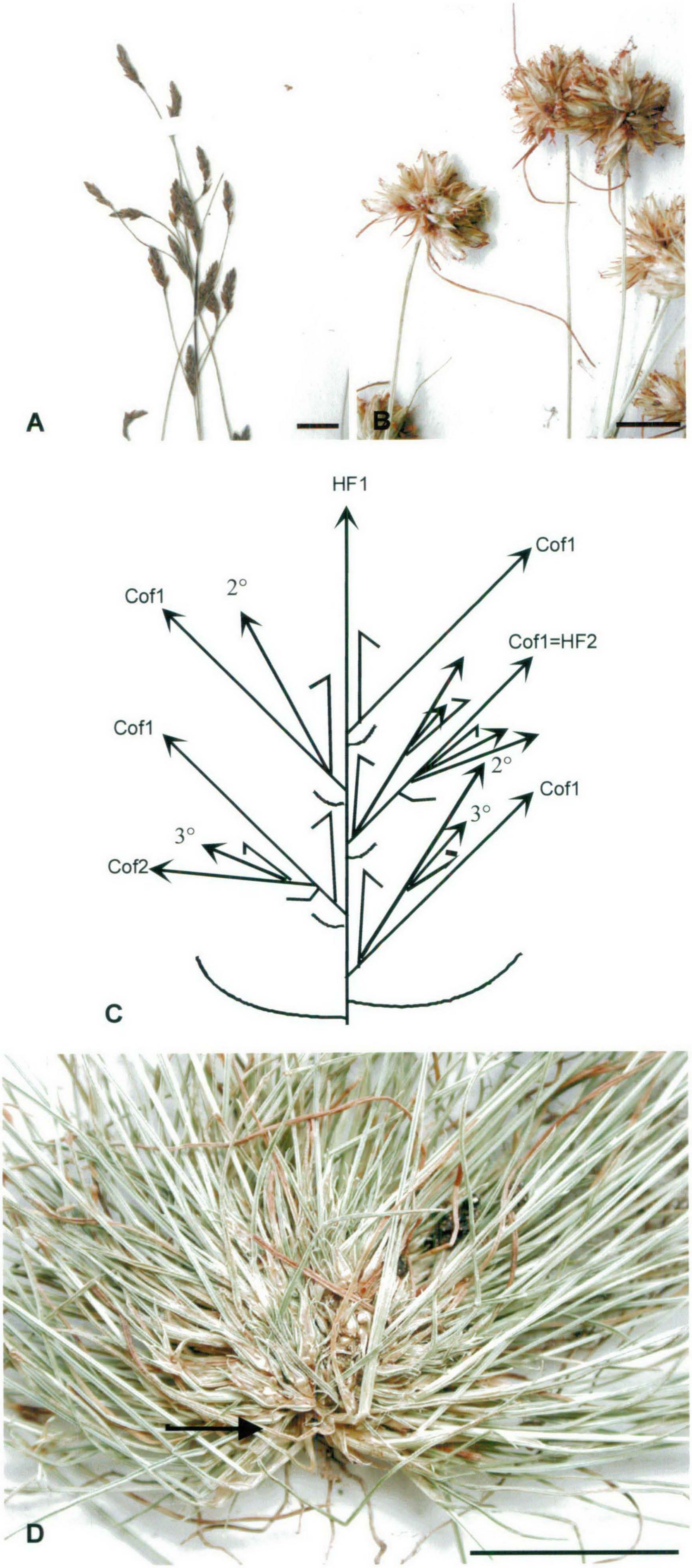
Inflorescence–synflorescence structure

Most species of the *Bulbostylis* included in the study possess primary-rayed spikelets (coflorescences). Solitary spikelets rarely occur, and if spikelets are solitary then there are at least some rayed spikelets present within the plant (Figure 5.15 A). Secondary orders within the synflorescence were frequent in *B. densa*, and *B.* sp. aff. *densa* 1, *B.* sp. aff. *densa* 2, *B. puberula*, *B. pyriformis* and *B. hispidula* subsp. *senegalensis*. Although intraprophyllar buds were often observed in the open rayed synflorescence, it was rare for the buds to mature and develop into spikelets.

The 'head' of sessile spikelets in specimens of *B. barbata* and *B.* sp. aff. *barbata* (Figure 5.15 B, C) is formed from multiple 'branched' sessile primary coflorescences, plus sessile spikelets that develop from within the inflorescence prophylls of the coflorescences. Spikelets arising from the intraprophyllar growth are distinct and contribute to the density of the 'head' of spikelets that occur in the two species. This synflorescence type of terminal capitulum (56-10) was not a synapomorphy; *B.* sp. aff. *barbata* was grouped within the 'rayed' synflorescence types of reduced anthelodium and reduced ramified anthelodium seen in the *B. pyriformis–B. turbinata–B. hispidula* clade (Figure 5.14).

Style bases in the Australian *Bulbostylis pyriformis*, and occasionally in *B. turbinata*, may persist on, or fall from the nut; the style always detaches from the

Figure 5.15 Variation of synflorescence structure for some species of *Bulbostylis*. A. Most *Bulbostylis* in the study possess 2–4 primary rayed spikelets (primary coflorescences on lengthened epipodia) as seen in *B*. sp. aff *densa* 1 (baffd2 pictured); 1–2 secondary coflorescences on rays (lengthened epipodia) may be present in the *B. densa* group, including *B. puberula*. Scale=5 mm. B. Sessile spikelets plus spikelets from prophyllar buds form a head in *B. barbata* and *B*. sp. aff. *barbata* (baffba1 pictured). Scale=5 mm. C. Representation of the prophyllar synflorescence structure seen in B. Sessile spikelets arise from the axils within the prophyll and contribute to the ramification of the synflorescence 'head' as indicated by 2° and 3° orders. D. 'Subradical' spikelets (arrow) may be present in *B. barbata* (bba8 pictured), *B. turbinata*, and *B. burbidgeae*; these spikelets have similar morphology to the aerial spikelets. Scale=10 mm. See Table 5.1 and Appendix 1 for OTU and specimen details.


A
B
HF1
Cof1
Cof1
2°
Cof1=HF2
Cof1
2°
Cof1
3°
3°
Cof2
C
D

style base leaving the style base on the nut, even if only for a short time. This is in contrast to style bases in the *B. hispidula* group, where the style may persist on the nut, or fall from the nut intact with the style. In some specimens of *B. hispidula* subsp. *senegalensis*, all the fallen styles observed had the style base intact. The large bulbous style base present in *B. pyriformis* and *B. turbinata* usually protrudes from the umbonate nut apex and tends to be easily removed. All other species scored in this study have smaller style bases that sit firmly at the apex of the nut.

Amphicarpy

The spikelets observed at the base of the plant in *B. humilis* show different morphology (73-3) to the basal spikelets of the African *B. densa* (*B.* sp. aff. *densa* 2). In *B. humilis* the basal spikelets are attenuate and florets may be bisexual. In the African *B. densa* (*B.* sp. aff. *densa* 2), the spikelets at the base of the plant are clustered in groups of 2 or 3 at the soil level (73-4) and have glumes that are much smaller than those in the aerial spikelets or in *B. humilis*. The basal glumes in *B. densa* may fall early and leave the nut exposed. Both types of basal spikelets are amphicarpic, with nuts in the basal spikelets being larger than in the aerial spikelets; the glumes also differ. Subradical spikelets (73-2) in some *B. barbata*, *B. turbinata*, and *B. burbidgeae* differ from classic amphicarpic plants, as the nuts and glumes resemble their aerial counterparts in size and shape; the spikelets occur on shortened culms (Figure 5.15 D).

Nut sculpturing

Nut epidermal shape and protuberances (or lack of) can be useful in identifying species (Figures 5.16–20), but were only broadly associated with the internal

Bulbostylis clades (Figure 5.14). Species with nuts that have papillate or granulate sculpturing (Figures 5.16–18) were split between the B1 and B2 clades, so that nuts with vertically elongated epidermal cells (Figure 5.19) were interspersed. *Bulbostylis burbidgeae* nut epidermal cell walls are barely to mildly sinuose, as are the *B. hispidula* and *B. pyriformis* samples (Figure 5.19). In contrast, *Bulbostylis barbata* and *B.* sp. aff. *barbata* have epidermal cell walls that are very strongly sinuose (Figure 5.20). Samples from the *Bulbostylis turbinata* group fall between the two extremes (Figure 5.18).

Embryo morphology

All species within this study, that formed the clade *Bulbostylis* share the general Bulbostylis-type embryo (synapomorphy 150-3; Figure 5.14). Variation in the size and general shape of embryos was observed (Figures 5.21–22). The embryos from *B.* sp. aff. *densa* 1 and *B.* sp. aff. *barbata* were the smallest sampled, with the very dense cellular contents obscuring visibility of the primordial leaf or leaves (Figure 5.21 B, D). Embryos from *B. hispidula* subsp. *pyriformis* (Figure 5.22 A, B) and *B. hispidula* subsp. *senegalensis* (Figure 5.22 C, D) are conspicuously larger than embryos of the other species; the basal orientated shoot and root are prominent, and the second primordial leaf is well-developed and almost the same size as the first leaf. The embryo of *Bulbostylis pyriformis* is slightly smaller than that in *B. hispidula* and the second primordial leaf was visible, although not well-developed (Figure 5.22 E, F). *Bulbostylis humilis* (Figure 5.22 G, H) has an embryo size and internal structure similar to that seen in the *B. hispidula* specimens.

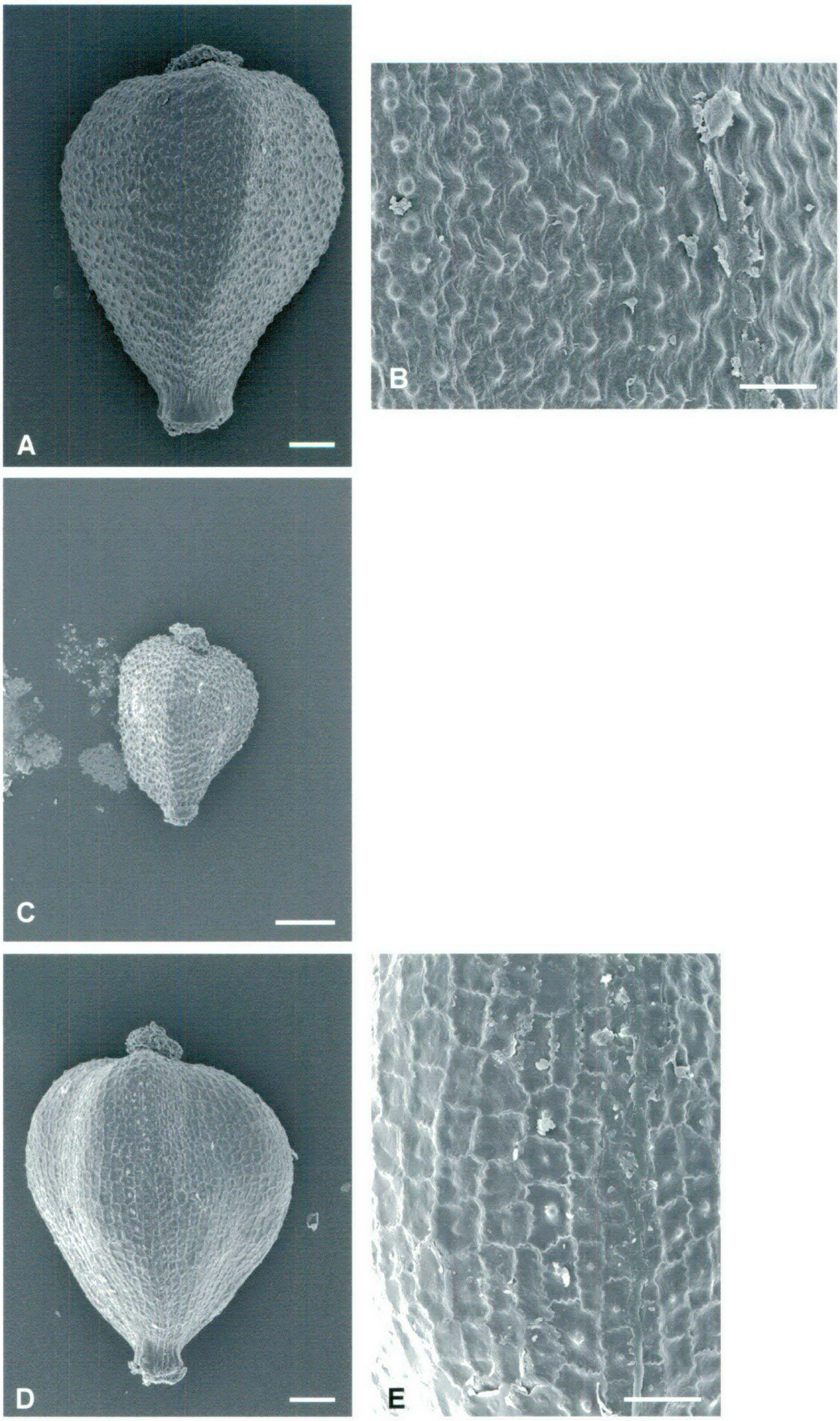


Figure 5.16 Scanning electron micrographs (SEM) showing the variation of nuts for some samples of the *Bulbostylis densa* group. A. *B. densa* (bde2) with B. epidermis at higher magnification; C. *B. densa* (bde3); and D. *B.* sp. aff. *densa* 1 (baffd1) with E. epidermis at higher magnification, showing epidermal cells with minute central silica body. Epidermal cell walls are sinuose. Scale bar for A, D=100 μm; B, E=50 μm; C=200 μm. See Table 5.1 and Appendix 1 for OTU and specimen details.

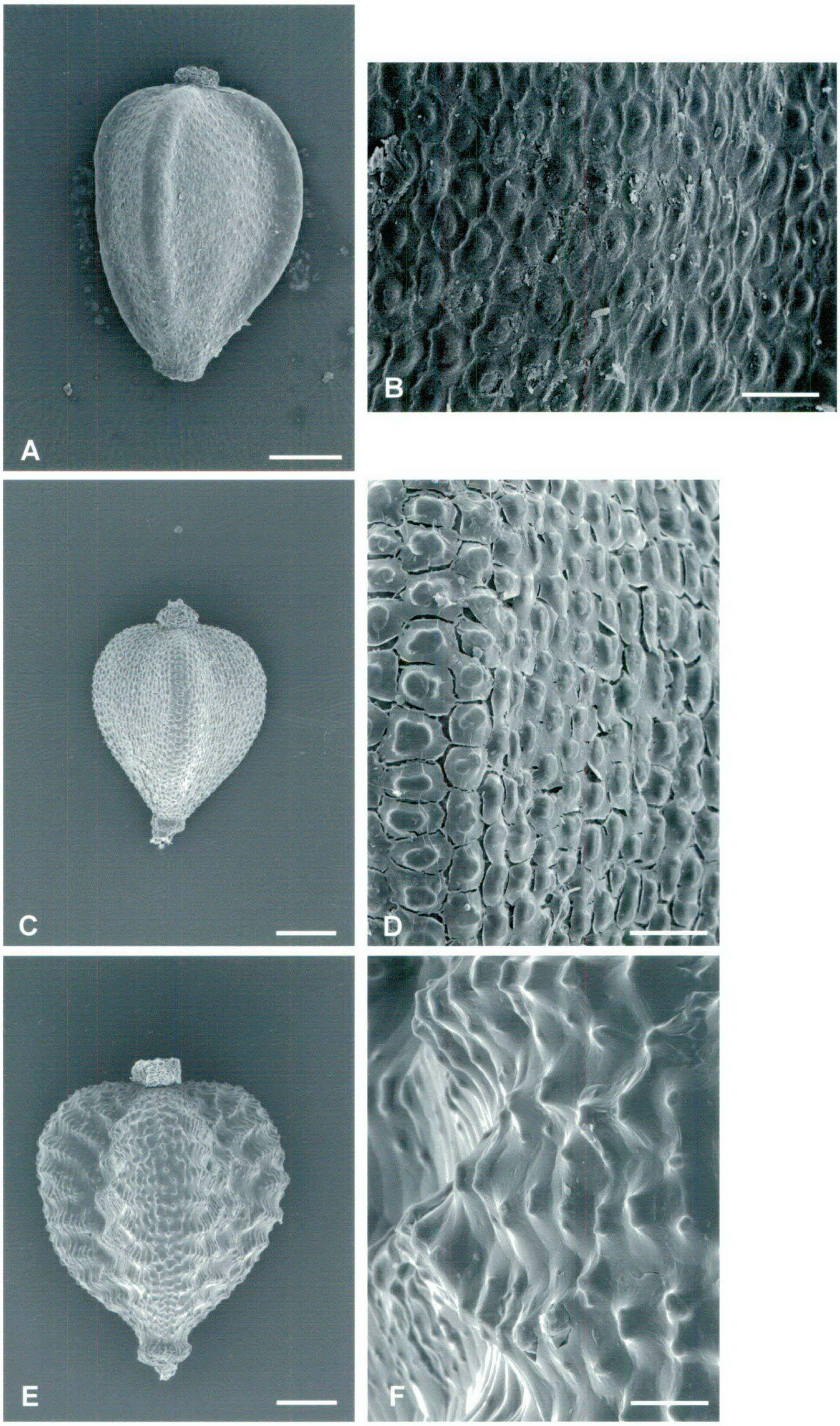


Figure 5.17 Scanning electron micrographs (SEM) showing the variation of nuts for samples of the *Bulbostylis burbidgeae* group. A. *B. burbidgeae* (bbu5) with B. epidermis at higher magnification; C. *B.* sp. aff. *burbidgeae* (baffbu); with D. epidermis at higher magnification; E. *B.* sp. aff. *puberula* 1 (baffpu) with F. epidermis at higher magnification, showing epidermal cells forming angular ridges. Scale bars A, D=100 μm; B, E=50 μm; C=200 μm. See Table 5.1 and Appendix 1 for OTU and specimen details.

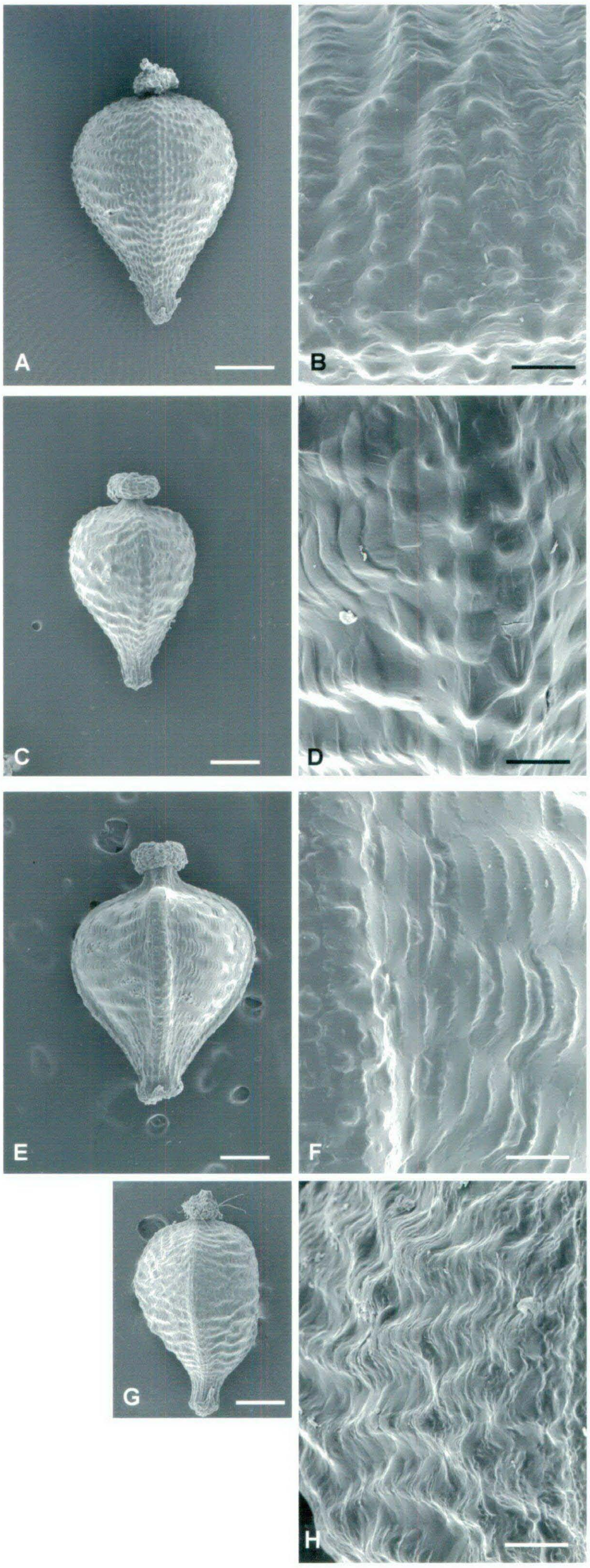


Figure 5.18 Scanning electron micrographs (SEM) showing the variation of nuts for samples of the *Bulbostylis turbinata* group. A. *B. turbinata* (bt3) with B. epidermis at higher magnification; C. *B. turbinata* (bt7) with D. epidermis at higher magnification; E. *B. turbinata* (bt9) with F. epidermis at higher magnification; G. *B. turbinata* (bt10) with H. epidermis at higher magnification. OTUs bt9 and bt10 formed a group separate to other *B. turbinata* samples (see Figure 5.2), consistent with the nut differences pictured. Scale bars for A, C, E, G=100 μm; B, D, F, G=50 μm. See Table 5.1 and Appendix 1 for OTU and specimen details.

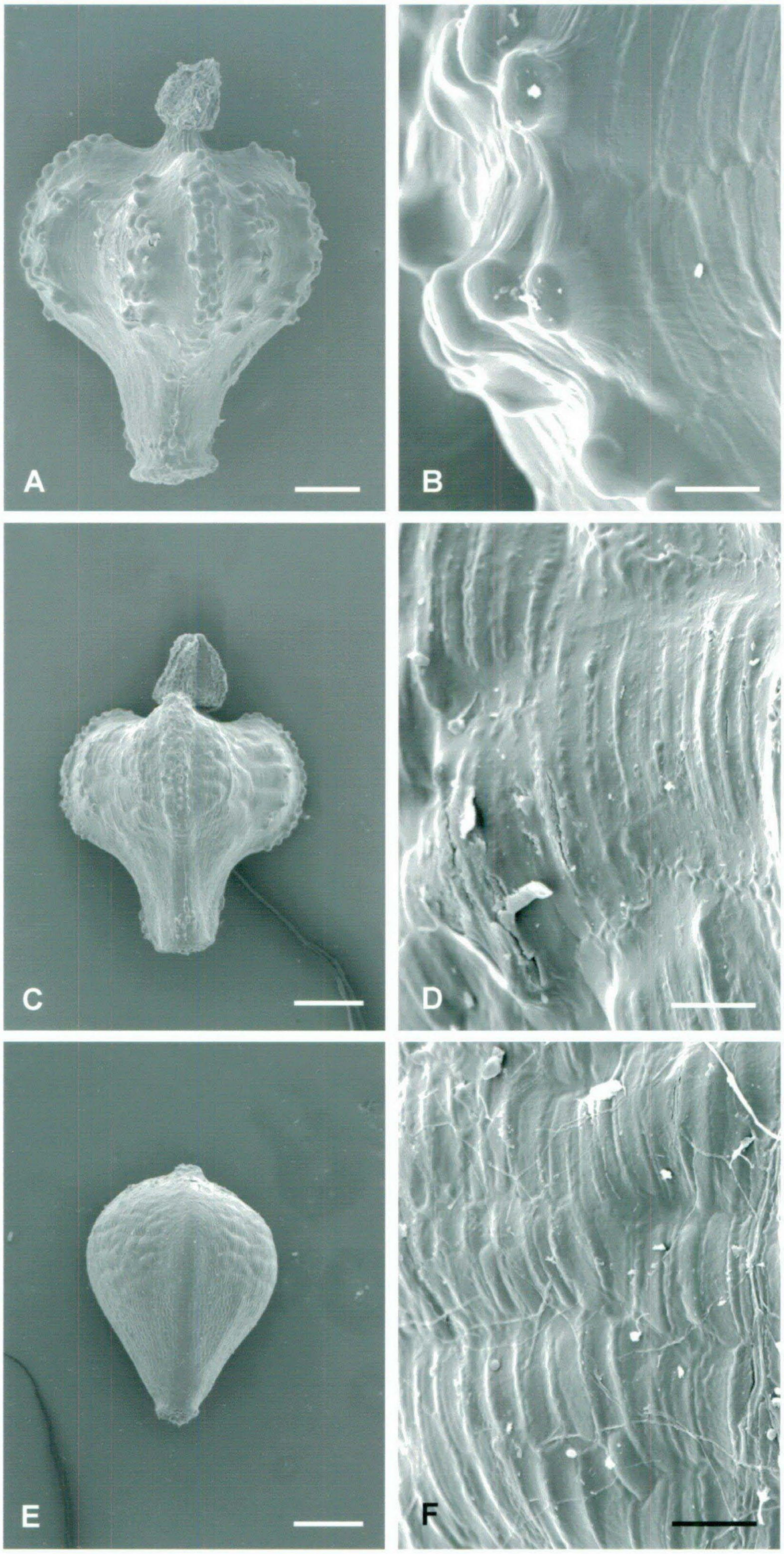


Figure 5.19 Scanning electron micrographs (SEM) showing the variation of nuts for samples from *Bulbostylis pyriformis* and the *B. hispidula* complex. A. *B. pyriformis* (bpy5) with B. epidermis at higher magnification; C. *B. hispidula* subsp. *pyriformis* (*M. Richards 23175B*); with D. epidermis at higher magnification; E. *B. hispidula* subsp. *senegalensis* (*J.T. Davey 10*) with F. epidermis at higher magnification. All samples have vertically elongated epidermal cells that may be raised so that the nut sculpturing is rugose. Scale bars A=200 µm; C, E=500 µm; B, D, F=50 µm. See Table 5.1 and Appendix 1 for OTU and specimen details.

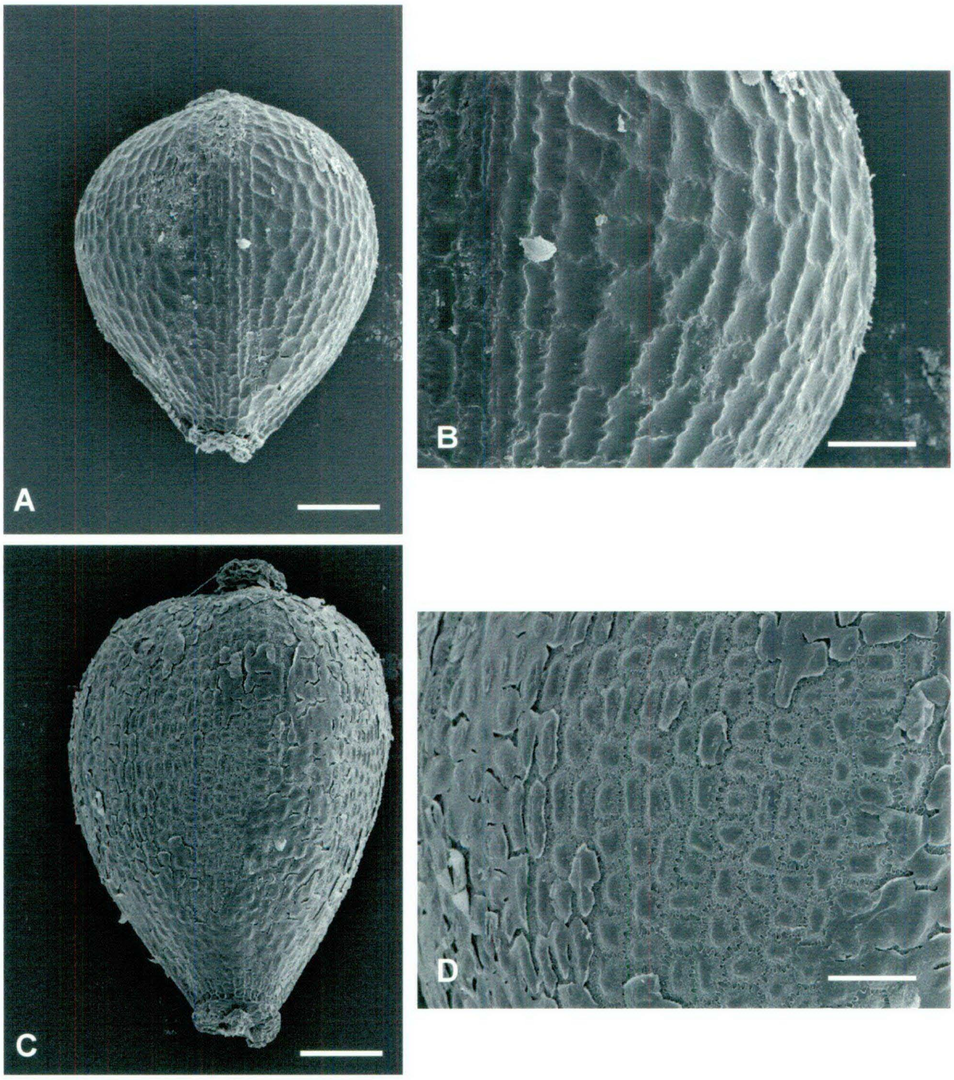


Figure 5.20 Scanning electron micrographs (SEM) showing the differences between nuts of *Bulbostylis barbata* and *B*. sp. aff. *barbata*. A. *B.*sp. aff. *barbata* (baffba5) with B. epidermis at higher magnification; C. *B. barbata* (bba5); and D. epidermis at higher magnification, showing wax plates on the surface that break away to reveal strongly sinuose cell walls around the isodiametric cells, creating a reticulate pattern over the surface of the nut. Scale bar A, C=200 µm; B, D=50 µm. See Table 5.1 and Appendix 1 for OTU and specimen details.

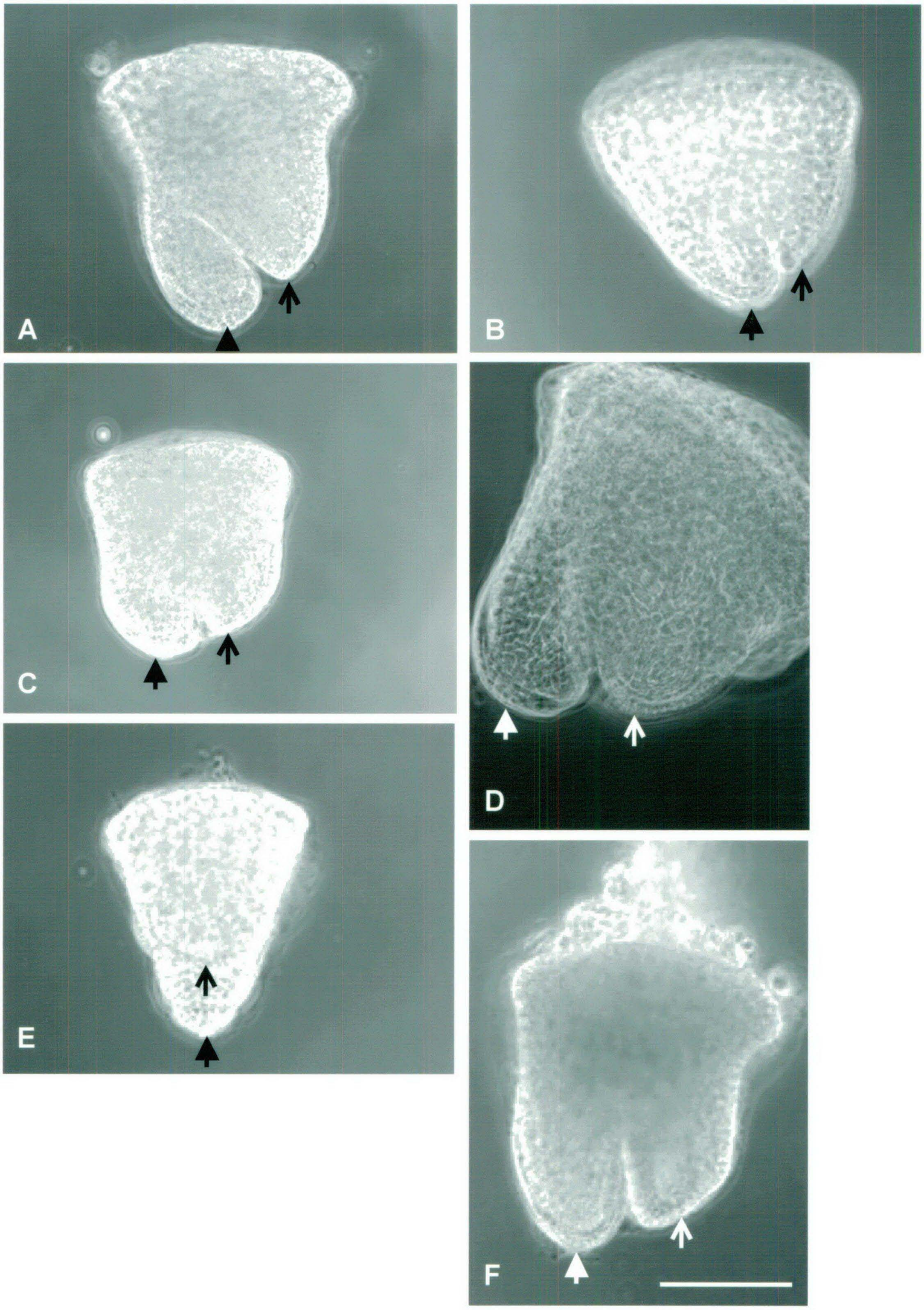


Figure 5.21 A. Embryo morphology in *Bulbostylis*. *B. capillaris* (*G. Davidse*) B. *B.* sp. aff. *densa* 1 (baffd1) C. *B.* sp. aff. *barbata* (baffba4) D. *B. barbata* (bba18) E. *B.* sp. aff. *burbidgeae* (baffbu) F. *B. puberula* (*G. Davidse 9037*). Collector and collection number, or specimen OTU label are given in brackets. Open arrow=shoot, closed arrow=root. Scale bar=100 μm (for all images). See Table 5.1 and Appendix 1 for specimen details.

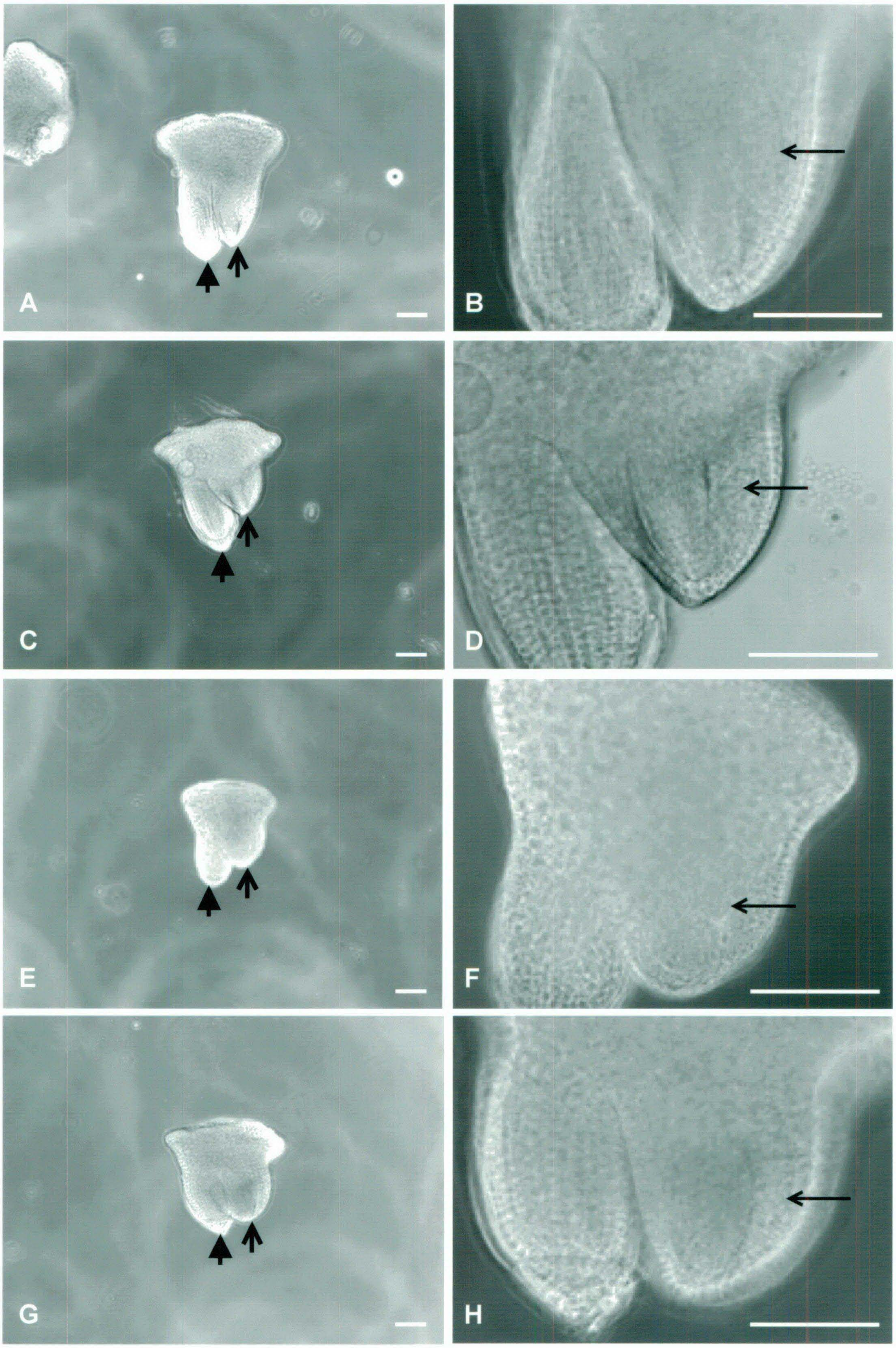


Figure 5.22 Variation in *Bulbostylis* embryo size, shape, and development of second primordial leaf. A. *B. hispidula* subsp. *pyriformis* (*M. Richards 23175B*) and B. the well-developed second primordial leaf (long arrow). C. *B. hispidula* subsp. *senegalensis* (*J.T. Davey 10*) and D. the second primordial leaf is well-developed. E. *B. pyriformis* (bpy2) with a slightly smaller sized embryo and F. second primordial leaf visible but not well developed. G. *B. humilis* (*C.P. Strong et al.)* embryo with H. second primordial leaf well-developed. Open arrow=shoot, closed arrow=root. Collector and collector number, or OTU label are given in brackets. Scale bar=100 μm. See Table 5.1 and Appendix 1 for specimen details.

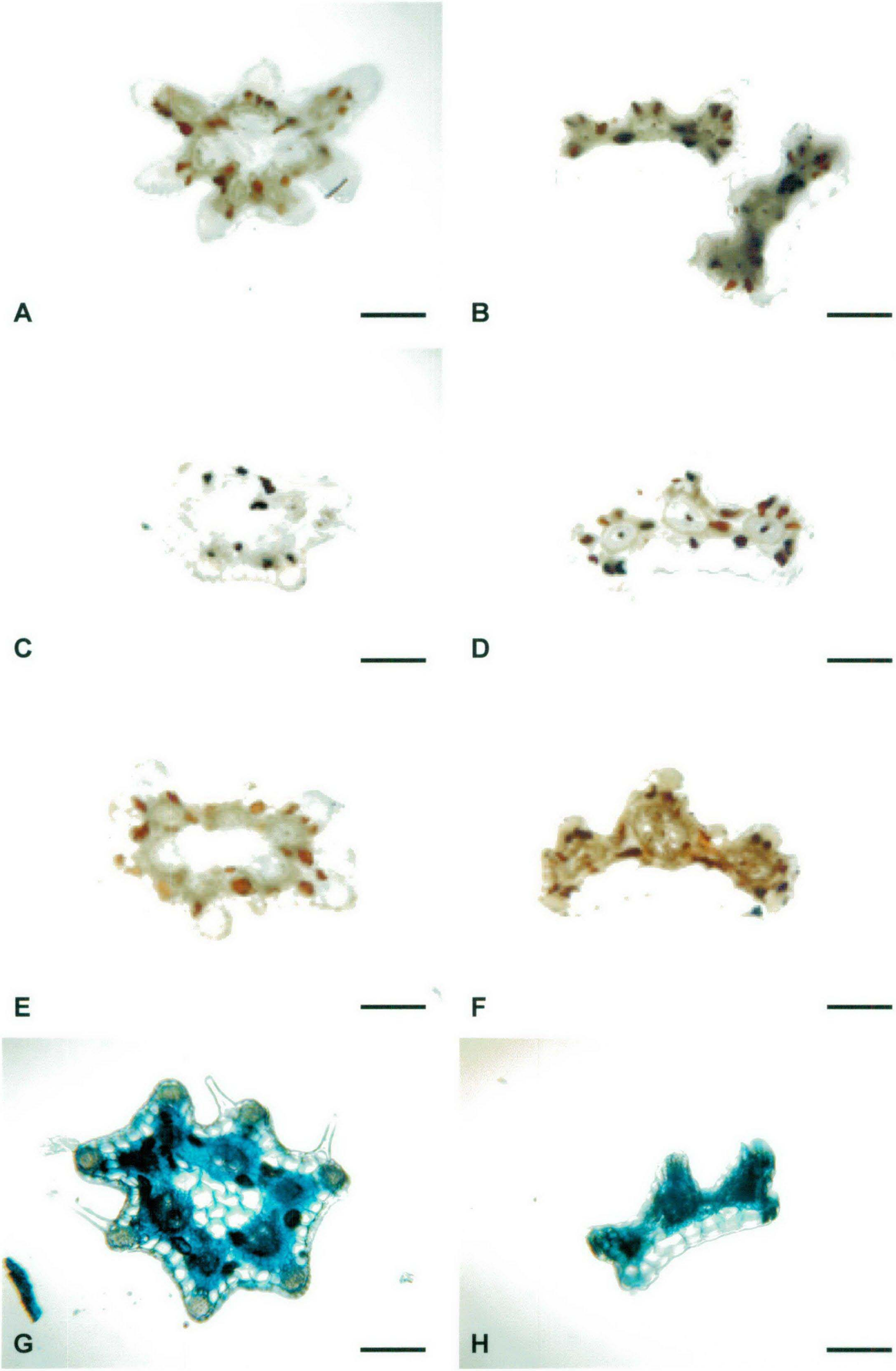


Figure 5.23 Culm and leaf blade transverse sections in *Bulbostylis*. A. Culm and B. leaf blade sections of *B. capillaris* (*G. Davidse*); C. culm and D. leaf blade sections of *B.* sp. aff. *densa* 1 (*A.R. Bean 3236*); E. culm and F. leaf blade *B.* sp. aff. *densa* 1 (*Field survey team 820*); G. culm and H. leaf blade sections of *B. densa* (bde2). Collector and collection number, or OTU label are given in brackets. Scale bar=100 µm. See Table 5.1 and Appendix 1 for specimen details.

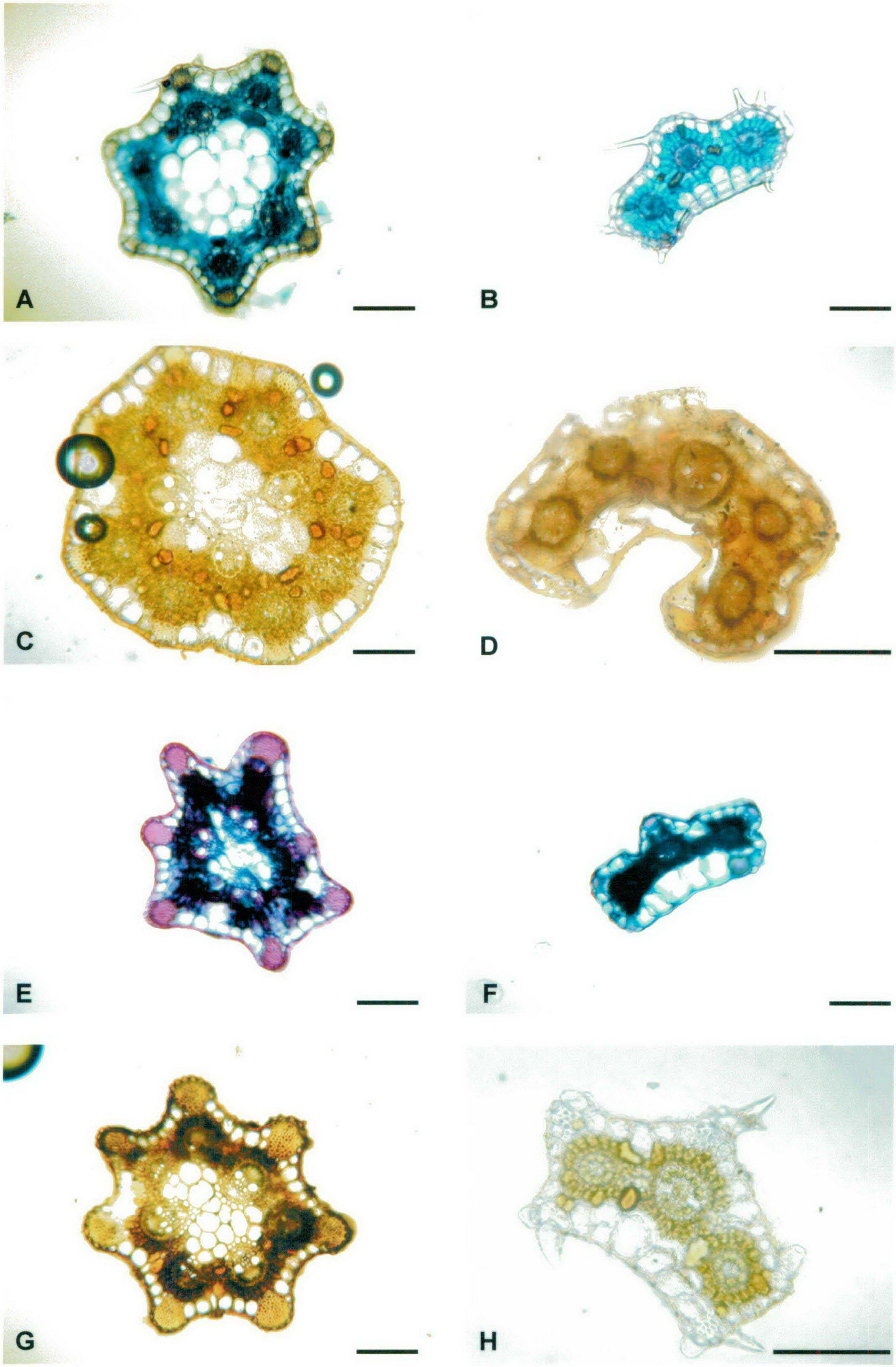


Figure 5.24 Culm and leaf blade transverse sections for *Bulbostylis*. A. Culm and B. leaf blade sections of *B. burbidgeae* (bbu5). Variation observed in C. culm and D. leaf blade sections of *B. barbata* (*K.L. Clarke 187 et al.*), and E. culm and F. leaf blade for OTU bba1. G. Culm and H. leaf sections for *B.* sp. aff. *barbata* (baffba1). Collector and collection number, or OTU label are given in brackets. Scale bar=100 µm. See Table 5.1 and Appendix 1 for specimen details.

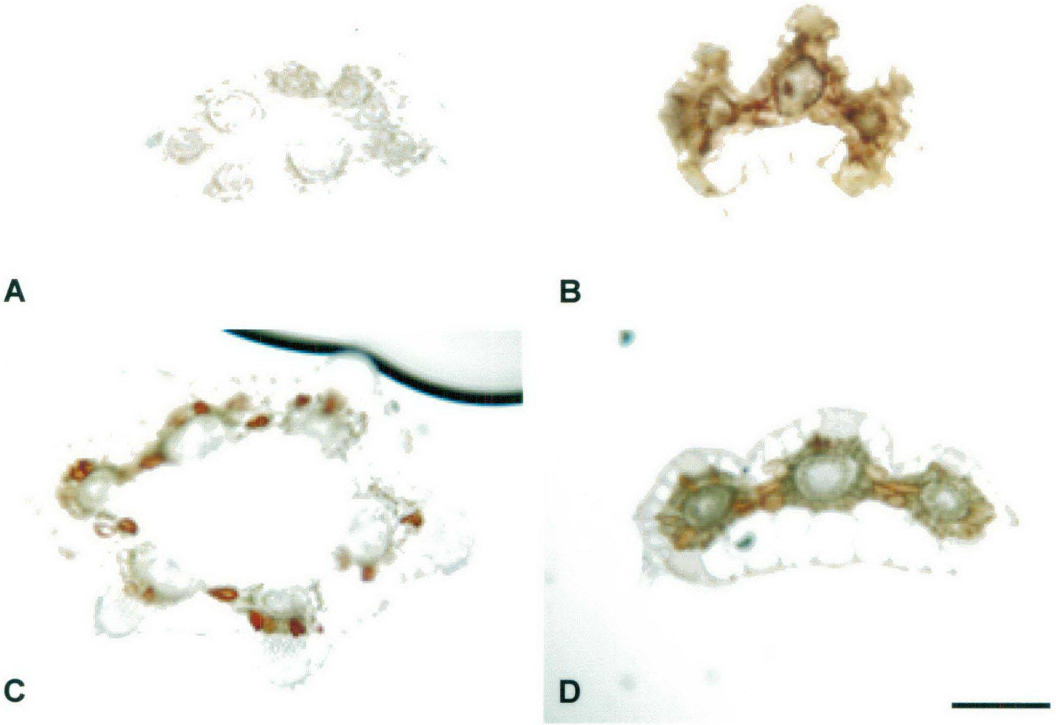


Figure 5.25 Culm and leaf blades transverse sections for *Bulbostylis*.
A. Culm and B. leaf blade sections of *B. puberula* (*G. Davidse 9037*); C. culm and D. leaf blade sections of *B. humilis* (*C.P. Strong et al.*) Collector and collection number are given in brackets. Scale bar=100 µm. See Table 5.1 and Appendix 1 for full specimen details.

Vegetative anatomy

The leaf blade anatomy of all species of *Bulbostylis* in this study conforms to the C_4 fimbristyloid photosynthetic pathway (Figures 5.23–25). Leaf blades in transverse section are either sub-triangular in outline, or channelled (canaliculate), usually with two shallow or acute ribs. Most species sampled have three vascular bundles within the leaf, occasionally five in *B. barbata* (Figure 5.24). A hypodermis is absent from the leaves of all sampled species and the adaxial epidermal cells are inflated roughly four times that of the abaxial epidermis. Culms are mostly regularly grooved and almost circular in outline, to irregularly circular and barely wavy (Figures 5.23–25). All species sampled have numbers of vascular bundles equal to the number of sclerenchyma strands. The vascular bundles form one concentric ring below the epidermal layer. Sclerenchyma strands are often bulbous, forming the ridges of the channels, but may be square to just rectangular (Figures 5.23–25).

Discussion

The group recovered in phenetic analyses as *Bulbostylis* sp. aff. *barbata* is a distinct new species, as indicated by its placement in the combined minor clades B1 and B2, sister to *B. barbata* (see Figure 5.14). The variation observed in *B. barbata* is consistent across the global geographic range. I have not seen the TYPE specimen for *B. barbata* subsp. *pulchella*, but the representative samples from India included in this study (Appendix 1) do not differ greatly from the other sampled specimens (as defined in phenetic analyses). To assess the limits of the species and subspecies, it is recommended that *B. barbata* subsp. *pulchella* be compared with a wider sample.

High levels of homoplasy for many of the *Bulbostylis* sampled could explain the lack of overall terminal branch support within the cladistic analyses of this chapter. In general, species of *Bulbostylis* form a monophyletic group sister to the clade of main *Fimbristylis* species (F1) and was in direct contrast to placement of *Bulbostylis* in Chapters 3 and 4, where the two species of *Bulbostylis* (*B. barbata* and *B. densa*) were nested within the same *Fimbristylis* species that form the F1 clade of this analysis. The consistency of the embryo type and vegetative anatomy appears to have been important in stabilising the results, despite extensive homoplasy across many of the morphological characters.

The presence and development of the second and third primordial leaves in the embryo could provide a strong character for grouping species into sections if these structures could be viewed in all the sampled embryos. The sampled species of *Bulbostylis* with larger nuts (*B. hispidula*, *B. humilis*) had larger embryos and a prominent second primordial leaf. *Bulbostylis pilosa* falls into this category, having the largest embryo sampled in Van der Veken's (1965) study of *Bulbostylis*, and was shown to have the second primordial leaf well-developed and almost as large as the first leaf. *Bulbostylis breviculmis* (a synonym of *B. striatella*) was shown to have a poorly developed second leaf (Van der Veken 1965), differing from the embryo observed in *B. humilis* within this study. These differences question the synonomy of *B. breviculmis*, or the consistency, and therefore usefulness as a character, of the development of the second primordial leaf.

The smaller embryo (although larger than the other Australian species), and nut size in general, plus the less developed second leaf in the Australian *B. pyriformis* contribute to maintaining species level status separate from *B. hispidula*. Clearly there are general similarities in nut shape, epidermal patterning (see Figure 5.19), and synflorescence morphology between specimens of *B. pyriformis* and the *B. hispidula*; however, a more comprehensive study is needed to assess the broad similarities between all entities of the *B. hispidula* complex and *B. pyriformis*.

Those species with the smaller embryos, where the primordial shoot and root is less prominent, are mostly grouped in the B1 clade (i.e. *B. densa* group, *B. puberula*, and *B. capillaris*). If the inner organs could be scored, however, the uncertainty with the placement of taxa that currently fall into the B2 clade may be resolved. These taxa, *B.* sp. aff. *barbata*, *B.* sp. aff. *burbidgeae*, *B.* sp. aff. *puberula* and *B. burbidgeae*, seem 'misplaced' due to general embryo morphology and nut characters. In samples with an abundance of fruits, sectioning embryos embedded in paraffin wax, would allow the scoring of the internal organs to assess specific groups.

Prophyllate spikelets, seen within the synflorescence for *B. barbata* and *B.* sp. aff. *barbata*, or prophyllate buds that were present in most of the *Bulbostylis* samples in the phenetic study, and as reported by Guaglianone (1970), have also been described for some species of *Schoenoplectus* (e.g. *S. calfornicus*) and *Rhynchospora* (e.g. *R. corymbosa*, *R. brownii*) (Kukkonen 1986; Vegetti 2003). Extending the sample across species in *Bulbostylis* is recommended to investigate the usefulness of the character more thoroughly.

Spikelets found at the base of the plant have been recorded previously for *B. humilis* (syn. *B. striatella*), *B. heterostachya* Cherm. (Chermezon 1929), *B. glaberrima* Kük. (Haines 1971), *B. basilis* Fosberg, *B. schaffneri* (Boeck.) C.B.Clarke, *B. sphaerocarpa* (Boeck.) C.B.Clarke (Fosberg 1977), and *B. funckii* (Steud.) C.B.Clarke (Goetghebeur and Gröger 1993). Amphicarpy occurs across a number of genera and has been reported in *Trianoptiles* i.e. *T. capensis* (Steud.) Harv., *T. solitaria* (C.B.Clarke) Levyns (Levyns 1943; Haines and Lye 1977), *Schoenoplectus* i.e. *S. erectus* (Poir.) Palla ex J.Raynal subsp. *raynalii* (Schuyler) Lye, *S. lateriflorus* (J.F.Gmel.) Lye subsp. *lateriflorus, S. microglumis* Lye, *S. articulatus* (L.) Palla, *S. senegalensis* (Hochst. ex A.Rich.) Palla, *S. leucanthus* (Boeck.) J.Raynal, *S. proximus* (Steud.) J.Raynal, *Eleocharis* i.e. *E. minima* Kunth (Browning 1992), *E. caespitosissima* Baker (Bruhl 1994), and *Crosslandia* (see Chapter 3). The African material of *B. densa* (baffd2: bde16, 17, 18) has classic amphicarpic nuts, and when combined with the generally larger anther length, fimbriolate glume margins of the mostly mucronate glumes, and the inflorescence of mainly solitary or reduced anthelodia (anthela of 2-3 rays), forms a group separate to the other *B. densa* OTUs. It is necessary to compare the African amphicarpic material more broadly with other species of the *B. densa* complex as per Haines and (1983), and Gordon-Gray (1995) to fully assess the species boundaries.

The variation in floret sex of the radical spikelets seen in *B. humilis* was reported as common among species of *Bulbostylis* by Chermezon (1929). Bisexual or female florets may occur in the radical spikelets, and the stamen number may be variable compared to the more consistent numbers in aerial spikelets.

Spikelets that may be present near the base of the plant as well as the aerial spikelets in *B. barbata* and *B. turbinata* do not exhibit amphicarpic features, and are termed subradical by Wilson (1980). None of the examined overseas specimens of *B. barbata* have subradical spikelets, the presence of which is a likely result of the extreme environmental conditions in which they grow. Most of the specimens that exhibit greatly reduced culms have been collected from the dry desert regions of central and north-western Australia (see Appendix 1). Subradical spikelets usually produce fruit earlier than aerial spikelets, but this could be due to the later development of aerial spikelets once conditions are more favourable. Experiments would be needed to test the effects of harsh environments on the production of subradical spikelets in *Bulbostylis barbata.* Further study could concentrate more specifically on the variation within *B. barbata*, by expanding the sample size and including molecular data within the study to fully explore the presence of subradical spikelets.

Raynal (1976) used the potential to develop amphicarpy in species of *Schoenoplectus* to redefine *Schoenoplectus* section Supini (Cherm.) J.Raynal. Assessing all the species currently assigned to *Bulbostylis* could provide similar results, when used in conjunction with data from embryo morphology and anatomy, and general vegetative morphology. Using Clarke's (1908) classification of *Bulbostylis*, all the species known then to be amphicarpic, are found in sections I and II.

The putative new species *Bulbostylis* sp. aff. *barbata* can now be named using the results of the phenetic and cladistic data as support. A distinctly smaller nut, different from all other Australian species, and the hairy glume margins of the almost hyaline glumes, supports the recognition of this new species, known only from Kakadu National Park, Northern Territory.

Given the limited sample size of the unknown identities, *B.* sp. aff. *densa* 1, bt9, bt10, *B.* sp. aff. *puberula* and *B.* sp. aff. *burbidgeae*, and the broad variation within the *Bulbostylis densa* and *B. hispidula* groups, it seems necessary to explore the limits of taxa in these groups more broadly by increasing the sample size and the number of species in subsequent analyses. Comparing the unknowns to other overseas species is also necessary to exclude the possibility of extended ranges, possibly introduced into Australia via human movement.

A new combination is now provisionally put forward prior to valid publication.

Nomenclature of *Bulbostylis* in Australia

Genus: ***Bulbostylis*** Kunth (nom. cons.) Enumeratio Plantarum 2: 205 (1837)

TYPE: ***Bulbostylis capillaris*** (L.) Kunth ex C.B.Clarke in J.D. Hooker, Fl. Brit. India 6:652 (1885)
Basionym: *Scirpus capillaris* L.

1. *Bulbostylis barbata* (Rottb.) C.B.Clarke
Basionym: *Scirpus barbatus* Rottb.
B. eustachyii Eardley

2. *Bulbostylis burbidgeae* K.L.Wilson

3. *Bulbostylis densa* (Wall.) Hand.-Mazz.
Basionym: *Scirpus densus* Wall.
Bulbostylis capillaris var. *trifida* (Nees) C.B.Clarke

4. *Bulbostylis humilis* (Kunth) C.B.Clarke
Basionym: *Isolepis humilis* Kunth
Fimbristylis arenaria Nees
Isolepis breviculmis Kunth
Scirpus arenarius (Nees) Boeck.
Bulbostylis breviculmis (Kunth) C.B.Clarke
Isolepis humillima Hochst. ex C.B.Clarke
Bulbostylis striatella C.B.Clarke
Abildgaardia humilis (Kunth) Lye
Abildgaardia striatella (C.B.Clarke) Lye

5. *Bulbostylis kakadu* K.L.Clarke & J.J.Bruhl sp. nov. ined.

6. *Bulbostylis pyriformis* S.T.Blake

7. *Bulbostylis turbinata* S.T.Blake

Specimens with uncertain species limits, *B.* sp. aff. *densa* 1, *B.* sp. aff. *densa* 2 (African amphicarpic), *B.* sp. aff. *turbinata* 1, *B.*sp. aff. *turbinata* 2, *B.* sp. aff. *burbidgeae*, and *B.* sp. aff. *puberula*, need to be assessed against a broader sample of species from *Bulbostylis* prior to publication.

Species of uncertain standing

Bulbostylis pilosa (Steud.) Beetle nom. illeg. Leaflets of Western Botany 4: 45 (1944)
Basionym: *Isolepis pilosa* Steud. Type: Hrbr. Drummond IV nr. 360 (nisi schedula commutata) N. Holl.

The TYPE specimen is not located in Australia, and until the TYPE sheet can be examined, placement of this taxon within Australian species cannot be determined.

Chapter 6

Testing monophyly of the tribe Abildgaardieae Lye

Introduction

The aim of this chapter is to test monophyly for the tribe Abildgaardieae Lye by subjecting representatives of all genera assigned to the tribe by Goetghebeur (1986, 1998) and Bruhl (1995) (Table 6.1) to cladistic analysis. The genera, *Abildgaardia* Vahl (the TYPE genus), *Fimbristylis* Vahl (including *Tylocarya* Nelmes (Kern 1974; Simpson 1993; Goetghebeur 1998), or *Tylocarya* treated as a distinct genus (Goetghebeur 1986; Bruhl 1995), *Bulbostylis* Kunth, *Crosslandia* W.Fitzg., *Nemum* Desv. ex Ham., and *Nelmesia* Van der Veken, are the focus of the study.

The general history of the tribe Abildgaardieae was outlined in Chapter 1, as were problem areas where disagreement on generic boundaries persists. The position of *Abildgaardia*, assigned as a section (or series) of *Fimbristylis* (Koyama 1961; Kern 1974; Simpson 1993): as Monostachyae Ohwi, or as a genus (Vahl 1805; Kral 1971; Haines and Lye 1983; Goetghebeur 1986; Bruhl 1995; Gordon-Gray 1995; Goetghebeur 1998), is specifically relevant in this study because of the large number of species that occur in, and are endemic to, Australia (see Chapter 4). The status of *Tylocarya* is either as a monotypic genus (Bruhl 1995), or more generally accepted, as a species of *Fimbristylis*, *F. nelmesii* J.Kern (Kern 1974; Simpson 1993; Goetghebeur 1998).

Although *Bulbostylis* currently has wide acceptance as a genus, separate from *Fimbristylis*, the distinction is tenuous. Koyama (1961) classified *Bulbostylis* as a subgenus of *Fimbristylis*, and Lye (in Haines and Lye 1983) placed *Bulbostylis* as a subgenus within *Abildgaardia*, although both authors have since reverted to using *Bulbostylis* at the generic rank (Lye 1995; Simpson and Koyama 1998).

The genus *Nemum* is thought to be close to *Bulbostylis* due to a similar embryo type and the presence of long coarse hairs that may be present at the mouth of the sheath-leaf junction (Raynal 1973); these two genera are otherwise quite different.

Arthrostylis R.Br. and *Actinoschoenus* Benth. have been variously combined, as *Arthrostylis* (Kunth 1837; Bentham 1861; Thwaites 1864; Kükenthal 1944) within *Fimbristylis* (Boeckeler 1874; von Mueller 1875; Clarke 1893; Fitzgerald 1918; Kern 1955; 1974; Latz 1990: recommending placement into *Actinoschoenus*). Rye (1992), in her treatment of the Kimberley Flora (Western Australia), placed the unnamed species into the reinstated genus *Actinoschoenus*. *Trachystylis* S.T.Blake has also been referred to *Fimbristylis* as *F. stradbrokensis (*Domin) J.Kern (Kern 1959).

Species and generic limits for *Crosslandia* (Chapter 3) and *Abildgaardia* (Chapter 4), and species limits for *Bulbostylis* in Australia (Chapter 5) were defined in the preceding chapters. A comprehensive assessment of species and generic limits for *Bulbostylis* and *Fimbristylis* was not possible because of the large number of species assigned to each genus, c. 200 and c. 300, respectively (World Checklist of Monocotyledons 2004). Representative samples from *Bulbostylis* and *Fimbristylis* were included in the cladistic study. To complete the cladistic data set for the tribe Abildgaardieae, data were collected from species of *Nemum* and from the monotypic genera *Nelmesia* and *Tylocarya*.

Materials and methods

Ingroup

To assess monophyly for the tribe, and therefore the relationships of genera within the tribe, all terminal taxa previously defined in the *Crosslandia*, *Abildgaardia* and *Bulbostylis* chapters (3, 4, and 5) were included in the tribal assessment. When combined with samples from *Nemum spadiceum* (Lam.) Desv.ex Ham., *N. megastachyum* (Cherm.) J. Rayn., *N. equitans* (Kuk.) J. Rayn., *Nelmesia melanostachya* Van der Veken, *Tylocarya cylindrostachya* Nelmes (= *F. nelmesii*), and selective species of *Fimbristylis*, the ingroup represented all genera currently accepted into the tribe Abildgaardieae.

Previous analyses revealed that *Fimbristylis* is not a monophyletic group (see Chapters 3, 4, and 5), however, it was not possible to extend the sample species for this analysis due to time constraints. Representative taxa from *Fimbristylis* used in earlier work within this thesis were maintained for cladistic analysis in this chapter. A total of 52 species across 8 genera (or 7 if *Tylocarya* is excluded as a separate genus) formed the basis for the final cladistic study (Table 6.1, see also Appendix 1 for specimen details).

Outgroup

Outgroup taxa used to polarise data were unchanged (Table 6.1; see also Appendix 1). The taxa comprised *Arthrostylis aphylla*, provisional *Actinoschoenus compositus*, *Trachystylis stradbrokensis* from the provisional Arthrostylideae (Goetghebeur 1986; Bruhl 1995) or Schoeneae (Goetghebeur 1998), plus *Schoenoplectus tabernaemontani* (C.C.Gmel.) Palla (= *S. validus*), *Schoenoplectiella lateriflora*

Table 6.1 Taxa included in cladistic analysis to assess monophyly of the tribe Abildgaardieae. Species from *Crosslandia*, *Abildgaardia*, and Australian species of *Bulbostylis* included here were defined in Chapter 3, 4, and 5 respectively. See Appendix 1 for specimen details.

Taxa	No. specimens sampled
Ingroup	
Abildgaardia macrantha (provisional)	10
Abildgaardia mexicana	5
Abildgaardia odontocarpa (provisional)	2
Abildgaardia ovata	13
Abildgaardia oxystachya (provisional)	13
Abildgaardia pachyptera (provisional)	11
Abildgaardia schoenoides	12
Abildgaardia triflora	4
Bulbostylis barbata	20
Bulbostylis sp. aff. *barbata*	7
Bulbostylis burbidgeae	5
Bulbostylis sp. aff. *burbidgeae*	1
Bulbostylis capillaris	4
Bulbostylis densa	15
Bulbostylis sp. aff. *densa* 1	2
Bulbostylis sp. aff. *densa* 2	3
Bulbostylis hispidula subsp. *pyriformis*	3
Bulbostylis hispidula subsp. *senegalensis*	2
Bulbostylis humilis	3
Bulbostylis puberula	7
Bulbostylis sp. aff. *puberula*	1
Bulbostylis pyriformis	8
Bulbostylis turbinata	8
Bulbostylis sp. aff. *turbinata* 1	1
Bulbostylis sp. aff. *turbinata* 2	1
Crosslandia anthelata (provisional)	5
Crosslandia setifolia	18
Crosslandia spiralis (provisional)	3
Crosslandia vaginata (provisional)	14
Fimbristylis bahiensis	4
Fimbristylis blakei	2
Fimbristylis cinnamometorum	5
Fimbristylis depauperata	2
Fimbristylis fimbristyloides	4
Fimbristylis furva	2
Fimbristylis hygrophila	2
Fimbristylis microcarya	2
Fimbristylis schultzii	2
Fimbristylis sp L.	2
Fimbristylis variegata	1
Nelmesia melanostachya	1
Nemum equitans	2
Nemum megastachyum	2
Nemum spadiceum	4
Tylocarya cylindrostachya	1
Outgroup	
Actinoschoenus compositus (provisional)	4
Arthrostylis aphylla	4
Schoenoplectiella laevis	5
Schoenoplectiella lateriflora	5
Schoenoplectus tabernaemontani	3
Trachystylis stradbrokensis	7

(J.F.Gmel.) Lye (= *Schoenoplectus lateriflorus*) and *Schoenoplectiella laevis* (S.T.Blake) Lye (= *Schoenoplectus laevis*) in the tribe Scirpeae (Bruhl 1995) or Fuireneae, (Goetghebeur 1986, 1998) depending on the system of classification accepted.

Characters and homology

Additional characters were added to the cladistic data set when species from *Nemum*, *Nelmesia* and *Tylocarya* were sampled. These new characters were mainly associated with the spikelets, i.e. persistence of glumes to the rachilla in species of *Nemum*, presence of an intraspicular prophyll in *Nelmesia*, and variation in anatomical attributes (Appendix 2).

Embryo morphology and anatomy

Most specimens on loan for *Nemum* and *Nelmesia* (ISOTYPE!) could not be sampled for characters from leaf blade and culm anatomy, or embryo morphology due to the limited amount of material available; missing data (mainly embryographical and anatomical data) were obtained from the literature (Van der Veken 1965; Metcalfe 1971; Raynal 1973; Goetghebeur 1986).

Prepared slides for leaf blade and culm anatomy were available for *Tylocarya* from a previous study by Bruhl (1990), however, embryo morphology for *Tylocarya* was obtained from Van der Veken (1965) and Goetghebeur (1986). Only material that was already loose on the sheets was used to obtain floret measurements, and for embryo morphology and SEM treatment (not TYPE sheets), if needed. Sampling across the taxa allowed leaf blade and culm anatomy to be compared where possible. Scanning electron microscopy of the nut epidermis enabled the comparison of nut characters, especially the micromorphological attributes e.g. epidermal cell shape and type of protuberance, between taxa.

Analyses

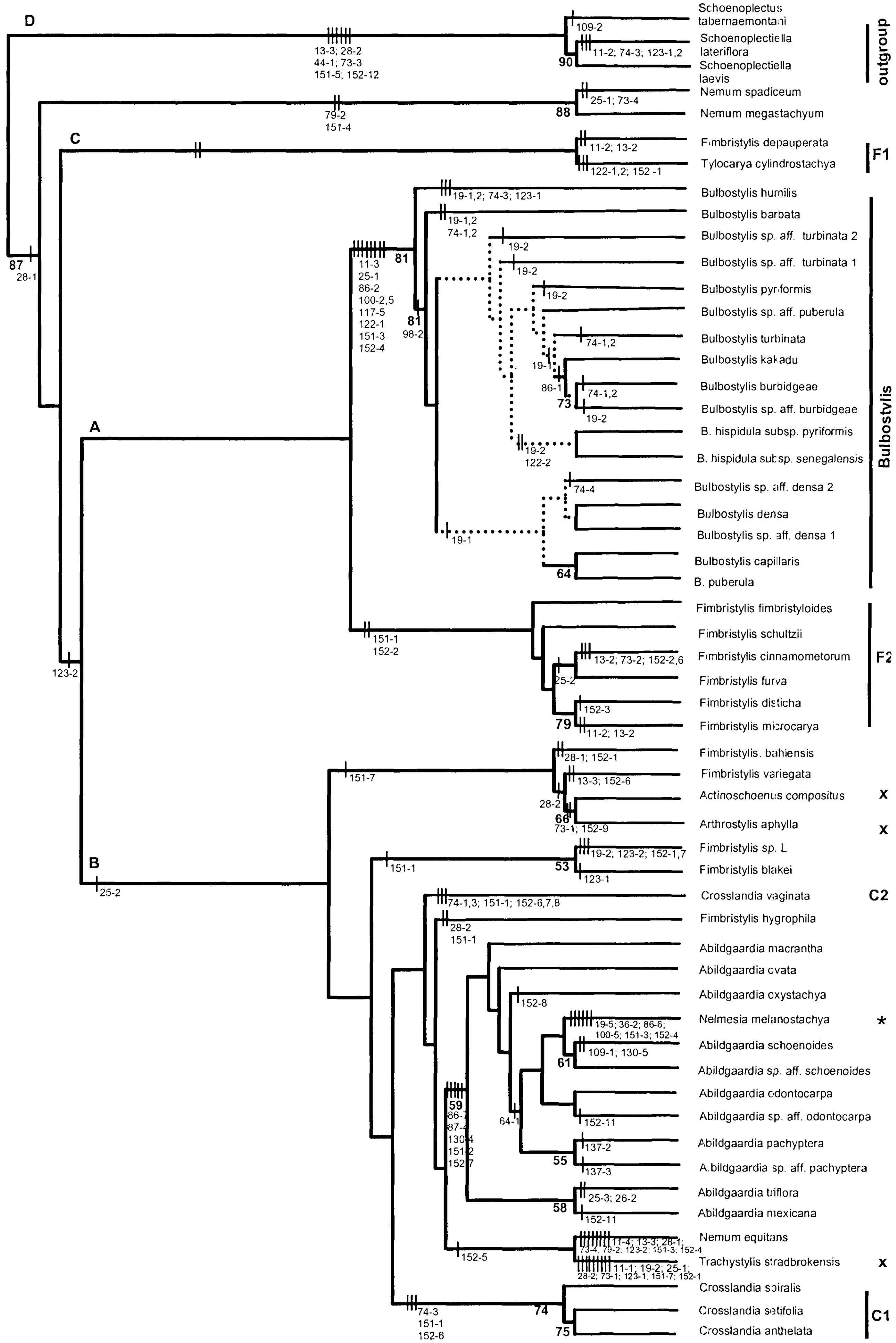
Data for 55 terminal taxa and 152 characters were subjected to parsimony analsysis within PAUP* using heuristic techniques (hsearch swap=TBR addseq=rand nreps=1000 hold=5 multrees=yes). Branch support was assessed using Bootstrap analysis (1000 bootstrap replications), as the computational time required to calculate the Bremer support indices past 3 extra tree length steps was protracted, even when limiting the addition-sequence replications to 10. Characters were traced in MacClade and the most relevant characters presented in the cladogram.

Results

Cladistic analysis

A heuristic search produced 91 most parsimonious trees (Tree length=1482, CI=0.3947, HI=0.6053, RI=0.5814, RC=0.2295). Tree 1 was one of the retrieved trees with similar topology to the strict consensus, and was selected to show branch support and character/branch associations.

Taxa from the 'Arthrostylideae', used with *Schoenoplectus* (including *Schoenoplectiella*) in the outgroup for Chapters 3, 4, and 5, violated the assumption for monophyly of the ingroup in this analysis. All taxa from the ingroup, plus members of the provisional Arthrostylideae, formed a broad clade sister to the outgroup species of *Schoenoplectus*, with strong branch support indicated (Bootstrap=87%) (Figure 6.1). *Arthrostylis aphylla* and *Actinoschoenus compositus*


D
13-3; 28-2
44-1; 73-3
151-5; 152-12
109-2
11-2; 74-3; 123-1,2
90
Schoenoplectus tabernaemontani
Schoenoplectiella lateriflora
Schoenoplectiella laevis
outgroup
79-2
151-4
25-1; 73-4
88
Nemum spadiceum
Nemum megastachyum
C
11-2; 13-2
122-1,2; 152 -1
Fimbristylis depauperata
Tylocarya cylindrostachya
F1
87
28-1
19-1,2; 74-3; 123-1
19-1,2
74-1,2
11-3
25-1
86-2
100-2,5
117-5
122-1
151-3
152-4
81
81
98-2
19-2
19-2
19-2
19-1
86-1
74-1,2
74-1,2
73
19-2
19-2
122-2
74-4
19-1
64
Bulbostylis humilis
Bulbostylis barbata
Bulbostylis sp. aff. turbinata 2
Bulbostylis sp. aff. turbinata 1
Bulbostylis pyriformis
Bulbostylis sp. aff. puberula
Bulbostylis turbinata
Bulbostylis kakadu
Bulbostylis burbidgeae
Bulbostylis sp. aff. burbidgeae
B. hispidula subsp. pyriformis
B. hispidula subsp. senegalensis
Bulbostylis sp. aff. densa 2
Bulbostylis densa
Bulbostylis sp. aff. densa 1
Bulbostylis capillaris
B. puberula
Bulbostylis
A
151-1
152-2
13-2; 73-2; 152-2,6
25-2
152-3
11-2; 13-2
79
Fimbristylis fimbristyloides
Fimbristylis schultzii
Fimbristylis cinnamometorum
Fimbristylis furva
Fimbristylis disticha
Fimbristylis microcarya
F2
123-2
151-7
28-1; 152-1
13-3; 152-6
28-2
66
73-1; 152-9
Fimbristylis. bahiensis
Fimbristylis variegata
Actinoschoenus compositus
Arthrostylis aphylla
X
X
B
25-2
151-1
19-2; 123-2; 152-1,7
53
123-1
Fimbristylis sp. L
Fimbristylis blakei
74-1,3; 151-1; 152-6,7,8
Crosslandia vaginata
C2
28-2
151-1
Fimbristylis hygrophila
152-8
19-5; 36-2; 86-6;
100-5; 151-3; 152-4
109-1; 130-5
61
59
86-7
87-4
130-4
151-2
152-7
64-1
152-11
137-2
55
137-3
25-3; 26-2
58
152-11
Abildgaardia macrantha
Abildgaardia ovata
Abildgaardia oxystachya
Nelmesia melanostachya
*
Abildgaardia schoenoides
Abildgaardia sp. aff. schoenoides
Abildgaardia odontocarpa
Abildgaardia sp. aff. odontocarpa
Abildgaardia pachyptera
A.bildgaardia sp. aff. pachyptera
Abildgaardia triflora
Abildgaardia mexicana
152-5
11-4; 13-3; 28-1;
73-4, 79-2; 123-2; 151-3; 152-4
11-1; 19-2; 25-1;
28-2; 73-1; 123-1; 151-7; 152-1
Nemum equitans
Trachystylis stradbrokensis
X
74-3
151-1
152-6
74
75
Crosslandia spiralis
Crosslandia setifolia
Crosslandia anthelata
C1

were nested with the species *F. variegata* and the C_4 *Fimbristylis bahiensis*, and were sister to the F3–A*bildgaardia–Crosslandia* clade. Within this clade *Trachystylis* (also assigned to the outgroup) was paired with *Nemum equitans* as a group sister to the *Abildgaardia* clade.

Two main clades, A and B, were sister to the clade *Fimbristylis depauperata–Tylocarya cylindrostachya* (clade C), and all were sister to the *Nemum spadiceum–N. megastachyum* clade that showed strong branch support (Bootstrap=87%). The species of *Nemum* sampled, therefore, did not form a monophyletic group.

In clade A, all the species of *Bulbostylis* sampled formed a monophyletic group, with moderate branch support (Bootstrap=77%), sister to the clade *Fimbristylis* 2 (*F. fimbristyloides*, *F. schultzii*, *F. cinnamometorum*, *F. furva*, *F. disticha*, *F. microcarya*). Clade B, however, contained the smaller F3 clade (*F.* sp. L. and *F. blakei* – with weak support), which was sister to the *Abildgaardia–Crosslandia* clade, which included *Fimbristylis hygrophila* (= *Abildgaardia hygrophila*), *Nelmesia*, *Trachystylis* and *Nemum equitans*.

The previously monophyletic *Abildgaardia* (Chapter 4) was rendered non-monophyletic by the placement of *Nelmesia melanostachya*, which was nested within the Australian endemics. The *Abildgaardia–Nelmesia* branch showed weak Bootstrap support (67%) and the terminal arrangement of taxa did not collapse in the consensus tree, as indicated by solid lines in Figure 6.1. There are no obvious synapopmorphies that unite *Nelmesia* and *Abildgaardia* other than the large stipitate nut.

Species assigned to *Crosslandia* in Chapter 3 formed a monophyletic group that included *C. setifolia*, and the provisional *C. anthelata* and *C. spiralis*, and received moderate branch support (Bootstrap=73%). *Crosslandia vaginata* (= *Abildgaardia vaginata*) was basal in the sister group to *Crosslandia* in this tribal analysis (Figure 6.1) and the *Bulbostylis* treatment (Chapter 5), although there was no internal support for the placement here.

Fimbristylis hygrophila (= *Abildgaardia hygrophila*) persists as a sister to the species of *Abildgaardia* and *Nelmesia melanostachya* in the tribal analysis, however, internal branch support was absent for the placement, as was support for the placement of *Nemum equitans* and *Trachystylis*.

Characters

There are no unambiguous synapomorphies that clearly delimit the internal clades due to the poor tree resolution caused by the high level of homoplasy within the data set. Characters from embryo morphology, such as the Schoenoplectus-type embryo (151-5), the germination pore parallel to the first primordial leaf (154-1), plus anatomy of the culm (44-1, 51-1), separate the outgroup species of *Schoenoplectus* and *Schoenoplectiella* from the remaining taxa.

The only strongly robust group, other than the outgroup (i.e. *Schoenoplectus*), is the clade of *Bulbostylis*. The synapomorphies for the *Bulbostylis* clade are: pilose hairs at the sheath-leaf junction (11-3); leaf vascular bundle number 5 or less (25-1); a minutely triangular style (117-5); style base persistent on the nut (always separates from the style) (122-1), although the specimens of *B. hispidula* may have deciduous style bases (it falls in tact with the style) (122-2); and Bulbostylis-type embryo (151-4).

Observations

Inflorescence–synflorescence

The inflorescence–synflorescence structure is very homoplastic, even when the structure of the head of sessile spikelets is broken down into different structural types. The simplest 'head' of 3 sessile spikelets (57-4) occurs in *Abildgaardia* (*A. mexicana*), *Fimbristylis bahiensis* and *Bulbostylis* (*B. humilis*) (see Figure 4.12). A synflorescence head formed as a compressed spike (multiple primary sessile coflorescences, of one spikelet per coflorescence, where the terminal spikelet sits above the sessile coflorescences (57-5), was observed in *Fimbristylis* (*F. schultzii*) and *Actinoschoenus*. The multiple branched reduced anthelodia, where all spikelets are sessile (branching as rays) is highly reduced but discernable under the dissecting microscope (57-8), is seen in *Crosslandia setifolia* and *Arthrostylis aphylla* (see Figure 3.16). *Crosslandia setifolia* was the only taxa sampled that produced lateral heads (see Figure 3.17), where a primary coflorescence has developed into a secondary main florescence of a head of sessile spikelets. The 'prophyllar' head is a combination of the multiple branched reduced anthelodium and prophyllate branching from primary and sometimes secondary inflorescence branches (57-10), (see Figure 5.15 B, C); this type is restricted to *Bulbostylis* in this study (*B. barbata* and *B. kakadu*). The only other genus in the study with intraprophyllar growth within the inflorescence is *Schoenoplectus–Schoenoplectiella*, which differs in structure through the paniculodium base plan. In *Schoenoplectiella laevis*, prophylls were not restricted to the production of spikelets, as some prophylls were fertile, possessing a solitary nut in the axil without any other bract visible; unique for taxa within the study. The most common synflorescence type was the reduced anthelodium with a sessile main primary florescence and primary coflorescences supported on rays (lengthened epipodia) (see Figures 3.14, 4.12, 4.15 A), which was found across most genera of the ingroup. Florescence ramification (57-7) within the synflorescence was common in members of *Fimbristylis* (*F. blakei*, *F.* sp. L., *F. cinnamometorum*; well-developed in *F. microcarya*, *F. depauperata*, *F. furva* and sometimes *F. cinnamometorum*; and in some species of *Bulbostylis* (e.g. *B. densa*, *B. pyriformis*, and may be well-developed in *B. puberula* and *B. hispidula* subsp. *senegalensis*).

The solitary spikelet is the simplest of all the inflorescence–synflorescence structural types, and, within the study, is most common in *Abildgaardia* (see Figure 4.12 A). The spike in *Nelmesia melanostachya* superficially resembles a solitary spikelet, but the intraspicular prophyll within the solitary spike is exceptional for the tribe (Figure 6.2). The prohpyll is in place where a lateral branch arises as a solitary, sessile floret (i.e. single floret spikelet); this inflorescence type is not homologous with the solitary spikelet in *Abildgaardia*. Despite the difference in the structure of the inflorescence, *Nelmesia* was placed with species of *Abildgaardia* in many of the trees retrieved, although there was no support for the placement (Figure 6.1).

Florets within all the studied taxa comply with the basic scirpoid floral arrangement: being tetracyclic, 2–3 carpels, 1–3 stamens, 0–6 perianth bristles enclosed by a glume (floral bract) (Vrijdaghs et al. 2005). Perianth was absent from all the sampled ingroup taxa, with the exception of one collection of *Abildgaardia schoenoides* (see Chapter 4). Perianth may be present in *Schoenoplectus–Schoenoplectiella* as bristles with retrorse barbs; *Schoenoplectus tabernaemontani* (= S. *validus*) has three perianth bristles present (see Figure 6.8 A). The unique perianth in the *Abildgaardia schoenoides* collection differed in having 2 perianth bristles with antrorse barbs (see Figure 4.13).

Figure 6.2 *Nelmesia melanostachya* ISOTYPE showing general habit, including solitary spikes where the lateral spikelet is reduced to a single floret. The insert shows a single floreted spikelet bearing a mature nut; the large prophyll is obvious and sits between the nut and the rachis. Scale bar=2 mm. See Appendix 1 for specimen details.

Nut epidermal pattern

The nut epidermis varies in the shape and orientation of epidermal cells, or sculpturing from single silica bodies (puncticulate to granulate), groups of multiple raised cells forming various shapes (turbercules), cells raised in ridges that may be broken or continuous (rugose), raised cell walls (reticulate), or cells with a sunken lumen (pitted), and is distinct at the species level. There is some consistency in the epidermal cell size and shape as seen in the group *Abildgaardia* – excluding *Nelmesia*, (see Chapter 4), where epidermal cells are distinctly rounded (*A. ovata*, *A. oxystachya*, *A. schoenoides*, *A.* sp. aff. *schoenoides*, *A. odontocarpa*, *A.* sp. aff. *odontocarpa*) or barely hexagonal in shape (*A. pachyptera*, *A. macrantha, A. triflora* and *A. mexicana*). Large tubercules are common across the species and vary in size and shape, and occasionally may be few or absent in *A. pachyptera, A. macrantha* and *A. triflora*. Cell walls are not sinuose.

The *Bulbostylis* species sampled may have nut epidermal cells that are isodiametric or longitudinally rectangular, and barely rectangular to linearly rectangular in shape (see Chapter 5). Cellular protuberances may be absent (e.g. *B. barbata*, *B. kakadu*) or individual cells may have a central raised silica body producing a puncticulate or granulate surface, depending on the size of the silica body (e.g. *B. densa*, *B. burbidgeae*, *B. turbinata*). Alternatively, the longitudinal rectangular cells are raised to some extent, giving degrees of rugose patterning as transverse wrinkles that may be continuous or broken (e.g. *B. puberula*, *B. pyriformis*, *B. hispidula*). The cell walls are sinuose to some extent (finely – distinctly) in all but *B. humilis*.

Even in the limited *Fimbristylis* sample the variation in the nut epidermis is evident. Epidermal cells vary from isodiametric hexagonal cells to barely circular, longitudinally rectangular, or transversely rectangular; cell walls may be straight, barely sinuous to sinuous. Protuberances, as single raised cells to multiple raised cells with various distribution patterns over the surface, occur frequently across the species sampled. Nut epidermal features do not seem to influence the group arrangement for the species of *Fimbristylis* F2 (Figures 6.3-4), although the poor resolution in the tree topology could mask the usefulness of the character at the sectional level. There are no similarities in the nut epidermal sculpturing for the paired *Tylocarya* and *Fimbristylis depauperata* (Figure 6.5). The nut in *Tylocarya* is smooth, with hexagonal shaped epidermal cells that have strongly sinuose walls, and contrasts with the striated epidermal cells in *F. depauperata*.

The nut epidermis in *Nemum spadiceum*, *N. megastachyum* and *N. equitans* is distinct in the completely smooth nut surface (Figure 6.6) that is lustrous and coloured black, dark brown or grey-brown. Taxa from the Arthrostylideae (*Arthrostylis*, *Actinoschoenus* and *Trachystylis*) that fall with the ingroup in this analysis have variable nut characters (Figure 6.7). The most striking characters are the bulbous base of the nuts in the provisional *Actinoschoenus compositus* (= *Fimbristylis composita*) (Figure 6.7 C), and the minutely papillose epidermis (Figure 6.7 D). Some species of *Fimbristylis* have an external gynophore that is brown and attached at the base of the nut (e.g. *F. depauperata*, *F. fimbristyloides*, *F. schultzii* and *F. bahiensis*), however, none is as large as the brown spongy structure seen in *Actinoschoenus compositus*. The papillose nut epidermis also in *A. compositus* has not been seen among any of the other taxa studied.

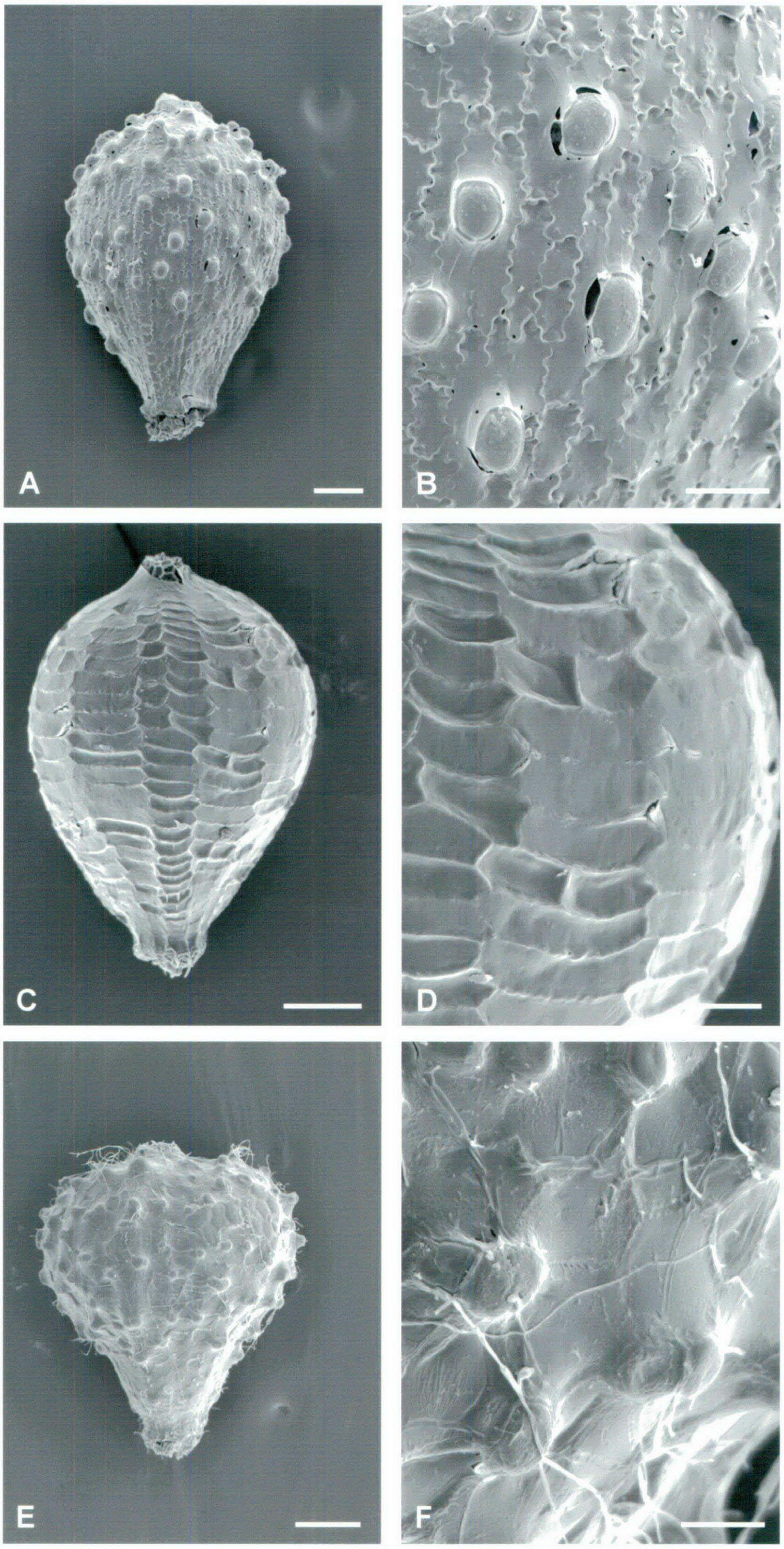


Figure 6.3 Scanning electron micrographs (SEM) showing the variation of nut outline and epidermal sculpturing in some species of *Fimbristylis*. A. Nut for *F. furva* (ff2) and B. epidermal sculpturing at higher magnification, with cells irregularly longitudinal and cell walls that are distinctly sinuose. C. Nut for *F. microcarya* (*K.L. Clarke 319, L. Little*) and D. at higher magnification, showing epidermal cells that are horizontally elongated and cell walls that are very finely sinuose. The waxy covering is not plate-like but continuous over the surface. E. Nut for *F. schultzii* (*K.L. Clarke 153 et al.*) and F. at higher magnification, showing epidermal sculpturing and hexagonal cell shape. Scale bars A=100 μm; C, E=200 μm; B, D, F=50 μm. See Appendix 1 for OTU and specimen details.

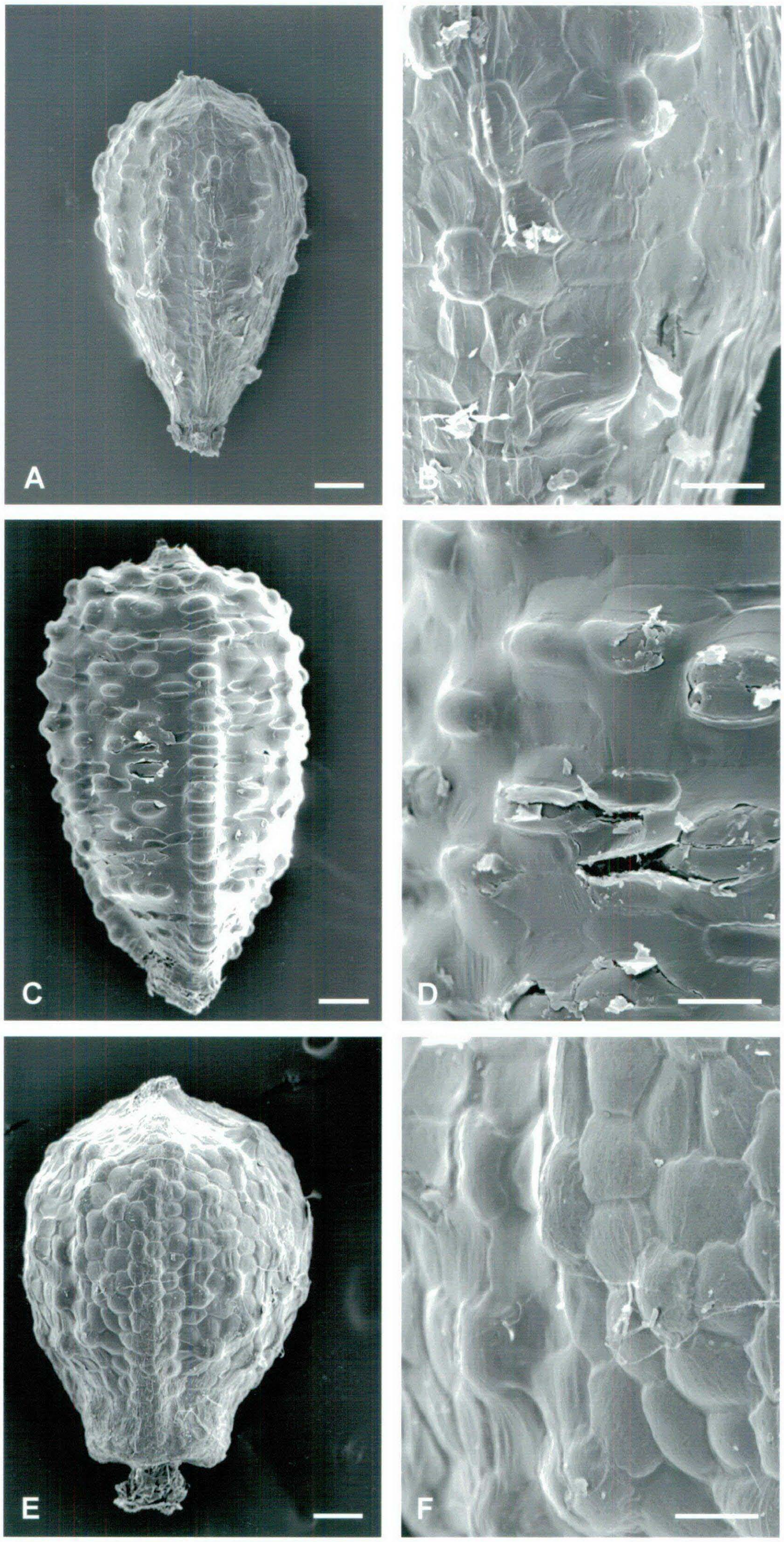


Figure 6.4 Scanning electron micrographs (SEM) showing the variation of nut outline and epidermal sculpturing in some species of *Fimbristylis*. A. Nut for *F. disticha* (fd2) and B. epidermal sculpturing at higher magnification, with cells mostly circular and straight cell walls. C. Nut for *F. cinnamometorum* (fc5) and D. at higher magnification, showing epidermal cells that are horizontally elongated and protuberances also elongated horizontally. The waxy covering is not plate-like but continuous over the surface. E. Nut for *F. fimbristyloides* (ffi3.) showing the truncate base and F. at higher magnification, epidermal sculpturing and hexagonal to circular cell outline. Scale bars A, C, E=100 μm; B, D, F=50 μm. See Appendix 1 for OTU and specimen details.

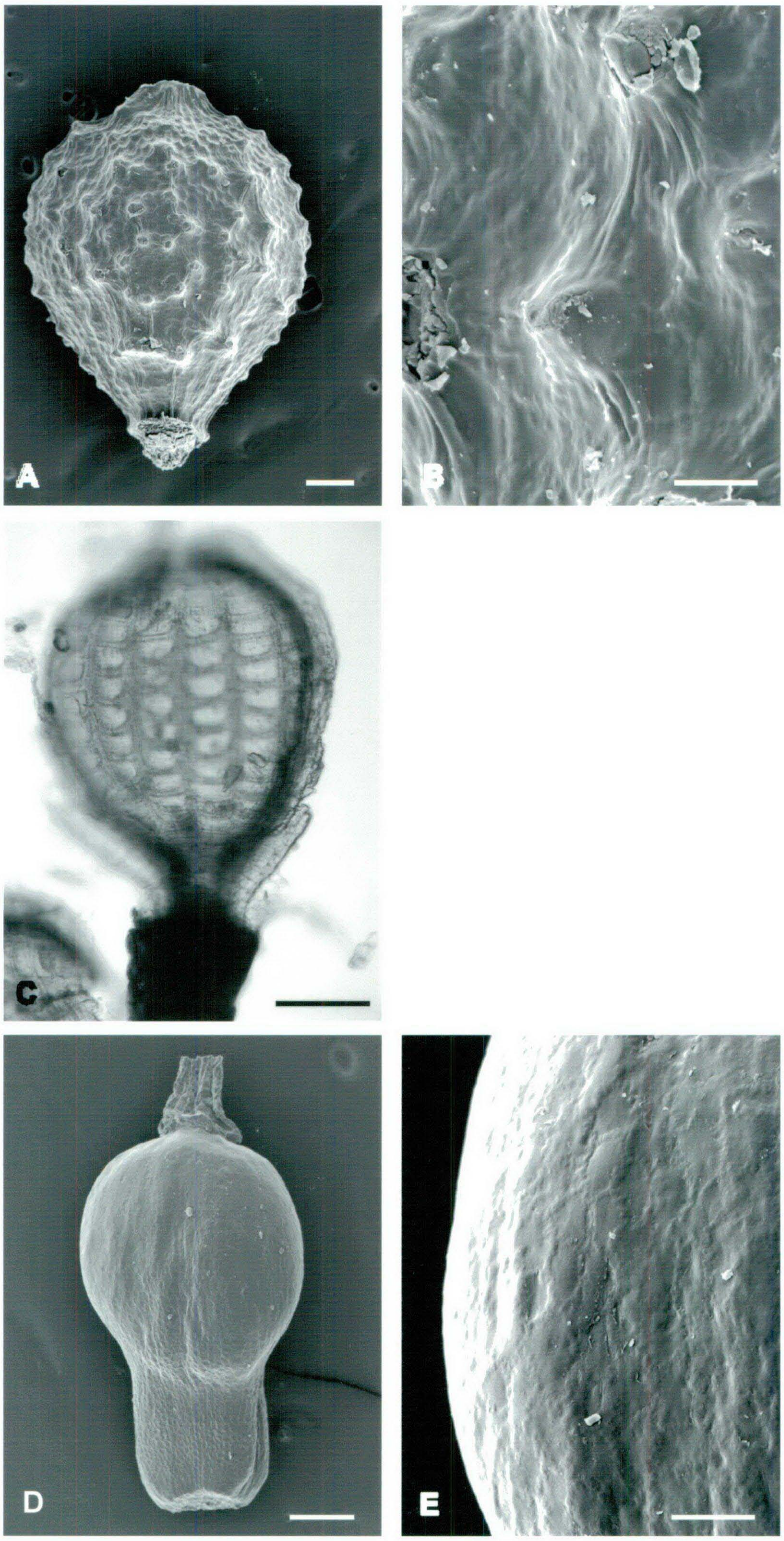


Figure 6.5 Scanning electron micrographs (SEM) and light micrograph (LM) showing the variation of nut outline and epidermal sculpturing in species of *Fimbristylis* (including *Tylocarya*). A. SEM of nut for *F. blakei* (fb1) and B. epidermal sculpturing at higher magnification, with cells mostly hexagonal to circular in outline. C. LM of nut for *F. depauperata* (*K.L. Clarke 305, L. Little*) showing the square epidermal cells arranged in rows. D. SEM of nut for *Tylocarya cylindrostachya* (*A.F.G. Kerr 21294*) (= *F. nelmesii*) showing the nut outline and E. at higher magnification, the epidermal surface that is smooth with hexagonal cells with sinuose walls. OTU or collector and collection number are given in brackets. Scale bars A, D=200 μm; C=20 μm; B, E=50 μm. See Appendix 1 for OTU and specimen details.

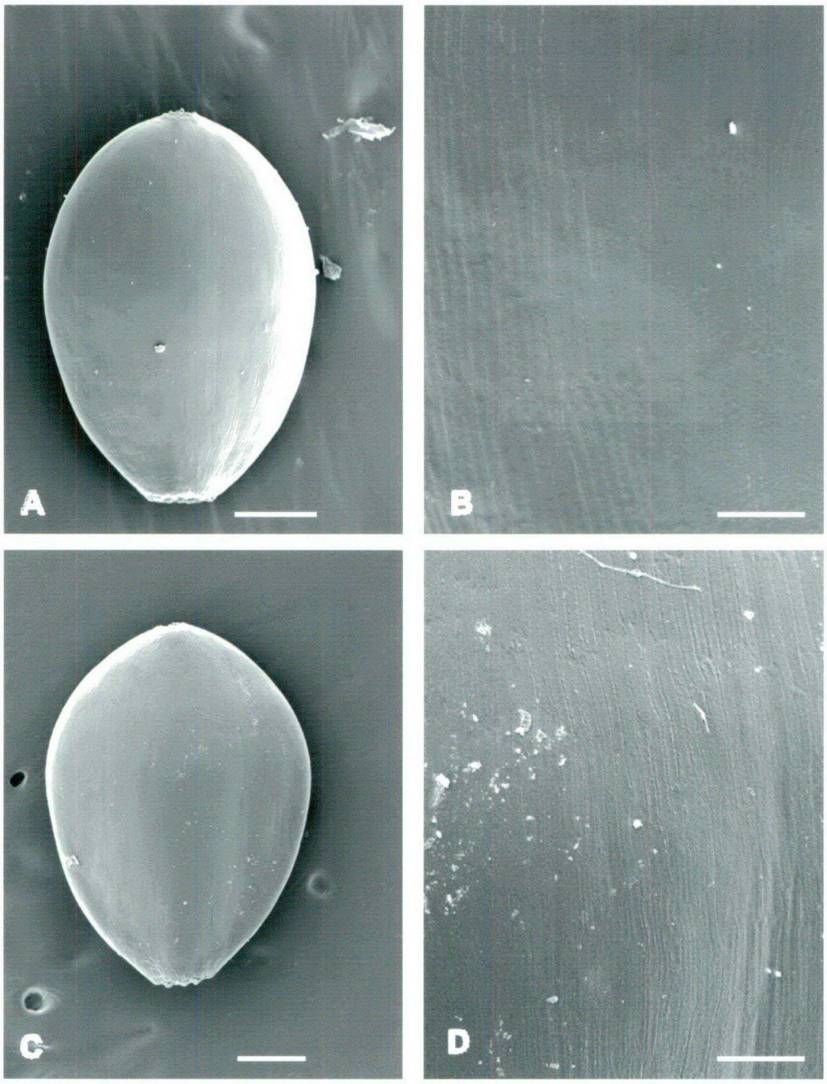


Figure 6.6 Scanning electron micrographs (SEM) showing the nut outline and epidermal surface in two species of *Nemum*. A. Nut for *N. spadiceum* (*E.A. Robinson 4677*) and B. epidermal aurface at higher magnification. C. Nut for *N. megastachyum* (*Germain 4420*) and D. at higher magnification. The nuts of both species are similar in outline and the epidermal surface is lineolate (marked with fine lines), as the cells are barely discernable at higher magnification. Collector and collection number are given in brackets. Scale bars A=100 µm; C=200µm; B, D=50 µm. See Appendix 1 for OTU and specimen details.

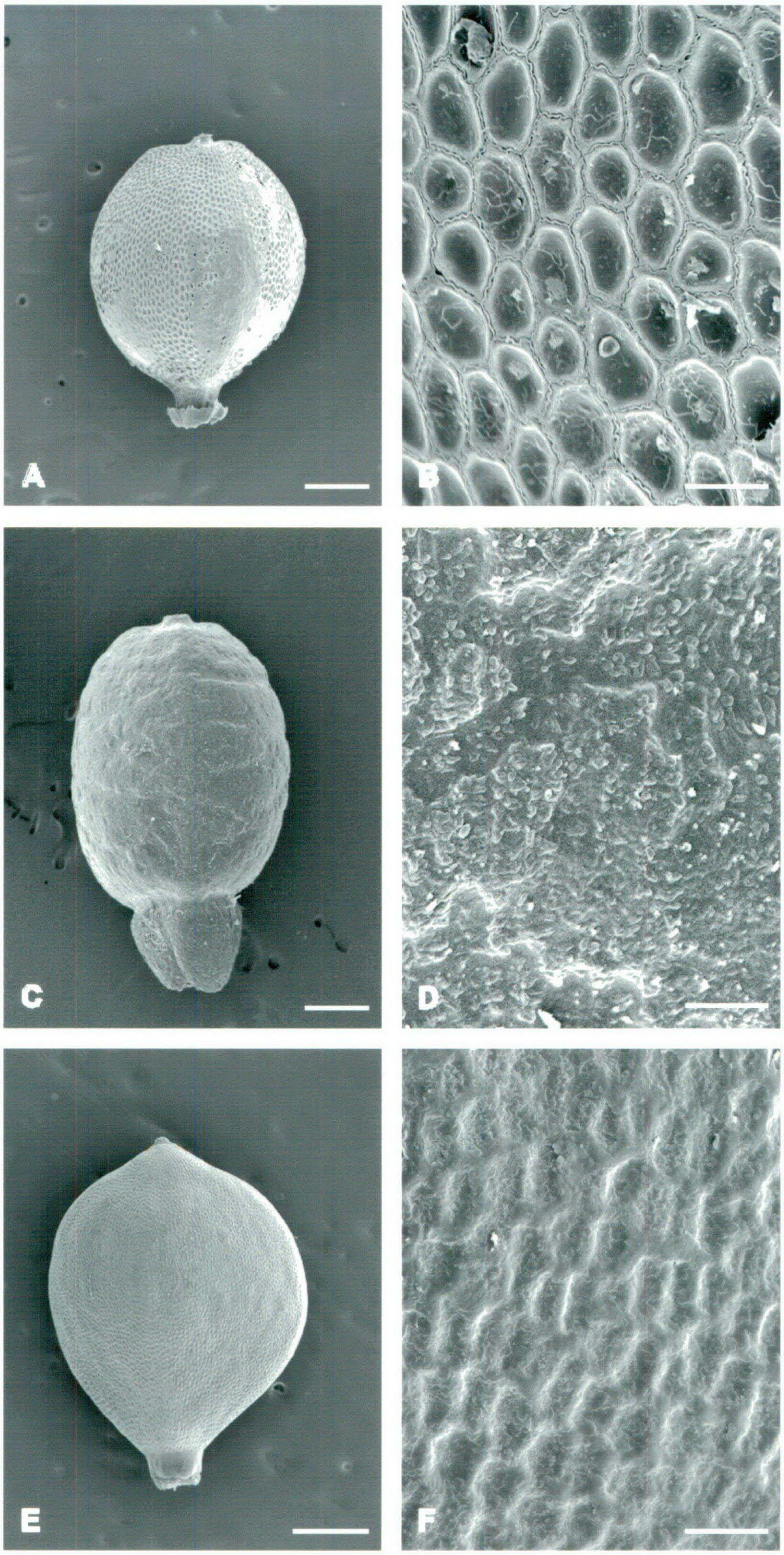


Figure 6.7 Scanning electron micrographs (SEM) showing the variation of nut outline and epidermal sculpturing in species from the provisional tribe Arthrostylideae. A. Nut for *Arthrostylis aphylla* (*G.N. Batianoff 10089*) and B. epidermal sculpturing at higher magnification, with cells circular in outline. C. Nut for provisional *Actinoschoenus composita* (*K.L. Clarke 178 et al.*) and D. at higher magnification, showing the small papillae that cover the nut surface, which are unique among taxa within the study. E. Nut for *Trachystylis stradbrokensis* (*E.J. Thompson 78*) showing the nut outline and E. at higher magnification, the epidermal cell pattern is reticulate–foveate. Collector and collection number are given in brackets. Scale bars A, C, E=500 µm; B, D, F=50 µm. See Appendix 1 for specimen details.

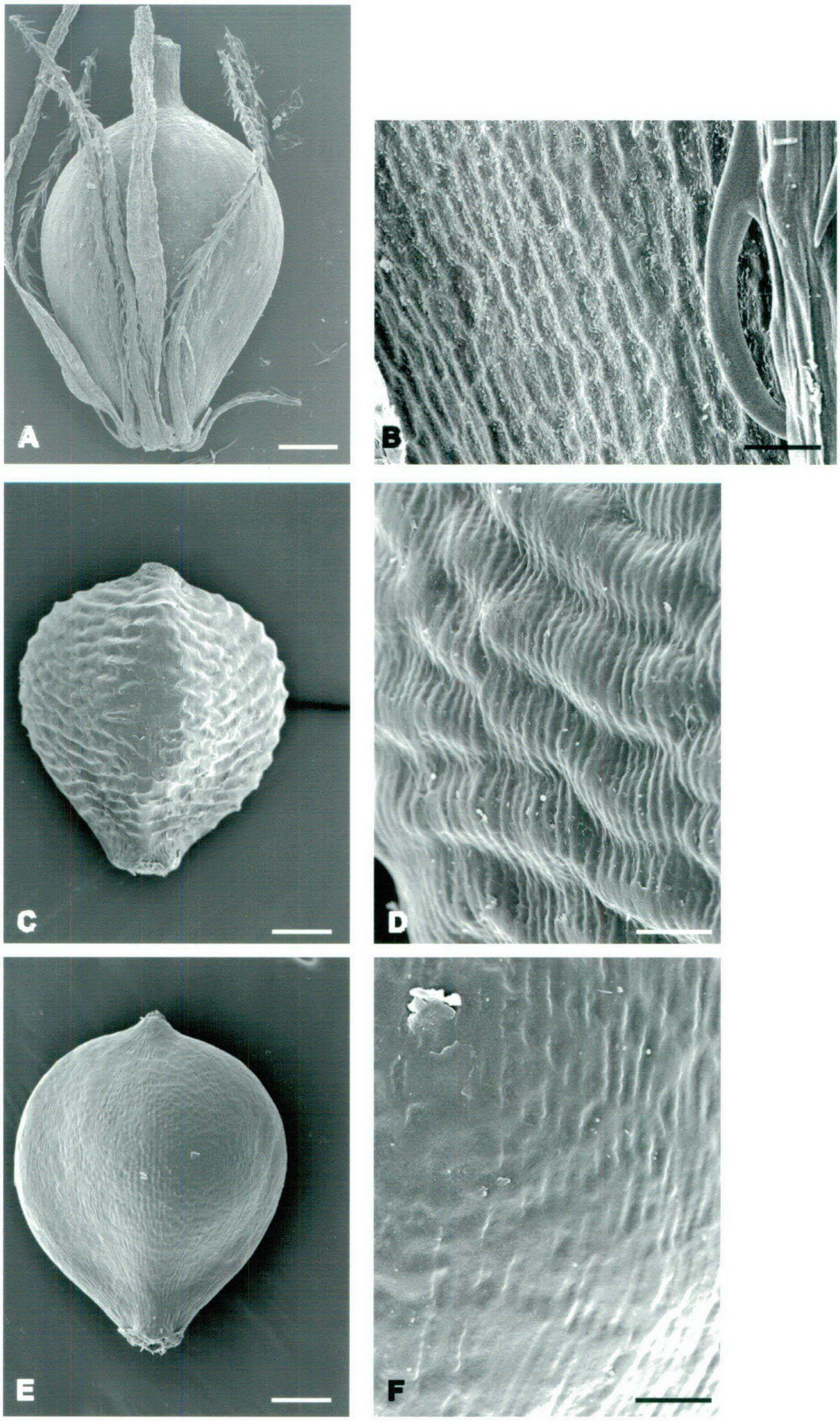


Figure 6.8 Scanning electron micrographs (SEM) showing the variation in nut outline and epidermal sculpturing for outgroup species of *Schoenoplectus* and *Schoenoplectiella*. A. Nut for *Schoenoplectus tabernaemontani*. (*K.L. Wilson 4278*) and B. epidermal surface at higher magnification, with cells narrowly elongated in outline. Perianth with retrorse barbs occur in this species. C. *Schoenoplectiella lateriflora* (*P.K. Latz 3761*) showing the rugose nut surface and D. the vertically linear epidermal cells at higher magnification. E. Nut for *S. laevis* (*P.M. Milthorpe 1777A,G. M. Cunningham*) showing the smooth epidermis and F. at higher magnification. Collector and collection number are given in brackets. Scale bars A=500 µm; C, E=200 µm; B, D, F=50 µm. See Appendix 1 for OTU and specimen details.

In the outgroup species sampled for *Schoenoplectus* and *Schoenoplectiella*, the nut shows variable nut sculpturing (Figure 6.8). *Schoenoplectus tabernaemontani* and *Schoenoplectiella laevis* have smooth nuts, while the nuts in *S. lateriflora* are tightly rugose. All nuts for the three species have vertically linear cells, which are raised in *S. lateriflora*.

Embryo

In species of *Fimbristylis*, the Fimbristylis-type embryo, although consistent in the orientation of the primordial shoot and root, is variable in size and shape across the species sampled (Figure 6.9). *Tylocarya cylindrostachya* (or *Fimbristylis nelmesia*) was shown to have a variant of the Fimbristylis-type embryo (Goetghebeur 1986) that is a synapomorphy for the *Tylocarya–F. depauperata* clade (Figure 6.1). Species of *Crosslandia* (including *C. vaginata*) also share the Fimbristylis-type embryo and are placed separate to species currently assigned to *Fimbristylis* (see also Chapter 3).

The embryo type in species of *Nemum* is not typical and varies between the Abildgaardia-type and Bulbostylis-type (Figure 6.10) (see also Chapters 4 and 5). The primordial shoot and root are of roughly equal size, or the shoot may be slightly larger (as in the Abildgaardia-type); the embryo size itself is closer to the Bulbostylis-type. In *Nemum equitans* the embryo is similar in outline to the Bulbostylis-type and is trigonous from the top view of the embryo (Figure 6.10), although the root is not prominent and the second leaf not detectable, possibly obscured by the cellular contents surrounding the organs. The elliptic rather than rounded or trigonous outline in the top view of the embryo in sampled *N. spadiceum* and *N. megastachyum* specimens coincides with the di-stigmatic style of both species; *Nemum equitans* has tri-stigmatic styles. The variation of the embryo features seen in *Nemum* was reflected in the analysis, as *Nemum equitans* and *Trachystylis stradbrokensis* formed a minor clade, well removed from the other species of *Nemum*, despite having different embryo types – the Nemum-type and Carex-type (Figure 6.10) respectively.

Nelmesia melanostachya is shown to have a variation of the Abildgaardia-type embryo (Van der Veken 1965; Goetghebeur 1986) (Figure 6.10, see also Chapter 4), where the primordial shoot is basal and larger than the parallel root. The main difference between the Nelmesia-type and Abildgaardia-type embryos is the size, although the embryo of *Nelmesia* in this study has been extrapolated from Van der Veken (1965) and Goetghebeur (1986) and, therefore, may not be a true representation of the embryo size. The Nelmesia-type embryo is an autapomorphy for *Nelmesia* and disrupts the Abildgaardia-type embryo synapomorphy for the species otherwise grouped as *Abildgaardia* (see also Chapter 4).

The Bulbostylis-type embryo was one of the synapomorphies for the *Bulbostylis* clade (also see Chapter 5), in contrast to the Fimbristylis-type embryo, which was homplastic across clades C, A, and B (Figure 6.1) and variable across the sampled taxa.

Taxa in the *Arthrostylis–Actinoschoenus* s.l. clade share the Schoenus-type embryo (Figure 6.10) as a synapomorphy on the internal branch that unites the four taxa (Figure 6.1).

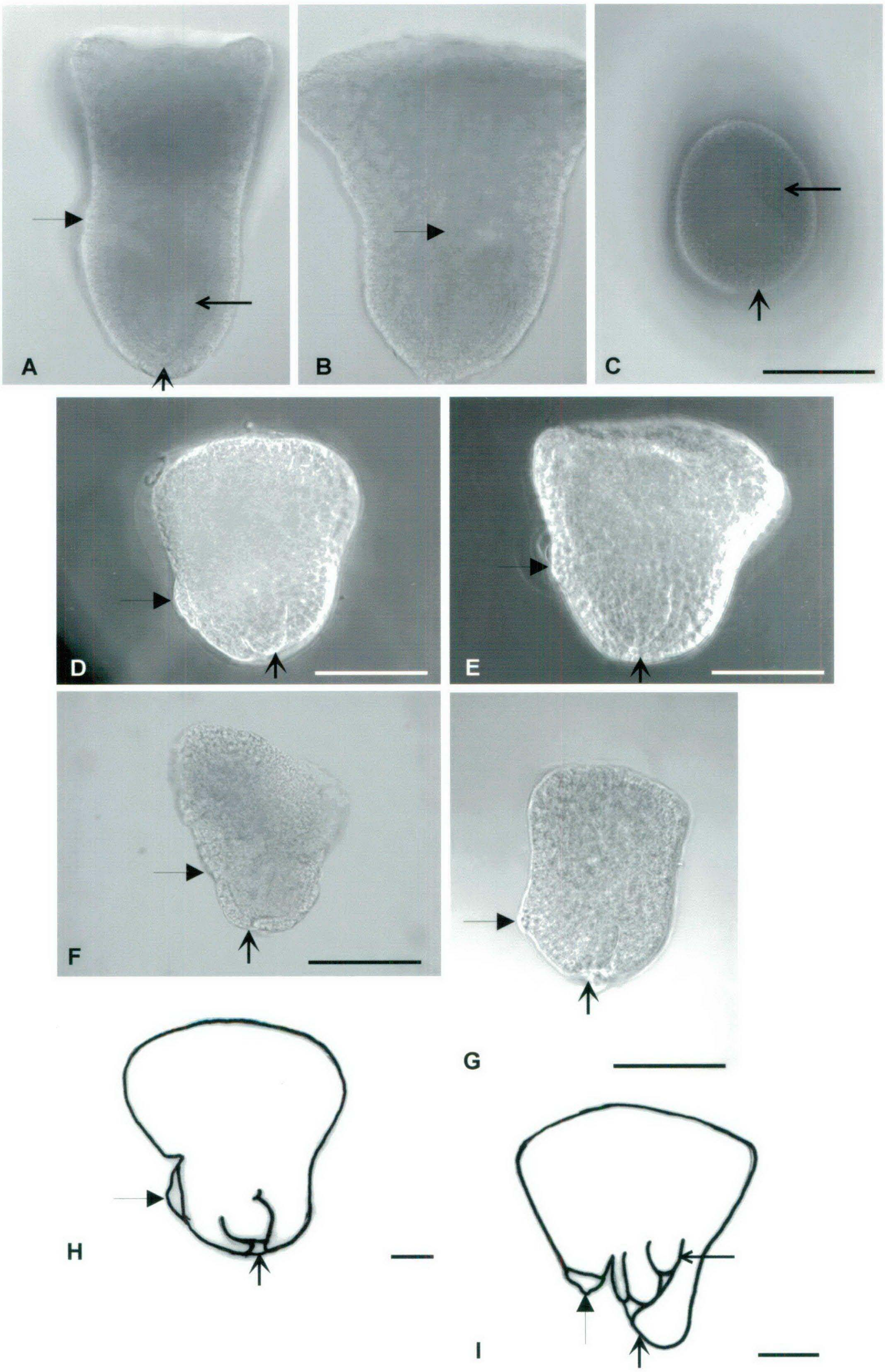


Figure 6.9 Light micrographs of whole cleared embryos showing the variation in shape and size for some species assigned to *Fimbristylis*, plus schematic embryos for *Tylocarya* and *Nelmesia*. *Fimbristylis depauperata* (*K.L. Clarke 305, L. Little*) A. side view, B. frontal view, and C. top view of shoot with the second primordial leaf in view (thin arrow) directly behind the first leaf. D. *F. shultzii (K.L. Clarke 108 et al.)*, E. *F. furva* (*K.L. Clarke 210 et al.*), F. *F. disticha* (fd1) and G. *F. cinnamometorum* (fc2) share the Fimbristylis–type embryo. H. The embryo for *Tyolocarya* is a variant of the Fimbristylis–type. I. In *Nelmesia* the embryo is a variation of the Abildgaardia– and Bulbostylis–types. Scale bars=100 µm. Solid arrow=root, open arrow=shoot, thin arrow=second primordial leaf. OTU label or collector and collection number are given in brackets. See Appendix 1 for specimen details. Embryo schematics H and I are adapted from Van der Veken (1965) and Goetghebeur (1986).

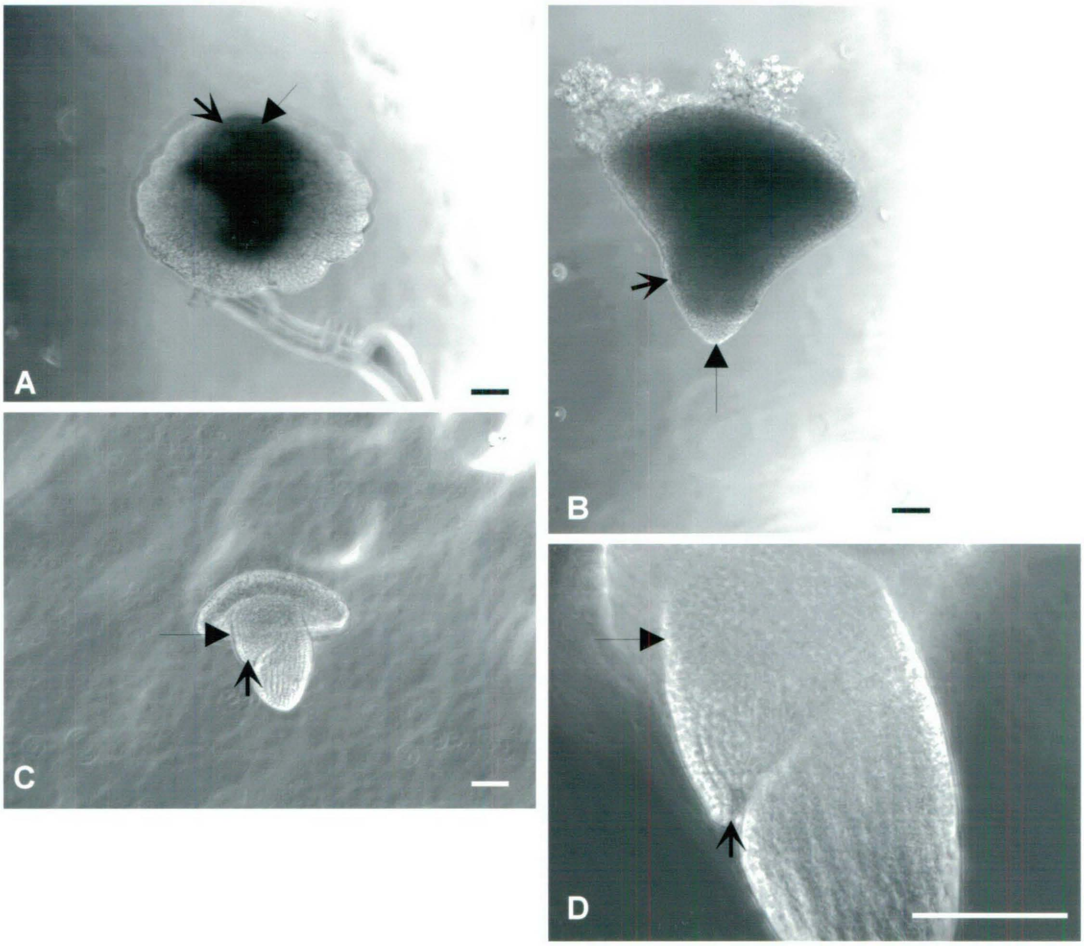


Figure 6.10 Light micrographs of whole cleared embryos for some species from the outgroup used in cladistic analyses: *Actinschoenus*, *Trachystylis* and *Schoenoplectiella*.
A. *Actinoschoenus composita* (*K.L. Clarke 178 et al.*) has the Schoenus-type embryo (indicated by the arrows) with the embryo outline wide and saucer shaped in side view, B. *Trachystylis stradbrokensis* (*S.T. Blake 13201*) has a Carex-type embryo with a widened cotyledon. C. The distinctive Schoenoplectus-type embryo is shown for *Schoenoplectiella laevis* (*K.L. Wilson 8041 et al.*), where the cotyledon extends past the primordial shoot, and D. at higher magnification showing the germ pore parallel to the first primordial leaf. Scale bars=100 μm. Solid arrow=root, open arrow=shoot. Collector and collection number are given in brackets. See Appendix 1 for specimen details.

Anatomy

Leaf blade and culm anatomy show 47 of the 55 taxa sampled, all from the ingroup, share the C_4 fimbristyloid photosynthetic pathway. The C_3 photosynthetic pathway arises several times amid the ingroup in the tribal analysis, and taxa with C_3 anatomy (*Arthrostylis aphylla*, *Actinoschoenus compositus*, *Fimbristylis variegata* and *Trachystylis stradbrokensis* (Figure 6.11) are placed with C_4 species (*Fimbristylis bahiensis* and *Nemum equitans*, respectively).

Despite variation in the general shape of transverse sections of leaf blade and culm, in the number of vascular bundles, the shape and number of sclerenchyma, and the shape and arrangement of parenchyma among the C_4 species, there was a general consistency with all having only sclerenchyma strands in leaf blades and culms. The exception is seen in the sections of *Tylocarya* (Figure 6.12). Leaf blade anatomy in *Tylocarya* shows similar structure to some of those seen in *Fimbristylis* and *Abildgaardia*. In addition to the usual abaxial row of sclerenchyma strands that occur below the epidermis, *Tylocarya* varies in that adaxial strands of sclerenchyma are present and associated with the largest vascular bundles (four in this sample, excluding the usual corner support) (Figure 6.12). Adaxial strands were observed in only one other species in this study, and that was *F. fimbristyloides* (Figure 6.12). Culm anatomy in *Tylocarya*, however, is distinct from any of the other specimens sampled; there are many layers of vascular bundles arranged in rough concentric rings (3 developed and the 4th newly formed), decreasing in size as the newer bundles develop below the outermost tissue layers. The large dome-shaped bundles of support sclerenchyma are in direct contact with many of the newest vascular bundles in the outermost ring, and are clearly girders and not strands. The vascular bundles have extra sclerenchyma support, with an inner cap of approximately six strands, with some extra rows of sclerenchyma supporting the largest bundles that have been pushed inwards (Figure 6.12 B).

Nemum spadiceum was the only species of *Nemum* sampled for anatomy. The culm is highly sclerified, showing an almost continuous undulating band of fibres. The central pith is absent and prominent air spaces occur between most of the vascular bundles. The number of vascular bundles arranged in the single ring corresponds to the crescentiform section of the undulations, with stomata protruding through and above the sclerenchyma fibres in the narrow fibre regions (Figure 6.12 E). The leaf blade outline in transverse section is almost elliptic, possessing only four vascular bundles (not presented). The hypodermis is restricted to a couple of cell layers and is three to four cells wide in the adaxial central region. The leaf margins in both *Nemum* and *Nelmesia* are folded in and joined at the leaf sheath junction (see Metcalfe 1971).

The transverse culm outline in *Arthrostylis aphylla* is four-sided. Tannins are present within the epidermal cells, forming a broken line between the strands of sclerenchyma. The vascular bundles are found around the perimeter of the culm, and do not correspond in number to the many small mounds of sclerenchyma strands (Figure 6.11 A, B).

Actinoschoenus compositus is the only sampled species with sclerenchyma girders and strands present within the culms. The prominent ribs have equally prominent thickly V-shaped or crescentiform strands adjacent to the smaller vascular bundles (Figure 6.11 C, D). The deep channels have twin stomata at the sides near the base of the channel, and hairs are prominent near the outer margin. The epidermal layer is

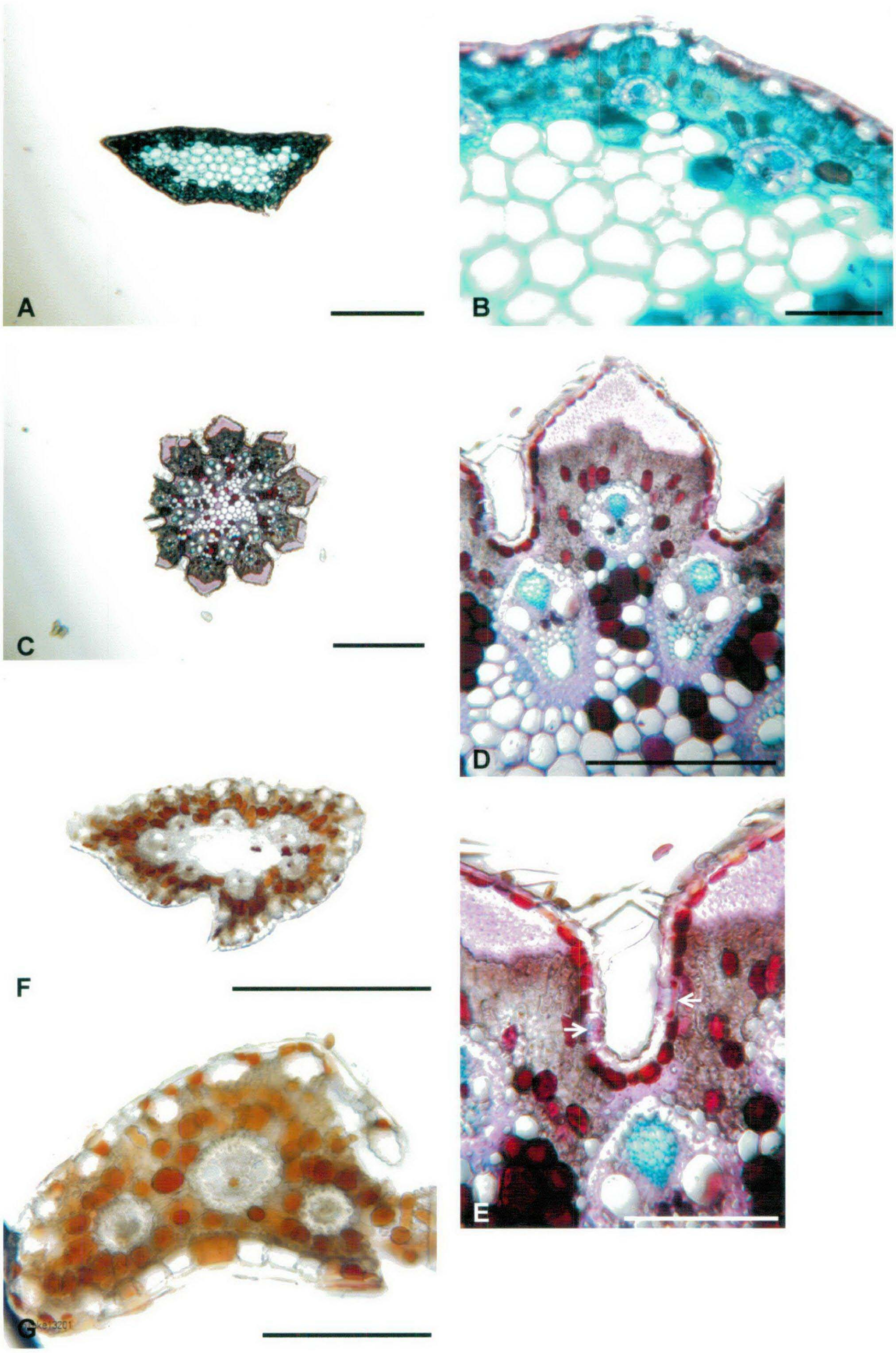


Figure 6.11 Culm and leaf blade transverse sections for some species from the provisional tribe 'Arthrostylideae' selected as outgroup taxa for use in cladistic analyis, showing the typical outlines, arrangement of sclerenchyma strands per vascular bundle, and C_3 anatomy. A. *Arthrostylis aphylla* (*A. Gunness AGL1965*) 4-sided culm and B. at higher magnification, showing the greater number of small mounded sclerenchyma strands than vascular bundles. C. *Actinoschoenus composita* (*K.L. Clarke 178 et al.*) culm that is regularly, deeply ribbed, with vascular bundles alternately large and small; at higher magnification D. thin rectangular girders are associated with the larger bundles and large crescentiform sclerenchyma strands are opposite the smaller vascular bundles. Twin stomata oppose each other at the base of each channel formed by the rib (indicated by the arrow heads). E. In *Trachystylis stradbokensis* (*S.T. Blake13201*) the culm is distinctly triangular in outline and F. the leaf blade is subtriangular, with vascular bundles completely immersed within the chlorenchyma. Scale bars A, C=500 µm; B, E, G=20 µm; D, F=50 µm. Collector and collection number are given in brackets. See Appendix 1 for specimen details.

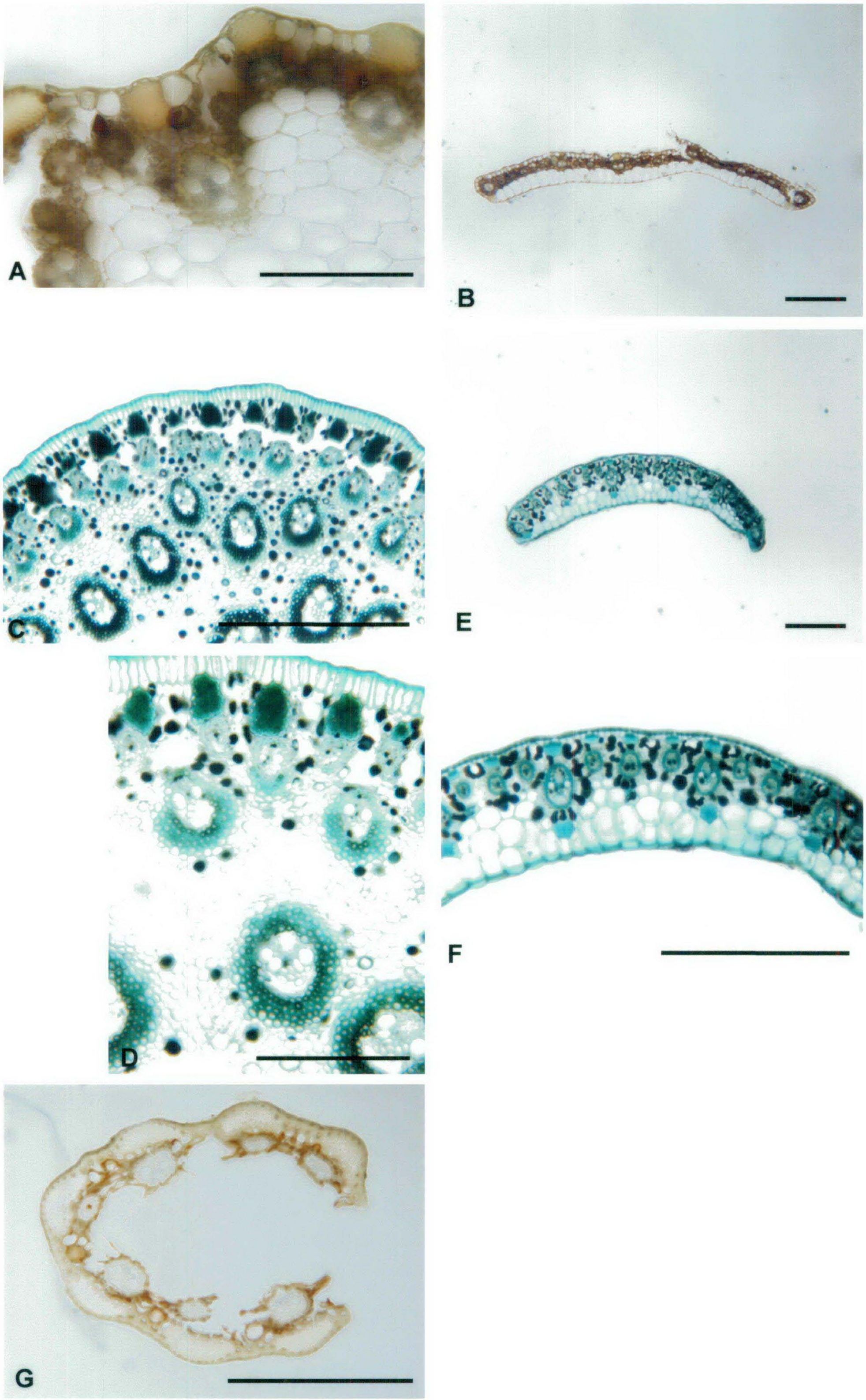


Figure 6.12 Culm and leaf blade transverse sections for *Fimbristylis, Tylocarya, and Nemum*. A. Culm and B. leaf blade sections of *Fimbristylis depauperata* (*K.L. Clarke 305, L. Little*). *Tylocarya cylindrostachya* (*A.G.F. Kerr 21294*) (= *F. nelmesii*) culm sections at C. low magnification and D. at high magnification, plus leaf blade sections at E. low magnification and F. at higher magnification, showing the variation and detail of vascularisation. G. Culm section for *Nemum spadiceum* (*E.A. Robinson 4676*) showing the continuous ring of undulating sclerenchyma. Collector and collection number are given in brackets. See Appendix 1 for specimen details. Scale bars A, D=20 μm; B, E= 500 μm; C, F, G=50 μm.

densely stained with tannins, seen as a continuous line, and has a thick cuticle layer (Figure 6.11 E).

In *Trachystylis*, both the leaf and culm are triangular in outline, and both are dense with tannin-filled cells. Some tannin is deposited in the epidermal tissues in both culms and leaves, although not so densely. The three vascular bundles of the leaf blade are completely surrounded by the chlorenchyma (Figure 6.11).

Tannin deposits in the epidermal layer do not occur in any of the other taxa sampled, including the outgroup, and were only found within the members of the provisional Arthrostylideae. In all of the other taxa studied, the tannin deposits were mostly observed within the chlorenchyma tissue.

Discussion

It is not possible to draw substantial conclusions from the main cladistic analysis, other than that the tribe Abildgaardieae, as it is currently accepted by Bruhl (1995) or Goetghebeur (1998), does not form a monophyletic group. The weak branch support in earlier analyses (see Chapters 3, 4, 5) for *Arthrostylis aphylla*, *Actinoschoenus compositus* and *Trachystylis stradbrokensis* with the outgroup clade gave an indication of the instability of the outgroup. Including *Eleocharis* within the current outgroup could resolve this instability, however, the lack of leaf blade characters and the solitary spikelets limit the usefulness of the genus as an outgroup here. Ghamkar et al. (2006, in press), in a molecular study of the tribe, found that samples from *Actinoschoenus* (*Fimbristylis composita* Latz), *K.L. Clarke et al. 214*, *K.L. Clarke et al. 213* (NE and NSW) and *Arthrostylis*, *K.L. Clarke et al. 212*, *K.L. Clarke et al. 183* (NE and NSW), all collected from Northern Territory, were nested within *Fimbristylis*; surprising considering the major differences seen in this study for vegetative anatomy and embryo morphology between the sampled *Actinoschoenus* and *Arthrostylis*, and the species of *Fimbristylis* (see Figures 6.9-10 and 6.11-12). Clearly, *Arthrostylis*, *Trachystylis,* plus overseas and Australian *Actinoschoenus* need to be assessed more thoroughly to fully determine their position, especially considering the taxonomic history of these taxa as species of *Fimbristylis*.

Species of *Bulbostylis* and *Fimbristylis* in clade A of this study are all C_4 taxa, however, any conclusions drawn regarding uniformity of the photosynthetic pathway across these genera are limited by the small samples sizes used in this study. The C_3 taxa that occur within the predominantly C_4 clade B of the *Abildgaardia–Crosslandia* group do not show any relative grouping patterns to explain their positioning within the cladogram. Stock et al. (2004) demonstrated a connection between phylogeny and geographical distribution in the tribes Cypereae, Scirpeae and Schoeneae; the sample size for the Abildgaardiaeae was too small to be informative. *Schoenoplectus* has both C_3 and C_4 species in the genus (Stock et al. 2004), however, Bruhl and Wilson (2005, in press) suggest that the C_4 *S. pulchella* sampled by Stock et al. may be misidentified, as all other species of *Schoenoplectus* are reportedly C_3. The species of *Shoenoplectus* and *Schoenoplectiella* sampled in this study i.e. *Schoenoplectus tabernaemontani* (= *S. validus*), *Schoenoplectiella lateriflora* (= *Schoenplectus lateriflorus*) and *Schoneoplectiella laevis* (= *Schoenoplectus laevis*) are all C_3 taxa. Alternatively, *Schoenoplectus pulchella* may be misplaced. The study by Bruhl and Wilson (2005, in press) reports the presence of C_3 and C_4 species in *Abildgaardia*. However, *A. hygropyhila* is the only C_3 species currently accepted in the genus, and is misplaced in *Abildgaardia* (see Chapter 4). Future studies in *Fimbristylis* could determine if C_3 species such as *Fimbristylis variegata* (with a Schoenus-type embryo and a prior history with *Abildgaardia*) should be removed from *Fimbristylis* that is currently accepted as containing both C_3 and C_4 species (Bruhl and Wilson 2005, in press).

The placement of *Tylocarya* with the representative species for the *Fimbristylis* TYPE section, *Fimbristylis* section *Fimbristylis* (*F. depauperata*) supports the current acceptance of *Tylocarya* as a species of *Fimbristylis* (*F. nelmesii*) (Kern 1974; Simpson 1993; Goetghebeur 1998). The differences in the culm anatomy and the variation in the Fimbristylis-type embryo need to be resolved against a broader *Fimbristylis* sample, especially when these two species have separated from the other species of *Fimbristylis* to be sister to most of the ingroup taxa.

The remaining species of *Fimbristylis* did not conform to Kern's (1974) sections. The only terminal branch in *Fimbristylis* with moderate support (Bootstrap=70%) was the paired *F. disticha* (section Fuscae) and *F. microcarya* (section *Trichelostylus*), which are clearly classified in separate sections. A similar result was obtained in the combined *trn*L-F and ITS regions data sets of Ghamkhar et al. (2005, in press), where a larger sample of species of *Fimbristylis* were included across the analysis, but sectional groups for the genus were not retrieved. A broader sampling of the embryos across the species assigned to *Fimbristylis* could provide more natural sectional groups, as there were distinct differences between the *Fimbristylis* embryos observed in this study and those by Van der Veken (1965) and Goetghebeur (1986).

Although intraprophyllar buds were observed in the *Bulbostylis* species studied (excluding *B. striatella*), their presence was not captured in the overall inflorescence–synflorescence structure; the buds can remain dormant and appear to be absent in some specimens. The difficulty also lies in the amount of material available for examination, as some specimens with only buds may be damaged or destroyed during examination. Nevertheless, the presence or absence of intraprophyllar buds, or growth, in species assigned to *Bulbostylis* could be a useful distinguishing character at the sectional level within *Bulbostylis*, if not at the higher rank of genus. There is potential for future work on this.

It is not surprising that Lye (in Haines and Lye 1983) used the appearance of the embryo to place *Bulbostylis* as a subgenus of *Abildgaardia*. The arrangement of the shoot and root primordia positioned basally, and the well-developed second primordial leaf are strikingly similar in all species of *Abildgaardia* and some species of *Bulbostylis* (*B. hispidula*, *B. striatella* and *B. pilosa*). However, the overall size of the embryo in *Abildgaardia* is consistently larger and the shoot is always more prominent than the root, while the reverse is true in all of the *Bulbostylis* species sampled in this study and those studied by Van der Veken (1965) and Goetghebeur (1986). The species of *Bulbostylis* examined by Van der Veken and Goetghebeur were: *B. caespitosa* Peter (= *B. oritrephes* (Ridl.) C.B.Clarke), *Fimbristylis cioniana* Savi (= *B. cioniana* (Savi) Lye, *B. coleotricha* (Hochst. ex A.Rich) C.B.Clarke, *B. conifera* (Nees) Kunth, *B. fendleri* C.B.Clarke, *B. lanifera* (Boeck.) Kük., *B. pringlei* (Britt.) Beetle (= *B. schaffneri* (Boeck.) C.B.Clarke), *B. vanderystii* Cherm., *B. melanocephala* (Ridl.) C.B.Clarke, and *B. oligostachya* (Hochst. ex A.Rich.) C.B.Clarke. The *Bulbostylis*-type embryo united the species of *Bulbostylis*, however, there are many species placed in this genus that require sampling; the embryo size, and the number and development of primordial leaves have potential for assessing the sectional limits of the genus.

The perianth bristles observed in *Abildgaardia schoenoides* (see Chapter 4 and Figure 6.3) are similar to those in *Eleocharis*, as both may have antrorse barbs

(Dahlgren et al. 1985; Wilson 1993), in contrast to the retrorse barbs in the species of *Schoenoplectus* with a perianth (see Figure 6.3). Many genera are composed of species with or without perianth (e.g. *Schoenoplectus*, *Schoenus* and *Rhynchospora*) and considering the rarity of the perianth within the tribe, the novel observation seems merely to be a remnant feature. The fact that the bristles were not well-developed in every floret (although many florets had aborted) and that the specimen is distinctly grouped with the other samples for *A. schoenoides*, adds support to the remnant hypothesis; it is less likely to me that the presence of perianth in this material is a reversal.

The surprise placement of *Nelmesia* within the *Abildgaardia* clade is not such a surprise when these results are compared to the systematic study of Goetghebeur (1986), where *Nelmesia* was placed in the same clade as *Abildgaardia*. The sample size of one collection, missing data, and the many autapomorphies associated with *Nelsmesia*, could have contributed to the placement. *Nelmesia* is known only from the Belgian Congo and placement within the Australian species of *Abildgaardia* is not a likely scenario. The intraspicular prophyll (cf. Haines 1967) present in *Carex* L., *Kobresia* Willd., *Schoenoxiphium* Nees (Snell 1936; Kern 1958; Timonen 1998; Starr et al. 2004), and *Lipocarpha* R.Br. (Goetghebeur 1998), although, the prophyll is modified into a utricle in genera of Carieaceae and the mixed floret sex, differs from the bisexual florets of *Nelmesia* with the non-modified prophyll. Lateral branches are consistently one-flowered spikelets in *Nelmesia* while the taxa shown in Kern (1958), Timonen (1998) and Starr et al. (2004) may have lateral branches with varying numbers of florets within the spikelet. Expanding the sample size to include taxa with features similar to *Nelmesia* and more collections of the species, could resolve some of the problems in assessing monophyly.

With *Nelmesia* excluded from the analysis, as occurred in Chapter 4, the species that form *Abildgaardia* are monophyletic and in a clade separate to most species of *Fimbristylis*, including *F. depauperata*, the representative for the TYPE section, *Fimbristylis* section *Fimbristylis*. Despite the problems within *Fimbristylis*, in the full analysis, *Abildgaardia* does not form a clade with the species of *Fimbristylis* (excluding *F. blakei* and *F.* sp. L (Kimberley Flora). If *Abildgaardia* is considered as a section in *Fimbristylis*, then my study shows that *Bulbostylis* and *Crosslandia* would need to be demoted from the generic rank to the rank of section as well. *Actinoschoenus* and *Trachystylis* would also need to be reassigned as sections of *Fimbristylis*, if the results from my analysis are interpreted as sections.

The Carex-type embryo is considered to be closest to the ancestral form (Goetghebeur 1998), and is unique to *Trachystylis* in this study. *Actinoschoenus thouarsii* Benth., *A. filiformis* and *A. repens* were shown to have the Carex-type embryo (Van der Veken 1965; Goetghebeur 1986), however *Actinoschoenus compositus* and *Arthrostylis aphylla* (see also Goetghebeur 1986) share the Schoenus-type embryo. It is worth noting that *Trachystylis* with the Carex-type embryo and C_3 anatomy, both considered as ancestral features, was not placed in any of the basal positions within the clades, but was among taxa with the derived embryo types and anatomy. I cannot see why *Trachystylis stradbrokensis* and *Nemum equitans* were placed together within the *Abildgaardia–Crosslandia* clade, other than the lack of informative characters from the many autapomorphies present in both taxa, inhibiting assessment of the relationships. Expanding the sample to include more species of *Nemum* and *Actinoschoenus*, plus other taxa from the tribe Schoeneae Dumort., the alternative valid tribe in which *Trachystylis*, *Arthrostylis* and *Actinoschoenus* are placed (Goetghebeur 1998), may assist in resolving the lack of monophyly achieved in this analysis. In addition, selecting a broader outgroup sample to include other closely related genera and so aid optimisation of the tree (Grandcolas et al. 2004), starting with *Eleocharis* R.Br., is recommended.

There is still much work to be done to assess the limits of the genera with the largest number of species, i.e. *Fimbristylis* and *Bulbostylis*, and the monotypic genera that have only minimal collections, i.e. *Nelmesia* and *Tylocarya*.

The lack of resolution for relationships in the current study is due in part to problems at both ends of the sampling spectrum, confounded by high levels of homoplasy and the difficulty in defining adequately characters for the cladistic analyses. Problematic data is not new, and many articles have been written about the use of characters in cladistic studies in an attempt to work through some of the lack of cladistic or phylogenetic resolve in analysis (Rieger 1979; Scotland and Williams 1993; Thiele 1993; Donoghue and Ackerly 1997; Poe and Wiens 2000; Wiens 2000; Desutter-Grandcolas et al. 2005). The next step that could be taken is the merging of the plant morphology, embryo morphology and anatomical data from this study with the molecular study for the tribe, and then seeing if the combined data set is more stable.

General conclusions

The tribe Abildgaardieae, as currently delimited, does not form a monophyletic group. The data analysed were obtained from morphology, vegetative anatomy and embryo morphology. Monophyletic groups were retrieved for some genera in Chapters 3, 4, and 5, where *Crosslandia*, *Abildgaardia*, *Fimbristylis*, and *Bulbostylis* formed the 'ingroup'.

Species of *Crosslandia* formed a monophyletic group: *C. setifolia*, *C. anthelata* ined., *C. spiralis* ined. (*Fimbristylis spiralis*) and *C. vaginata* ined. (*Abildgaardia vaginata*). *Crosslandia vaginata*, although consistently retrieved, had little support and in the *Bulbostylis* analysis (Chapter 5) and the 'whole tribe' analysis (Chapter 6) was placed as sister to the *Crosslandia* clade; it is important to note that *Crosslandia vaginata* did not fall within the *Fimbristylis* or *Abildgaardia* s.s. clades (although it was placed in the broad *Abildgaardia–Crosslandia* clade). The variation in embryo morphology (Fimbristylis-and Schoenus-types) and inflorescence–synflorescence structure indicates that the sample size needs to be increased to fully define the limits before validly publishing new combinations. Extending the molecular sample is also recommended to explore the genetic variability across the geographical range. The remaining three species of *Crosslandia* have support for their placement as separate species within *Crosslandia*.

There is no evidence to support maintaining *Abildgaardia* as a section of *Fimbristylis*, as the species of *Fimbristylis* did not form a monophyletic group in any of the analyses, and *Bulbostylis* was placed more closely to *Fimbristylis* than were the species of *Abildgaardia*. A well-supported, monophyletic group was formed by species of *Abildgaardia* in the analyses in Chapters 3, 4, and 5, but not in the final analysis in Chapter 6, where *Nelmesia melanostachya* rendered the group non-monophyletic. Nevertheless, the *Abildgaardia* clade did not fall within the species of *Fimbristylis*, although two species of *Fimbristylis* (*F. blakei* and *F.* sp. L) were grouped in the same broad clade as *Abildgaardia* and *Crosslandia*. *Abildgaardia hygrophila* was not supported as a species of *Abildgaardia*, even though it is placed near the provisional *Crosslandia vaginata* and the other species of *Abildgaardia*. Similarities between *A. hygrophila* (= *Fimbristylis hygrophila*) and species of *Abildgaardia*, as defined here, are purely superficial. The fact that this species was not grouped with any of the species of *Fimbristylis* begs for further investigation into the correct placement of this C_3 species bearing a Fimbristylis-type embryo. There was no support for the inclusion of *Abildgaardia baeothryon* within *Abildgaardia*. A study of the embryo and anatomy of *Abildgaardia papillosa* is recommended because of the findings for *Fimbristylis bahiensis* (= *A. baeothryon*) in this study and the affinity between the two species. Broader sampling to capture the variation between *Abildgaardia oxystachya* and *A. pachyptera* to define their limits is needed prior to publishing. In contrast, species status for the samples *A.* sp. aff. *odontocarpa* and *A.* sp. aff. *pachyptera* is merited and descriptions are being prepared. Meanwhile, determining where the name *A. schoenoides* R.Br. should be applied and if *Fimbristylis squarrulosa* (TYPE) is a synonym of *A. schoenoides* must be sought by examining the *A. schoenoides* TYPE specimen held at BM. Comparing the TYPES assigned to both names with the groups retrieved from phenetic analyses is necessary to determine the correct application of the names.

Species of *Bulbostylis* formed a monophyletic group that was well supported in Chapters 5 and 6. *Bulbostylis kakadu* ined. is a distinct species separate to *B. barbata* and a description can now be prepared for valid publication.. Any relationship between the Australian *B. pyriformis* and the *B. hispidula* group was inconclusive. A more thorough study is recommended to explore fully the relationship between all the entities of the *B. hispidula* complex and the Australian *B. pyriformis*.

No sections from Kern's (1974) classification of *Fimbristylis* were retrieved in this study, however, the placement of *Tylocarya* with *Fimbristylis depauperata* (from the TYPE section, *Fimbristylis* section *Fimbristylis*) supports Kern's (1958) decision to place *Tylocarya* in *Fimbristylis* as *F. nelmesii*.

Members of the provisional Arthrostylideae loosely formed the outgroup beside species of *Schoenoplectus* and *Schoenoplectiella*. However, the shift of *Actinoschoenus*, *Arthrostylis* and *Trachystylis* into the ingroup when *Nemum*, *Nelmesia* and *Tylocarya* were added, reflected the tenuous support for the outgroup placement in previous chapters (Chapters 3, 4, and 5). *Actinoschoenus* and *Arthrostylis* require further investigation to explore the species and generic limits – a study is currently underway. Expanding the study to include other members of the *Schoeneae*, considered close to *Actinoschoenus* and *Arthrostylis*, is necessary. Better tree topology may result by adding these taxa and a broadened sample of species from *Fimbristylis* and *Bulbostylis*, where work is also required to assess species and generic limits.

The tribe Abildgaardieae may need to be reclassified in the near future. Expanding Abildgaardieae to include *Actinoschoenus*, *Arthrostylis* and *Trachystylis* is one option, or defining smaller tribal groups where the name Abildgaardieae is applied to taxa in the broad *Abildgaardia–Crosslandia* clade, and Fimbristylideae Cherm ex Raynal reinstated to accommodate taxa in the *Fimbristylis–Bulbostylis* clade is a second option. However, further cladistic studies to resolve monophyletic groups are needed.

Combining the morphological, anatomical, and embryographic data from this study with the molecular data from a sister study by Ghamkar (2004), to assess congruence and monophyly of the combined data, may move towards resolving monophyletic groups.

In the tribe Abildgaardieae and the Cyperaceae in general, the search for monophyletic groups to develop natural systems of classification may well rely on more collaborative projects, especially where genera with large numbers of species cover vast areas globally – and all of us with limited resources.

References

Adams CD (1994) Cyperaceae. In 'Flora Mesoamericana'. (Eds GD Davidse, M Sousa S and AO Chater). (Ciudad Universitaria : Universidad Nacional Autónoma de México, Instituto de Biología, Missouri Botanical Garden: Mexico)

Belbin L (1993) PATN pattern analysis package. (Division of Wildlife and Ecology, CSIRO: Canberra)

Bentham G (1861) 'Flora hongkongensis: A description of the Flowering Plants and Ferns of the island of HongKong.' (L. Reeve: London)

Bentham G (1878) Cyperaceae. In 'Flora Australiensis: A Description of the Plants of the Australian Territory'. (L. Reeve & Co.: London)

Bentham G, Hooker JD (1880) Cyperaceae. In 'Genera Plantarum' pp. 1037-1073. (L. Reeve & Co.: London)

Blake ST (1940) Monographic studies in the genus *Fimbristylis* (Cyperaceae). *Proceedings of the Royal Society of Queensland* **13**, 1-14.

Blake ST (1941) Notes on Australian Cyperaceae, V. *Proceedings of the Royal Society of Queensland* **52**, 55-61.

Blake ST (1947) Notes on Australian Cyperaceae, VIII. *Proceedings of the Royal Society of Queensland* **58**, 35-50.

Blake ST (1969) Studies in Cyperaceae. *Contirbutions from the Queensland Herbarium* **8**, 1-48.

Boeckeler O (1874) *Fimbristylis planiculmis*. *Linnaea* **38**, 391.

Bremer K (1994) Branch support and tree stability. *Cladistics* **10**, 295-304.

Brown R (1810) 'Prodromus Florae Novae Hollandiae.' (Hafner Publishing Co.: New York)

Browning J (1992) Hyogynous bristles and scales in basal florets in amphicarpous *Schoenoplectus* species (Cyperaceae). *Nordic Journal of Botany* **12**, 171-175.

Bruhl JJ (1990) Taxonomic relationships and photosynthetic pathways in the Cyperaceae. PhD thesis, Australian National University.

Bruhl JJ (1994) Amphicarpy in the Cyperaceae, with novel variation in the wetland sedge *Eleocharis caespitosissima* Baker. *Australian Journal of Botany* **42**, 441-448.

Bruhl JJ (1995) Sedge genera of the world: relationships and a new classification of the Cyperaceae. *Australian Systematic Botany* **8**, 125-305.

Bruhl JJ, Perry S (1995) Photosynthetic pathway-related ultrastructure of C_3, C_4 and C_3-like C_3-C_4 intermediate sedges (Cyperaceae), with special reference to *Eleocharis*. *Australian Journal of Plant Physiology* **22**, 1-10.

Bruhl JJ, Stone NE, Hattersley PW (1987) C_4 acid decarboxylation enzymes and anatomy in sedges (Cyperaceae). *Australian Journal of Plant Physiology* **14**, 719-728.

Bruhl JJ, Wilson KL (2005, in press) Towards a comprehensive survey of C_3 and C_4 photosynthetic pathways in Cyperaceae. In 'Monocots: comparative biology and evolution'. (Eds JT Columbus, EA Friar, CW Hamilton, JM Porter, LM Prince and MG Simpson) pp. xx-xxx. (Rancho Santa Ana Botanic Garden: Claremont)

Chermezon H (1929) Sur quelques *Scirpus* à épillets basicaules. *Archives de Botanique, Bulletin Mensuel, Caen* **3**, 193-197.

Clarke CB (1893) Cyperaceae 2. In 'The Flora of British India'. (Ed. JD Hooker) pp. 585-672. (L. Reeve and Co.: London)

Clarke CB (1900) Cyperaceae. In 'Flora Capensis: A systematic description of the Plants of the Cape Colony, Caffraria, and Port Natal (and neighbouring territories)'. (Ed. SWT Thiselton-Dyer) pp. 149-310. (Lovell Reeve & Co. Ltd: London)

Clarke CB (1908) New genera and species of Cyperaceae. *Bulletin of Miscellaneous Information* **8**, 1-196.

Crisp MD, Weston PH (1993) Geographic and ontogenetic variation in morphology of Australian waratahs (*Telopea*: Proteacae). *Systematic Botany* **42**, 49-76.

Dahlgren RMT, Clifford HT, Yeo PF (1985) 'The Families of the Monocotyledons.' (Springer-Verlag: Berlin)

Dallwitz MJ, Paine TA, Zurcher EJ (1999) DELTA Editor. (CSIRO Entomology: Canberra)

Davis GL (1966) 'Systematic Embryology of the Angiosperms.' (John Wiley and Sons, Inc.: New York)

Desutter-Grandcolas L, Legendre F, Grandcolas P, Robillard T, Murienne J (2005) Convergence and parallelism: is a new life ahead of old concepts? *Cladistics* **21**, 51-61.

Donoghue MJ, Ackerly DD (1997) Phylogenetic uncertainties and sensitivity analyses in comparative biology. In 'Plant Life Histories: Ecology, Phylogeny, and Evolution'. (Ed. J Silvertown, Franco, M., and Harper, J.L.) pp. 17-35. (Cambridge University Press: Cambridge)

Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**, 783-791.

Fitzgerald WV (1918) The Botany of the Kimberleys, North-West Australia. *Journal and Proceedings of the Royal Society of Western Australia* **3**, 102-224.

Fosberg FR (1977) Miscellaneous notes on the flora of Aldabra and neighbouring islands: IV. A new *Bulbostylis* and observations on *Cyperus* (Cyperaceae). *Kew Bulletin* **31**, 829-835.

Ghamkhar K, Marchant AD, Wilson KL, Bruhl JJ (2006, in press) Phylogeny of Abildgaardieae (Cyperaceae) inferred from ITS and trnL-F data. In 'Monocots: comparative biology and evolution'. (Eds JT Columbus, EA Friar, CW Hamilton, JM Porter, LM Prince and MG Simpson) pp. xx-xxx. (Rancho Santa Ana Botanic Garden: Claremont)

Gilliland MG, Gordon-Gray KD (1978) Kranz and non-Kranz cells in Cyperaceae. Proceedings of the Electron Microscopy Society of Southern Africa **8,** 85-86.

Goetghebeur P (1986) *Genera Cyperacearum*. Een bijdrage tot de kennis van de morfologie, systematiek en fylogenese van de Cyperaceae-genera. Doctoral thesis, Rijksuniversiteit Gent. [Flemish]

Goetghebeur P (1998) Cyperaceae. In 'The Families and Genera of Vascular Plants'. (Ed. K Kubitzki) pp. 141-190. (Springer-Verlag: Berlin)

Goetghebeur P, Coudijzer J (1984) Studies in Cyperaceae 3. *Fimbristylis* and *Abildgaardia* in Central Africa. *Bulletin Jardin Botanique National Belgium* **54**, 65-89.

Goetghebeur P, Coudijzer J (1985) Studies in the Cyperaceae. 5: The genus *Bulbostylis* in Central Africa. *Bulletin Jardin Botanique National Belgium* **55**, 207-259.

Goetghebeur P, Gröger A (1993) Studies in Cyperaceae II. The unispiculate species of *Bulbostylis* in the Americas. *Biologisch Jaarboek* **60**, 64-75.

González-Elizondo MS, Peterson PM, Granzow-de La Cerda I (1997) A cladistic and phenetic analysis of the Pauciflorae group of *Eleocharis* (Cyperaceae). *BioLlania, Edición Especial; Monografías Cientificas del Museo de Ciencias Naturales de la UNELLEZ Guanare* **6**, 341-368.

Gordon-Gray KD (1971) *Fimbristylis* and *Bulbostylis*: generic limits as seen by a student of southern African species. *Mitteilungen (aus) der Botanischen Staatssammlung München* **10**, 549-574.

Gordon-Gray KD (1988) Studies in Cyperaceae in southern Africa:13. The *Bulbostylis schoenoides* complex (Cyperaceae) in Africa, south of the Sahara. *South African Journal of Botany* **54**, 565-570.

Gordon-Gray KD (1995) Cyperaceae in Natal. *Strelitzia* **2**.

Grandcolas P, Guilbert E, Robillard T, D'Haese CA, Murienne J, Legendre F (2004) Mapping characters on a tree with or without the outgroups. *Cladistics* **20**, 579-582.

Greuter W, Brummitt RK, Farr PM, Kilian N, Kirk PM, Silva PC (Eds) (1993) 'Names in Current Use for Extant Plant Genera.' Regnum Vegetabile (Koeltz Scientific Books: Konigstein, Germany)

Guaglianone ER (1970) Un nuevo carácter, útil en la distinción genérica entre *Fimbristylis* Vahl y *Bulbostylis* Kunth. (Cyperaceae). *Darwiniana* **16**, 40-48.

Haines RW (1967) Prophylls and branching in Cyperaceae. *Journal of the East Africa Natural History Society and National Museum* **26**, 51-70.

Haines RW (1971) Amphicarpy in east African Cyperaceae. *Mitteilungen (aus) der Botanischen Staatssammlung München* **10**, 534-538.

Haines RW, Lye KA (1977) Studies in African Cyperaceae. 15. Amphicarpy and spikelet structure in *Trianoptiles solitaria*. *Botaniska Notiser* **130**, 235-240.

Haines RW, Lye KA (1983) 'The Sedges and Rushes of East Africa.' (East African Natural History Society: Nairobi)

Hennig W (1979) 'Phylogenetic Systematics.' (University of Illinois Press: Urbana)

Holmgren PK, Holmgren NH, Barnett LC (1990) 'Index Herbariorum. Part I: The Herbaria of the World.' (New York Botanical Garden: Bronx)

Hooper SS (1973) Cyperaceae. In 'The Families of Flowering Plants'. (Ed. J Hutchinson) pp. 863-871. (Clarendon Press: Oxford)

Hutchinson J (1934) 'The Families of Flowering Plants II. Monocotyledons.' (Macmillan and Co. Ltd: London)

Hutchinson J (1959) 'The Families of Flowering Plants.' (Clarendon Press: Oxford)

Johansen DA (1940) 'Plant Microtechnique.' (McGraw-Hill Book Co.: New York)

Johri BM, Ambegaokar, K.B., Srivastava, P.S. (1992) 'Comparative Embryology of Angiosperms.' (Springer-Verlag: Berlin)

Kearns CA, Inouye DW (1993) 'Techniques for Pollination Biologists.' (University Press of Colorado: Niwot, Colorado)

Kern JH (1955) Florae Malesianae precursores X. Notes on Malaysian and some S.E. Asian Cyperaceae 3. *Blumea* **8**, 110-169.

Kern JH (1958) Florae Malesianae Precursors XXI. Notes on Malaysian and some S.E. Asian Cyperaceae VII. *Acta Botanical Neerlandica* **7**, 786-800.

Kern JH (1959) Florae Malesianae precursores XXII. *Cladium* and *Machaerina* (Cyper.). *Acta Botanica Neerlandica* **8**, 263-268.

Kern JH (1963) *Acriulus* once more reduced (Cyperaceae). *Blumea* **12**, 41-44.
Kern JH (1974) Cyperaceae. In 'Flora Malesiana'. (Ed. CGGJ van Steenis) pp. 435-753. (Noordhoff International Publishing: Leyden)

Koyama T (1961) Classifification of the family Cyperaceae: 1. *Journal of the Faculty of Science* **8**, 37-148.

Kral R (1971) A Treatment of *Abildgaardia*, *Bulbostylis* and *Fimbristylis* (Cyperaceae) for North America. *Sida* **4**, 57-227.

Kral R (2002) *Abildgaardia*. In 'Flora of North America: North of Mexico'. (Ed. FoNAE Committee). (Oxford University Press: New York)

Kral R, Strong MT (1999) Eight novelties in *Abildgaardia* and *Bulbostylis* (Cyperaceae) from South America. *Sida* **18**, 837-859.

Kraus JE, de Sousa HC, Rezende MH, Castro NM, Vecchi C, Luque R (1998) Astra Blue and Basic Fuchsin double staining of plant materials. *Biotechnic and Histochemistry* **73**, 235-243.

Kükenthal G (1944) Vorarbeiten zu einer Monographie der *Rhynchosporideae*. 15. *Feddes repertorium specierum novarum regni vegetabilis* **53**, 186-197.

Kukkonen I (1986) Special features of the inflorescence structure in the family Cyperaceae. *Annales Botanici Fennici* **23**, 107-120.

Kukkonen I (1991) Problems in *Carex* section *Physodeae* and *Cyperus congolmeratus* within the Flora Iranica area. *Flora et Vegetatio Mundi* **9**, 63-73.

Kunth CS (1837) 'Enumeratio Plantarum. 2.' (Stutgardiae & Tubingae)

Latz PK (1990) Taxonomic studies of *Fimbristylis* (Cyperaceae) in Northern Australia. *Nuytsia* **7**, 161-182.

Le Roux LG, Kellogg EA (1999) Floral development and the formation of unisexual spikelets in the Andropogoneae (Poaceae). *American Journal of Botany* **86**, 354-366.

Levyns MR (1943) A revision of *Trianoptiles* Fenzl. *Journal of South African Botany* **9**, 21-26.

Lye KA (1971) The generic concept of *Bulbostylis* Kunth ex C.B. Clarke. *Mitteilungen (aus) der Botanischen Staatssammlung Munchen* **10**, 539-547.

Lye KA (1973) Studies in African Cyperaceae VIII. The taxonomic position of *Abildgaardia* Vahl and *Nemum* Hamilton. *Botaniska Notiser* **126**, 325-329.

Lye KA (1995) Cyperaceae. In 'Flora of Somalia'. (Ed. sLN Herbarium))

Lye KA (1996) A new species of *Bulbostylis hispidula* (Cyperaceae) from Somalia. *Willdenowia* **25**, 595-600.
Lye KA (2000) Achene structure and function of structure in Cyperaceae. In 'Monocots II: Systematic and Evolution'. Sydney. (Ed. KL Wilson, and Morrison, D.A.) pp. 615-628. (CSIRO)

Maddison WP, Maddison DR (1992) MacClade: Analysis of phylogeny and character evolution. In. (Sinauer Associates, Inc.: Sundlerland, Massachusetts)

Maheshwari P (1964) 'Embryology in relation to taxonomy.' (Pergamon Press Limited: Oxford)

Metcalfe CR (1969) Anatomy as an aid to classifying the Cyperaceae. *American Journal of Botany* **56**, 782-790.

Metcalfe CR (1971) Cyperaceae. In 'Anatomy of the Monocotyledons'. (Ed. CR Metcalfe). (Clarendon Press: Oxford)

Microsoft (1999) Microsoft Excel 2000.

Mitchell CH, Diggle PK (2005) The evolution of unisexual flowers: morphological and functional convergence results from diverse developmental transitions. *American Journal of Botany* **92**, 1068-1076.

Muasya AM, Bruhl JJ, Simpson DA, Culham A, Chase MW (2000) Suprageneric phylogeny of Cyperaceae: a combined analysis. In 'Monocots: Systematic and Evolution'. (Eds KL Wilson and DA Morrison) pp. 593-601. (CSIRO Publishing: Melbourne)

Nelmes E (1949) Notes on Cyperaceae: XIX. A new genus of Scirpeae. *Kew Bulletin* **4**, 139-140.

Page RDM (1996) TREEVIEW: An application to display phylogenetic trees on personal computers. *Computer Applications in the Biosciences* **12**, 357-358.

Penet L, Nadot S, Ressayre A, Forchioni A, Dreyer L, Gouyon PH (2005) Multiple developmental pathways leading to a single morph: monosulcate pollen (examples from the Asparagales). *Annals of Botany* **95**, 331-343.

Poe S, Wiens JJ (2000) Character selection and the methodology of morphological phylogenetics. In 'Phylogenetic Analysis of Morphological Data'. (Ed. JJ Wiens) pp. 20-36. (Smithsonian Institution Press: Washington)

Ramirez MJ (2005) Resampling measures of group support: a reply to Grant and Kluge. *Cladistics* **21**, 83-89.

Raynal J (1973) Notes Cypérologioques: 19. Contribution a la classification de la Sous-famille des Cyperoideae. *Adansonia* **13**, 145-171.

Raynal J (1976) Notes Cypérologioques: 26 Le Genre *Schoenoplectus* 11. L'amphicarpie et la sect. *Supini*. *Adansonia* **16**, 119-155.

Rieger RaT, S. (1979) The homology theorem in ultrastructural research. *American Zoologist* **19**, 655-664.

Robyns W, Tournay R (1955) 'Flore des Spermatophytes du Parc National Albert.'

Rye BL (1992) Cyperaceae. In 'Flora of the Kimberley Region'. (Ed. JR Wheeler) pp. 1035-1107. (Western Australian Herbarium, Department of Conservation & Land Management: Como, W.A.)

Scotland RW, Williams DM (1993) Multistate characters and cladograms: when are two stamens more similar to three stamens than four? A reply to Lipscomb. *Cladistics* **9**, 343-350.

Sharpe PR (1986) Keys to the Cyperaceae, Restionaceae and Juncaceae of Queensland. *Queensland Botany Bulletin* **5**, 1-34.

Simpson DA (1992) 'A revision of the genus *Mapania*.' (Royal Botanic Gardens, Kew: Surrey, UK)

Simpson DA (1993) Genera of Cyperaceae recognised at Kew. *Cyperaceae Newsletter* **12**, 8-12.

Simpson DA, Koyama T (1998) Cyperaceae. *Flora of Thailand* **6**, 247-485.

Simpson DA, Muasya AM, Alves M, Bruhl JJ, Dhooge S, Chase MW, Furness CA, Ghamkhar K, Goetghebeur P, Hodkinson TR, Marchant AD, Reznicek AA, Nieuwborg R, Roalson EH, Smets E, Starr JR, Thomas WW, Wilson KL, Zhang X (2005, in press) Phylogeny of Cyperaceae based on DNA sequence data - a new *rbcL* analysis. In 'Monocots: comparative biology and evolution'. (Eds JT Columbus, EA Friar, CW Hamilton, JM Porter, LM Prince and MG Simpson) pp. xx-xxx. (Rancho Santa Ana Botanic Garden: Claremont)

Snell RS (1936) Anatomy of the spikelets and flowersof *Carex*, *Kobresia* and *Uncinia*. *Bulletin of the Torrey Botanical Club* **63**, 277-295.

Soros CL, Bruhl JJ (2000) Multiple evolutionary origins of C_4 photosynthesis in the Cyperaceae. In 'Monocots: Systematics and Evolution'. (Eds KL Wilson and DA Morrison) pp. 629-636. (CSIRO: Melbourne)

Soros CL, Dengler NG (2001) Ontogenetic derivation and cell differentiation in photosynthetic tissues of C_3 and C_4 Cyperaceae. *American Journal of Botany* **88**, 992-1005.

Starr JR, Harris SA, Simpson DA (2004) Phylogeny of the unispicate taxa in Cyperaceae tribe Cariceae I: Generic relationships and evolutionary scenarios. *Systematic Botany* **29**, 528-544.

Statsoft I (1996) Statistica for Windows. (Statsoft Inc.: Tulsa)

Steudel EG (1855) Cyperaceae Juss. In 'Synopsis Plantarum Cyperacearum'. (J.B. Metzler: Stuttgartine)

Stock WD, Chuba DK, Verboom GA (2004) Distribution of South African C_3 and C_4 species of Cyperaceae in relation to climate and phylogeny. *Austral Ecology* **29**, 313-319.

Stuessy TF (1990) 'Plant Taxonomy.' (Columbia United Press: New York)

Swofford DL (2001) PAUP*: Phylogenetic analysis using parsimony (*and other methods). In. (Sinauer Associates: Sunderland, Massachusetts)

Thiele K (1993) The holy grail of the perfect character: the cladistic treatment of morphometric data. *Cladistics* **9**, 275-304.

Thwaites GHK (1864) 'Enumeratio Plantarum Zeylaniae.' (Dulau: London)

Timonen T (1998) Inflorescence structure in the sedge tribe Cariceae (Cyperaceae). *Publications in Botany from the University of Helsinki* **26**, 1-35.

Vahl M (1805) 'Enumeratio Plantarum. 2.' (Hauniae : Impenis auctoris, & prostat apud J.H. Schubothe: Copenhagen)

Van der Veken P (1955) Trois taxa nouveaux de Cypéracées du Congo Belge. *Bulletin du Jardin botanique de Etat a Bruzelles* **25**, 143-147.

Van der Veken P (1965) Contribution a l'embryographie systematiques des Cyperaceae: *Cyperoideae. Bulletin du Jardin botanique de Etat a Bruzelles* **35**, 285-354.

Vegetti AC (2003) Synflorescence Typology in Cyperaceae. *Annals Botanici Fennici* **40**, 35-46.

von Mueller F (1875) 'Fragmentia Phytographiae Australiae.' (Melbourne)

Vrijdaghs A, Caris P, Goetghebeur P, Smets E (2005) Floral ontogeny in *Scirpus*, *Eriophorum* and *Dulichium* (Cyperaceae), with special reference to the perianth. *Annals of Botany* **95**, 1199-1209.

Weberling F (1989) 'Morphology of flowers and inflorescences.' (Cambridge University Press: Cambridge)

Wiens JJ (2000) Coding morphological variation within species and higher taxa for phylogenetic analysis. In 'Phylogenetic Analysis of Morphological Data'. (Ed. JJ Wiens) pp. 115-145. (Smithsonian Institution Press: Washington)

Wilson KL (1980) Notes on some Australian species of Cyperaceae. *Telopea* **1**, 457-467.

Wilson KL (1991) Systematic studies in *Cyperus* section *Pinnati* (Cyperaceae). *Telopea* **4**, 361-559.

Wilson KL (1993) Cyperaceae. In 'Flora of New South Wales. Vol. 4.' (Ed. GL Harden) pp. 293-396. (New South Wales University Press: Kensington)

World Checklist of Monocotyledons (2004) The Board of Trustees of the Royal Botanic Gardens, Kew. In 'Published on the Internet; http://www.kew.org/monocotChecklist/'.

Appendix 1. List of all specimens used in phenetic and/or cladistic analyses. The OTU label corresponds to the code for each specimen used in phenetic analyses. Herbarium codes (Herb. Code.) are provided for all sampled specimens followed by the sheet number where available. Specimens collected in Australia show the state in which they were collected, if collected overseas then the country or continent is given. Specimens used for Scanning electron microscopy (SEM=*), embryo morphology (embryo=#) or leaf blade and/or culm anatomy (anatomy=+) are indicated in the phenetic code column next to the OTU label, if given. N.T.=Northern Territory, W.A.=Western Australia, Qld=Queensland, Vic=Victoria. (JJB)=prepared sections provided by J.J. Bruhl. Names given here are prior to analyses and are based on *Abildgaardia* and *Tylocarya* as genera.

Generic groups studied and species names	OTU label	Herb. code	State or Country	Collector
Ingroup				
***Crosslandia* W.Fitzg.**				
Crosslandia anthelata nom. prov. Goetgh. ined.	C18	MEL 1590282	N.T.	Dunlop C.R. 6854, Wightman G.
	C19#	BRI 313723	N.T.	Dunlop C.R. 3446
	C20#	NE 61439	N.T.	Bruhl J.J., Hunter V., Egan J. 1268
	C21	NSW 452330	N.T.	Dunlop C.R. 3408
	C22	NSW 452331	N.T.	Wilson K.L. 5150, Dunlop C.R.
	C23	CANB as CBG 8309188	N.T.	Thompson H.S. 403
Crosslandia setifolia W.Fitzg.	C1	BRI 313715	N.T.	Chippendale G. 1268
	C2	MEL 2048535	W.A.	Poulton G. 5
	C3	NSW 452305	W.A.	Wilson K.L. 4885
	C4	MEL 2048435	N.T.	Craven L.A. 7928, Whitbread G.
	C5	BRI 313716	N.T.	Blake S.T. 17420
	C6	NSW 460200	N.T.	Cowie I.D. ID 4639
	C7	CANB 264103	W.A.	Pullen R.
	C8	NE(exNSW 416310)	N.T.	Wilson K.L. 5260
	C9	NSW 303698	W.A.	Wilson K.L. 4859
	C10	NSW 460198	W.A.	Wilson K.L. 4803
	C11	MEL 2048448	N.T.	Lazarides M. 8, Adams L.G.
	C12	BRI 313711	W.A.	Burbidge N. 5703
	C13	MEL 2048434	N.T.	Dunlop C.R. 6789
	C14	NE	W.A.	Clarke K.L. 166, Bruhl J.J., Wilson K.L.

	C15	CANB 159880	N.T.	Blake S.T. 16585
	C16	CANB 78686	W.A.	Van Rijn P.J. 19
	C17	NE	N.T.	Clarke K.L. 155, Bruhl J.J., Wilson K.L., Cowie I.D.
Fimbristylis spiralis R.Br.	F1#	MEL 2048472	N.T.	Specht R.L. 235
	F2	DNA 36442	N.T.	Dunlop C.R. 2957
	F3	NSW 422184	N.T.	Leach G. 3601, Cowie I.D.
Abildgaardia vaginata R.Br.	Av1	BRI 300861	Qld	Blake S.T. 15540, Webb L.J.
	Av2#	NSW 285362	N.S.W.	Floyd A.G.F. AGF2205
	Av3#	BRI 300844	Qld	Brass L.J. 18362
	Av4	BRI 300865	N.S.W.	O'Hara J. 3472 and Coveny R.
	Av5	MEL 2048450	Qld	Blake S.T. 8598
	Av6	DNA 128735	N.T.	Cowie I.D. 6801
	Av7+	DNA 72733	N.T.	Brennan K. 2588
	Av8	NE 54172A	N.S.W.	Bell D.M.
	Av9#	MEL 716909	Qld	Forster P.I. PIF9732, Machim P.
	Av10	BRI 601359	Qld	Forster P.I. PIF16257
	Av11	MEL 2048451; BRI 300850 CBG 8309188	Qld	Blake S.T. 8222
	Av12	CANB 506846; BRI 300856	Qld	Blake S.T. 22499
	Av13	BRI 300848	Qld	Brass L.J. 1924
	Av14	BRI 549964; CANB 505073	Qld	Sharpe P.R. 5299 and Bird L.
***Abildgaardia* Vahl**				
Abildgaardia baeothryon A.St.-Hil.	*#+	K 2525	Brazil	Mattes Silva L.A. 394, Ribeiro A.J., da S. Brito H.
(all as *Fimbristylis bahiensis* Steud.)	#+	K 2528	Brazil	Almeida de Jesus J. 1466
		KEW 2529	Brazil	Bento Pickel D. 3140
		K 2527	Brazil	Mori S. 10389, dos Santos S., White I.
Abildgaardia hygrophila (Gordon-Gray) Lye	*	NE 71642	South Africa	Ward C.J. 2794
	#+	NU	South Africa	Tinley K.L. 307
Abildgaardia macrantha (Boeck.) comb. prov. Goetgh.	Am1	CANB 280535	W.A.	Hartley T.G. 14405

	Am2	NSW 454230	N.T.	Cowie I.D. 6202 & Booth R.
	Am3*	NSW 452333	N.T.	Wilson K.L. 4971
	Am4	BRI 301881	N.T.	Dunlop C.R. 4102
	Am5	MBA	Qld	Clarkson J. 8324
	Am6	NSW 338994	Qld	Wilson K.L. 8073, Clarkson J., Jacobs S.W.L.
	Am7*#	BRI 437357	Qld	Clarkson J. 6624
	Am8	DNA 122604	N.T.	Cowie I.D. 5260, Taylor S.
	Am9	CANB 242626	N.T.	Dunlop C.R. 3453
	Am10	NE	N.T.	Clarke K.L. 249, Bruhl J.J., Wilson K.L., Cowie I.D.
Abildgaardia mexicana (Palla) Kral	*#+	MEL 268631	Mexico	Pringle C.G. 3127
		MO 3524080	Mexico	Breedlove D.E. 54895, Davidse G.
		MO 1917406	Mexico	Kral R. 25115
		MO 3058759	Mexico	Pringle C.G. 9294
		MO 3632024	Mexico	Gonález S. 1116
		MEL 2050681	Mexico	Arséne G.
Fimbristylis odontocarpa S.T.Blake	Aod1	BRI341121	Qld	Blake S.T. 13582 (HOLOTYPE)
		MEL 2048459		(ISOTYPE)
		MEL 2048468		(ISOTYPE)
	Aod2*#+	BRI 574804	Qld	Turpin G.P., Thompson E.J.
F. sp. aff. *odontocarpa*	Aaffod *#+	BRI 302127	W.A.	Carey J.
Abildgaardia ovata (Burm.f.) Kral	Aov1	BRI 476426	Qld	Specht R.L. 408, Reeves R.D.
	Aov2*	BRI 457532	Qld	Batianoff G.N. 11056
	Aov3	MEL 2048512	Qld	O'Shanessy P.A. 1656
	Aov4	NSW 468324	N.S.W.	Wilson K.L. 5818
	Aov5	NSW 87198	N.S.W.	Johnson L.A.S.
	Aov6	NSW 468325	N.S.W.	Rodd A.N. 2277
	Aov7	MEL 2048525	N.S.W.	Mueller F.
	Aov8*	NSW 468326	N.S.W.	Rodd A.N. 2434
	Aov9	BRI 384713	Qld	Stanley T. 8019
	Aov10	BRI 591266	Qld	Neldner V.J. 3905
	Aov11 *	NE	Qld	Clarke K.L. 99, Bruhl J.J., Wilson K.L.

A. ovata (cont'd)		CANB	Timor	Wiriadinata H. 449
		MEL 2050881	India	Mueller F.
		MEL 2050886	U.S.A.	Medley Wood J. 4918
		MEL 2050863	India	Thomson G.
		MEL 2050864	India	Unknown
Abildgaardia oxystachya (F.Muell.) comb. prov. Goetgh.	Aox1*	NSW 452336	W.A.	Latz P.K. 4038
	Aox2	BRI 302157	Qld	Blake S.T. 15725, Webb L.J.
	Aox3*#	NE 61223	N.T.	Bruhl J.J. 1252
	Aox4+	NE	N.T.	Latz P.K. 8667
	Aox5*+	NSW 452337	N.T.	Wilson K.L. 5369
	Aox6+	NE	W.A.	Clarke K.L. 124, Bruhl J.J., Wilson K.L.
	Aox7	BRI 336290	Qld	Blake S.T. 19620
	Aox8	BRI 386514	W.A.	Cane S. 53
	Aox9	CANB 280532	W.A.	Hartley T.G. 14357
	Aox10	CANB 353598	W.A.	Carr G.W. 4377, Beauglehole A.C.
	Aox11	DNA 123491	N.T.	Booth R. 618K.L.
	Aox12+	CANB 505055; BRI 203628	Qld	Blake S.T. 13611
	Aox13	DNA 21755	N.T.	Wightman G. 424 and Dunlop C.R.
Abildgaardia pachyptera (S.T.Blake) comb. prov. Goetgh.	Ap1	NE 61427A	N.T.	Hunter J.T. 1547, Bruhl J.J.
	Ap2	MEL 1615159	N.T.	Dunlop C.R. 9041
	Ap3	MEL 252996	N.T.	Jones M., Booth R. 24
	Ap4	NSW 452342	W.A.	Dunlop C.R. 5339
	Ap5	NSW 452335	N.T.	Wilson K.L. 5109, Taylor S.
	Ap6	NSW 452334	N.T.	Wilson K.L. 5207
	Ap7	MEL 2048462	N.T.	Chippendale G
	Ap9+	NE	N.T.	Clarke K.L. 253, Bruhl J.J., Wilson K.L., Cowie I.D.
	Ap10+	NE	N.T.	Clarke K.L. 181, Bruhl J.J., Wilson K.L., Cowie I.D.
	Ap11	CANB 166722	N.T.	Adams L.G. 1715
A. sp. aff. *pachyptera*	Aaffpach	NE	N.T.	Clarke K.L. 201, Bruhl J.J., Wilson K.L., Cowie I.D.
Abildgaardia schoenoides R.Br.	As1	NSW 468344	W.A.	Wilson K.L. 4888

A. schoenoides (cont'd)	As2	BRI 480019; NSW 468346	W.A.	Dunlop C.R. 7838
	As3	NSW 468347	W.A.	Mitchell A.A. 2129
	As4	NSW 468343; MEL 1601269	N.T.	Dunlop C.R. 8651, White N.G.
	As7+	BRI 533192	Qld	Bruhl J.J. 487
	As8	NSW 229593	Qld	Jacobs S.W.L. 5903
	As9*+	NE	Qld	Clarke K.L. 70, Bruhl J.J., Wilson K.L.
	As10*	NE	W.A.	Clarke K.L. 157, Bruhl J.J., Wilson K.L.
	As11+	NE	N.T.	Clarke K.L. 216, Bruhl J.J., Wilson K.L., Cowie I.D.
	As12+	NE	W.A.	Clarke K.L. 120, J Bruhl J.J., Wilson K.L.
	As13*+	NE	N.T.	Clarke K.L. 230, Bruhl J.J., Wilson K.L., Cowie I.D.
	As14	CANB 16035	N.T.	Perry R. 222.
Abildgaardia sp. aff. *schoenoides*	As5*#+	NE 61432	N.T.	Bruhl J.J. 1261, Hunter J.T., Egan J.
	As6*#	BRI 329001	N.T.	Dunlop C.R. 5863, Craven L.A.
Abildgaardia triflora (L.) Abeywickr.	*	MO 4579353	Zaire	Malaisse F. 400, Goetghebeur P.
	#+		Tanzania	Greenway P.J. 1859
			South Africa	Ward C.J. 1708
			Sri Lanka	Koyama T. 13910, Koyama M.
***Fimbristylis* Vahl**				
Fimbristylis blakei Latz	fb1*#+	DNA D0120436	N.T.	Dunlop C.R. 10015, Latz P.K.
	fb2	BRI 435191	N.T.	Latz P.K. 10375
		DNA A0086876	N.T.	Latz P.K. 11214
(as *Fimbristylis* sp.)	#+	DNA 134230	N.T.	Orr T.M. 442
Fimbristylis cinnamometorum (Vahl) Kunth	fc1+	NE	Qld	Clarke K.L. 61, Bruhl J.J., Wilson K.L
	fc2#+	NE	N.T.	Clarke K.L. 132, Bruhl J.J., Wilson K.L., Cowie I.D.
	fc3#	NE	Qld	Clarke K.L. 276
	fc4	NE	N.T.	Clarke K.L. 228, Bruhl J.J., Wilson K.L., Cowie I.D.
	fc5*#+	NE	W.A.	Clarke K.L. 139, Bruhl J.J., Wilson K.L.

Fimbristylis depauperata R.Br.	#+	NE	Qld	Clarke K.L. 305, Little L.
		NE		Clarke K.L. 263, Bruhl J.J., Wilson K.L.
Fimbristylis fimbristyloides (F.Muell.) Druce	ffi1	MEL 269463	Qld	Dallachy
	ffi2+	BRI 336296	Qld	Blake S.T.18678
	ffi3#	QRS 43342	Qld	Flecker H.
Fimbristylis furva R.Br.	ff1	NE	N.T.	Clarke K.L. 267, Bruhl J.J., Wilson K.L., Cowie I.D.
	ff2*#+	NE	Qld	Clarke K.L. 52, Bruhl J.J., Wilson K.L
	#+	NE	N.T.	Clarke K.L. 210, Bruhl J.J., Wilson K.L., Cowie I.D.
Fimbristylis fusca (Nees) Benth.	ffu1	BRI 329000	N.T.	Dunlop C.R. 5922 Craven L.A.
	ffu2	BRI 301745	N.T.	Blake S.T. 16571
Fimbristylis sp. L (Kimberley flora)	fsL1	PERTH 2272911	W.A.	Kenneally K.F. 11171
	fsL2+	PERTH 2272962	W.A.	Kenneally K.F. 11168
	#	PERTH 2272911	W.A.	Kenneally K.F. 11167
Fimbristylis microcarya F.Muell.	#+	NE	W.A.	Clarke K.L. 131, Bruhl J.J., Wilson K.L.
		NE	N.T.	Clarke K.L. 268, Bruhl J.J., Wilson K.L.
		NE	Qld	Clarke K.L. 319, L. Little
Fimbristylis schultzii Boeck.	*	NE	W.A.	Clarke K.L. 108, Bruhl J.J., Wilson K.L.
		NE	W.A.	Clarke K.L. 153, Bruhl J.J., Wilson K.L.
Fimbristylis variegata Gordon-Gray	*#	NE 65205	South Africa	Browning J. 834
***Bulbostylis* Kunth**				
Bulbostylis barbata (Rottb.) C.B.Clarke	bba1+	DNA 24124	Qld	Wilson K.L. 5442
	bba2	DNA 49868	N.T.	Beauglehole A.C. 2608
	bba3	DNA 62627	W.A.	Mitchell A.S. 1150
	bba4	CANB 410874	N.S.W.	Tindale M.D. 2058
	bba5	NE 61441	N.T.	Bruhl J.J., Hunter J.T, Egan J. 1269B
	bba6#	NE 60472	N.S.W.	Bell D.B.
	bba7	BRI 316049	N.T.	Latz P.K. 8263
	bba8	NE	W.A.	Clarke K.L. 160, Bruhl J.J., Wilson K.L.
	bba9	CANB 325418	N.T.	Knight F. 14185
	bba10	NE	N.T.	Clarke K.L. 221, Bruhl J.J., Wilson K.L., Cowie I.D.
	bba11	NE	W.A.	Clarke K.L. 113, Bruhl J.J., Wilson K.L.

B. barbata (cont'd)	bba12	NE	Qld	Clarke K.L. 100, Bruhl J.J., Wilson K.L.
	bba13	K	Singapore	Burkhill H.M., Shah M. HMB235
	bba14	MO 4280627	U.S.A.	Hill S.R. 24361
	bba15	EA	Kenya	Napper D.M., Kanuri 2079
	bba16	NSW 468581	India	Raizada M.B
	bba17	NSW	U.S.A.	Correll D.S. 52337
	bba18# +	BRI 512812	India	Rajn R.R.V
	bba19	EA	South Africa	Polhill R. 847, Paulo S.
	bba20	L 2623	Thailand	Larsen K. 1299, Smitinand T., Warnck E.
	+	NE	N.T.	Clarke K.L. 187, Bruhl J.J., Wilson K.L., Cowie I.D.
Bulbostylis sp. aff. *barbata*	baffba1 +	NE	N.T.	Clarke K.L. 184, Bruhl J.J., Wilson K.L., Cowie I.D.
	baffba2	DNA 22621	N.T.	Rice B.L.
	baffba3	NE	N.T.	Clarke K.L. 245, Bruhl J.J., Wilson K.L., Cowie I.D.
	baffba4 #	NE	N.T.	Clarke K.L. 241, Bruhl J.J., Wilson K.L., Cowie I.D.
	baffba5	CANB 421033	N.T.	Bruhl J.J. 369A
	baffba6	NE	N.T.	Clarke K.L. 251, Bruhl J.J., Wilson K.L., Cowie I.D.
	baffba7	NE	N.T.	Clarke K.L. 239, Bruhl J.J., Wilson K.L., Cowie I.D.
Bulbostylis burbidgeae K.L.Wilson	bbu1	PERTH 4275098	W.A.	Hart R.P. 2092
	bbu2	PERTH 1083007	W.A.	Carolin R. 7640
	bbu3	PERTH 5223741	W.A.	Mitchell A.A. 1929
	bbu4	BRI 311667	W.A.	Burbidge N. 1102
	bbu5#+	NSW 452309	W.A.	Payne A.L. PRP976
Bulbostylis sp. aff. *burbidgeae*	baffbu	DNA 14302 NSW 452328	N.T.	Dunlop 4725
Bulbostylis capillaris (L.) Kunth ex C.B.Clarke	+	MO	U.S.A.	Davidse G.
		MEL 268550	U.S.A.	Curtiss A.H.
	+	MEL 268552	U.S.A.	Styains A.H.
	#	L 65104	U.S.A.	Horr W.H. E170
Bulbostylis densa (Wall.) Hand.-Mazz.	bde1	NE 60798	N.S.W.	Bruhl J.J. 1197, Quinn F.C.
	bde2	NE 63629	N.S.W.	Hunter J.T., Hunter V. 2737

B. densa (cont'd)	bde3	NSW 468227	Qld	Forster P.I. PIF8482
	bde4	BRI 304640	Qld	Blake S.T. 21453
	bde5	BRI 472840	Qld	Bean A.R. 1570
	bde7	CANB 50320 BRI 311651	Qld	Hubbard C.E. 3128
	bde8	CANB 117835	Qld	McKee H.S. 9317
	bde9	BRI 407433	N.S.W.	Williams J.B.
	bde10	CANB 282965	N.S.W.	Gray M. 3255
	bde11	CANB 410867	P.N.G.	Croft, Lelean 34706
	bde12	CANB 87831	P.N.G.	Robbins R.G. 2660
	bde13	MEL 268539	Philippines	Ramos M., Edaro G.
	bde15	BRI 342062	Sri Lanka	Davidse G. 7614
Bulbostylis sp. aff. *densa* 1	baffd1*#+	BRI 506795	Qld	Bean A.R. 3236
	baffd2+	MO 4501576	China	Field survey team 820
Bulbostylis sp. aff. *densa* 2	bde16	PRE	South Africa	Meeuse A.D.J. 10158
	bde17	PRE	South Africa	Scheepers J.C. 1141
	bde18	PRE	Swaziland	Haines R.W. 7048
Bulbostylis hispidula subsp. *pyriformis* (Lye) R.W.Haines	*#+	K	Kenya	McCallum-Webster
	*#+	K	Tanzania	Richards M. 23175B
		NSW 452317	Eritrea	Pappi A.
Bulbostylis hispidula subsp. *senegalensis* (Cherm.) Van den Berghen	*#+	K	Sudan	Davey J.T. 10
		MO 5018124	Senegal	Vanden Berghen C. 7484
Bulbostylis puberula C.B.Clarke	#+	K	Sri Lanka	Davidse G. 9037, Sumithraarachchi D.B.
		K CANB 67185	Borneo	Jacobs M. 5691
		L 65128	Singapore	Sinclair J.
		CANB 216795	Sri Lanka	Clayton D. 5112
		K	Thailand	van Beusekom C.F. 2247, Smitinand T
		K	Brunei	Coode M.J.E. 774, Kirkup D.W.
		DNA 70798	Indonesia	Elsol J.A.
Bulbostylis sp. aff. *puberula*	baffpu	NSW 452329	N.T.	Latz P.K. 11364
Bulbostylis pyriformis S.T.Blake	bpy1	NSW 400826	N.S.W.	Johnson L.A.S.

B. pyriformis (cont'd)	bpy2#+	NSW 452308	N.T.	Latz P.K. 10622
	bpy3	NE 60921A	N.S.W.	Hunter J.T., Bell D.B.
	bpy4	BRI 311664	N.T.	Latz P.K. 488?
	bpy5	NSW 452307	N.S.W.	Wilson K.L. 1479A
	bpy6	NSW 400827	N.T.	Latz P.K. 9852
	bpy7	BRI 9336	Qld	Sharpe P.R. 232
	bpy8	BRI 542784	Qld	Bean A.R. 4227
Bulbostylis humilis (Kunth) C.B.Clarke		PRE 2827DD	South Africa	Jarman N. 134
		PRE 2927BC	South Africa	Ruch M. 9
	#+	NE 58064	N.S.W.	Strong C.P., Fletcher J.R., Sharp G.C.
Bulbostylis turbinata S.T.Blake	bt2	DNA 62665	W.A.	Mitchell A.A. 479
	bt3	DNA 51665	N.T.	Latz P.K. 7126
	bt4	DNA 72393	N.T.	Latz P.K. 6339
	bt5	PERTH 2091526	W.A.	Royce R.D. 1491
	bt7	PERTH 2073552	W.A.	George A.S. 820
	bt8	PERTH 5221005	W.A.	Payne A.L. PRP1854
	bt9	BRI 476931	Qld	Harris P.L. 342
	bt10	MEL 1620712	N.T.	Beauglehole A.C. 26568
***Nelmesia* Van der Veken**				
Nelmesia melanostachya Van der Veken		NY	Congo	Gérard 57 (ISOTYPE)
***Nemum* Desv. ex Hamilt.**				
Nemum equitans (Kük.) J.Raynal	#	NU	Zambia	Robinson E.A. 2681
		EA	Zambia	Robinson E.A. 3912
		EA	Zambia	Greenway P.J.
Nemum spadiceum (Lam.) Desv.			Zambia	Robinson E.A. 5165
	#+	NU	Zambia	Robinson E.A. 4676
	*	NU	Zambia	Robinson E.A. 4677
Nemum megastachyum (Cherm.) J.Raynal	*	K EA	Congo	Germain 4420
***Tylocarya* Nelmes**				
Tylocarya cylindrostachya Nelmes	*+(JJB)	L 65198	Thailand	Kerr A.F.G. 21294
Outgroup				
Actinoschoenus compositus (Latz) nom. prov. ined.	*#+	NE	N.T.	Clarke K.L. 178 Bruhl J.J., Wilson K.L., Cowie I.D.
		NE	N.T.	Clarke K.L. 231 Bruhl J.J., Wilson K.L., Cowie I.D.
		NE	N.T.	Clarke K.L. 235 Bruhl J.J., Wilson K.L., Cowie I.D.
	*#+	NE	N.T.	Clarke K.L. 211 Bruhl J.J., Wilson K.L., Cowie I.D.
	*	NE	N.T.	Cowie I.D. 5643, Brennan K.

A. compositus (cont'd)		NE	N.T.	Clarke K.L. 227 Bruhl J.J., Wilson K.L., Cowie I.D.
		NSW 196791	N.T.	Wilson K.L. 7520
		MEL 1619328	N.T.	Cowie I.D. 4643
Arthrostylis aphylla R.Br.		BRI 311099	Qld	Brass L.J. 18669
	*	BRI 429959	Qld	Batianoff G.N. 10089
	*+	BRI 399429	Qld	Gunness A. AG1937
Schoenoplectus tabernaemontani (C.C.Gmel.) Palla (=S. *validus* Vahl)		NSW ex Herbario Kewensis 24110	New Hebrides	McKee H.S. RSNH 24110
		NSW 259584	Vic	Wilson K.L. 6804
		NSW ex AD 75517	S.A.	Hunt D. 1788
		NSW	Qld	Wilson K.L. 4278
		NE 30785	N.S.W.	Wallace B.J.
		NE 58440A	N.S.W.	Bruhl J.J. 150
Schoenoplectiella lateriflora (J.F.Gmel.) Lye (=*S. lateriflorus* G.F.Gmel)		NSW	W.A.	Jacobs S.W.L. 4226
	*	NSW	N.T.	Latz P.K. 3761
		NSW	Qld	Wilson K.L. 3389, Sharpe P.R., Johnson L.A.S., Blaxell D.
	*	NSW	Philippines	Ramos M.
		NSW	India	Unknown
Schoenoplectiella laevis (S.T.Blake) Lye (=*S. laevis* S.T.Blake)		NSW	W.A.	Dunlop C.R. 5405
		NSW	W.A.	Brennan K.
	*	NSW 251326	N.S.W.	Milthorpe P.L. 1777A, Cunningham G.M.
		NSW	N.T.	Wilson K.L .5399 and Scarlet C.
	*#+	NSW 338962	Qld	Wilson K.L. 8041, Clarkson J. and Jacobs S.W.L.
Trachystylis stradbrokensis (Domin.) Kük.	*	BRI 156925	Qld	White C.J.
	#+	BRI 156923	Qld	Blake S.T. 13201
		BRI 399437	Qld	Gunness A. Ag1965
		BRI 10875	Qld	Durrington L 312
		MEL 716466	Qld	Sharpe P.R. 5199, Wilson K.L., Jacobs S.W.L.
		MEL 2048446	Qld	Blake S.T. 23328
		BRI 227559	Qld	Sharpe P.R. 2280, Dowling R.
	*	BRI 541420	Qld	Thompson E.J. 78
	*	BRI 156931	Qld	Blake S.T. 15945
		CANB 193493	Qld	Brass L.J. 18660

Appendix 2 Full character list used in the assessment of monophyly for the tribe Abildgaardieae. All characters used in cladistic analyses in Chapters 3, 4, and 5 are subsets from this list. Characters presented in the cladograms from subset analyses are given in square brackets after the tribal character name, with the related chapter indicated as: Chapter 3=!, Chapter 4=^, and Chapter 5=~ following the subset character number.

1. Longevity whether
    1. annual
    2. perennial (with remains of old sheaths and or culms)
       Some young perennial plants may appear to be annual therefore care must be taken when scoring this character - if possible check plants in the area when collecting and note
2. Perennial rhizome whether
    1. caespitose - indistinct due to compaction giving clumped base, detectable by persistent sheaths from last years growth
    2. base clumped but rhizome visible sometimes growing vertically
    3. base not distinctly clumped but has obvious 'running rhizome' giving smaller clumps spread
    4. distinct thick horizontal rhizome with many scales, not spreading widely
    5. very distinct and elongated horizontally - base widely spreading
3. Sheath surface cover
    1. glabrous
    2. scabrid backs
    3. scabrid margins
    4. medium to dense cover of short to medium hairs
    5. mixture of short and long hairs
    6. short plus or minus horizontal hairs 60–100 µm
    7. sparsely bristly (hispid - hairs horizontal or nearly so)
    8. densely bristly
    9. sparse to medium distribution of long flexuose hairs (c. 300 µm, as in *Arthrostylis aphylla*)
    10. dense matt of long hairs
4. Sheath fitting whether at maturity
    1. tight fitting around culm, especially evident at sheath apex - sheath closed (as in *Schoenoplectus mucronatus*)
    2. fits against culm but not really tight and not loose
    3. sheath reduced to near base of plant and is open - recognised from sheath margins (as in *F. fimbristyloides*)
    4. seems absent and reduced to extreme culm base (leaf blade seems to go all the way to the base of the plant)
    5. open at apex but not loose (as in *Abildgaardia oxystachya*)
    6. sheath loose evenly around the culm and the sheath length, not more so around the apex - sheath closed (as in *Schoenoplectus tabernaemontani*)
    7. loose and open around culm, especially at sheath apex (as in *Crosslandia setifolia* and *Abildgaardia vaginata*)
    8. sheath apparently open along it's length, at least at maturity - if fused then only in young culms
5. Sheath margins texture
    1. sheath margins barely discernable
    2. hyaline (thin and translucent (transmits light - very easily damaged))
    3. membranous (thin and semi-translucent (like frosted glass), membrane-like)
    4. thinly chartaceous (thinner than chartaceous)
    5. chartaceous (papery, opaque (light not transmitted) and thin)
    6. subcoriaceous (thickish and strong)
    7. coriaceous (thick and leathery but flexible)
6. Sheath bases whether
    1. sheath base intact as interveinal tissue persists
    2. breaking down to fibres from remaining nerves - distinct
7. Sheath backs texture
    1. hyaline (thin and translucent)
    2. membranous (thin and semi-translucent – membrane-like)
    3. thinly chartaceous (papery, opaque (not transparent, dull not shining) and thin) damaged with forceps not flexible
    4. distinctly chartaceous (colour and feel of thin papyrus)

   5. scarious (thin and dry appearing shrivelled)
   6. subcoriaceous (thick and leathery) not easily damaged
   7. cartilaginous (hard and tough but flexible)
   8. fibrous (having loose woody fibres)
   9. pannose (with a felty texture)
8. Sheath apex shape excluding hair extensions
   1. pointed (apex longest on margin receding back to culm giving pointed triangular affect)
   2. truncated (margins abrubtly end and are the same width the length of the sheath)
   3. rounded (margins rounded and are or at least close to the full width of margins along rest of sheath)
   4. tapered (margins narrowed at leaf junction gradually widening to full margin width of sheath along rest of length)
   5. auriculate (sheath tapering then with rounded ends forming auricle)
   6. extended (extends beyond sheath-blade junction abaxially)
9. Sheath orifice adaxial
   1. open when mature
   2. deep V
   3. fused at apex
10. Sheath colour in dried material
    1. cream
    2. straw coloured (golden)
    3. yellow-brown
    4. light brown
    5. dark golden brown
    6. pale orange brown
    7. orange brown
    8. pink-brown
    9. red brown
    10. mid brown
    11. dark red brown
    12. dark brown (at least nerves are very dark)
11. Sheath leaf junction whether [12^]
    1. glabrous
    2. short hairs unrelated to ligule (hairs restricted to sheath apex margin and not across the width of the blade junction)
    3. pilose (at sheath apex but not continuing across the full width of blade junction)
    4. long coarse hairs
12. Leaf to culm ratio (mature culms and leaves, with or without leaf blade)
    1. 1:4
    2. 1:3
    3. 1:2
    4. 2:3
    5. 1:1
13. Ligule (whether present)
    1. absent
    2. as a fringe of stout hairs (near the sheath apex adaxial across the blade or subulate point as in *Fimbristylis depauperata*)
    3. as a membranous flap (formed as a continuation of the sheath margins adaxial across the blade or subulate point as in *Schoenoplectus*)
14. Leaf blade whether present or absent
    1. absent (binseniform)
    2. reduced to subulate points only
    3. mixture (of absent or reduced and well developed blades within an individual)
    4. present (always)
15. Leaf number per culm (includes bladeless sheaths associated with an individual culm)
    1. one per culm
    2. two to three per culm
    3. greater than three and up to five per culm
    4. greater than 5 less than 10
    5. greater than 15

doesn't include open sheaths that are restricted to base of 'groups' of culms

16. Leaf blades shape (see Radford 1974 p. 129)
    1. narrowly elliptic (with widest axis at midpoint of structure and with margins symmetrically curved; more then L W 6:1–3:1)
    2. linear (with widest axis at midpoint of structure and with margins essentially parallel; more than L W 12:1)
    3. linear-lanceolate
    4. ovate (with widest axis below middle and with margins symmetrically curved; L W 2:1–3:2)
    5. ovate-lanceolate
    6. lanceolate (with widest axis below middle and with margins symmetrically curved; more than L W 6:1–3:1)
    7. obovate (inversely ovate)
    8. falcate (broad blade that is sickle-shape, arcing back from centre of plant)
17. Leaf blades habit whether
    1. erect (follows line of and is usually intermingled with culms)
    2. erect then recurved near apex
    3. curly ascending (slightly horizontal then upright)
    4. ascending (slightly horizontal and then upright from mid of leaf usually at side of culms)
    5. ascending spreading
    6. loosely ascending as leaves all 'mishappened'
    7. strongly falcate (leaves bent backwards from near base of plant)
18. Leaf blade shape in transverse section (along mid-third)
    1. sub-triangular (adaxially concave and abaxial midrib distinct as a point with convex sides)
    2. concave triangular (abaxial sloping concave faces)
    3. shallow channel (crown-like abaxial central rib as point and concave sides giving shallow channelled appearance from the three points adaxial side usually concave as in *B.* sp aff. *barbata.*)
    4. strongly channelled (with deep channels as in *B. turbinata*)
    5. thickly crescentiform
    6. v-shaped
    7. thickly v-shaped
    8. U-shaped
    9. crescentiform
    10. half-circular or obliquely so
    11. depressed elliptic
    12. thinly crescentiform (as in *F. schultzii*)
    13. broadly linear (almost flat - horizontal and thin
    14. fused at the margins and is almost subcylindrical
    15. fused at the margins and is almost triangular
19. Leaf blade width (at midpoint of blade)
    1. to 0.3 mm
    2. greater than 0.3 to 0.5 mm
    3. greater than 0.5 to 0.73 mm
    4. 0.75 to 0.8 mm
    5. 0.85 to 1.4 mm
    6. 1.5 to 2.0 mm
    7. 2.1 to 3.0 mm
    8. greater than 3.0 to 4.8 mm
20. Leaf blade vestiture
    1. glabrous
    2. minutely scabrid margins
    3. scabrid margins
    4. scabrid over abaxial surface
    5. hairy not scabrid (hairs almost horizontal to slightly antorse)
    6. densely hirsute backs
    7. sparsely bristly
    8. bristly hispid
21. Leaf anatomy sclerenchyma presence
    1. apparently absent
    2. in abaxial area only

   3. in abaxial and to a lesser extent adaxially (not including sclerenchyma at leaf margins)

22. Leaf anatomy sclerenchyma
    1. present as strands (not in contact with vascular bundle but adjacent to)
    2. present as girders (in contact with vascular bundle)
    3. present as cap above the phloem
    4. present as a cap on the inner side of the vascular bundle
23. Leaf blade anatomy sclerenchyma shape for abaxial surface
    1. square to square with concave sides
    2. rhombic (with upper epidermal edge shorter than inner one)
    3. reverse rhombic (with upper epidermal edge longer than the inner edge)
    4. low mound
    5. dome (wide base towards VB)
    6. high dome
    7. oval-elliptic
    8. circular-rounded
    9. crescentiform
    10. pulviniform (rounded rectangular)
    11. rectangular
    12. triangular (point towards VB)
24. Number of sclerenchyma strands or girders (compared to vascular bundle number)
    1. less than the number of vascular bundles
    2. equals the number of vascular bundles
    3. greater than number of vascular bundles
25. Leaf anatomy vascular bundle number
    1. less than five
    2. five to seventeen
    3. greater than twenty
26. Leaf anatomy vascular bundles, whether
    1. vascular bundles form one layer below the abaxial epidermis
    2. vascular bundles form a partial or complete second row as new VB's form near the abaxial epidermal region
27. Leaf anatomy size of vascular bundles., whether
    1. same size
    2. 2 sizes with midrib VB being the larger
    3. varying sizes with largest bundle at midib
28. Leaf and culm anatomy type of vascularisation [27^; 26!]
    1. C_4 fimbristyloid (primary and secondary bundles have PCR tissue interrupted laterally by the metaxylem vessel elements, the mestome sheath complete and surrounded by PBS)
    2. C_3 type (having two sheath layers, formed by the mestome sheath which is surrounded by large achlorenchymatous parenchyma sheath)

The inner border parenchyma cells are large and chlorenchymatous, constituting the PCR tissue, and interrupted laterally by the metaxylem vessel elements; the mestome sheath of small, achlorenchymatous, thick-walled cells; and a complete (unless interrupted by sclerenchyma) PBS, which is usually smaller and less chloroplast laden than the surrounding PCA tissue (a PBS also surrounds the secondary bundles). Definitions from Bruhl (1990).

The C_4 anatomical types are described in terms of primary vascular bundles, the latter being recognised by the possession of meta- and proto-xylem, often associated with a protoxylem lacuna. C_4 has either fimbristyloid, chlorocyperoid, eleocharoid, or rhynchosporoid type

Fimbristyloid C_4 comprises three bundle sheaths in primary and secondary bundles: the inner border parenchyma cells are large and chlorenchymatous (=PCR tissue) and is interrupted laterally by the metaxylem vessel elements; the mestome sheath of thick-walled, achlorenchymatous cells; and a complete PBS of smaller cells that are less chloroplast laden than the surrounding PCA tissue.

Chlorocyperoid C_4 anatomy is essentially similar, but here the PBS is restricted to one or a few cells lateral to the metaxylem vessel elements, or sometimes completely absent (being always absent from secondary bundles).

The border parenchyma cells also constitute the PCR tissue in eleocharoid C_4 anatomy, but are usually not interrupted by the metaxylem vessel elements, and the PBS is absent.

The mestome sheath constitutes the PCR site in rhynchosporoid C_4 species, and the PBS is present but irregularly incomplete.

29. Leaf anatomy parenchymatous bundle sheath (PCA) [27!]
    1. colourless (no chlorophyll present) as seen in *Schoenoplectus* and *Arthrostylis*
    2. contains chlorophyll
30. Leaf vascular bundles whether
    1. embedded within chlorenchymatous tissue
    2. not embedded within chlorenchymatous tissue but intrudes into the clear parenchyma tissue
    3. chlorenchymatous tissue apparently absent, or at least highly reduced and undiscernable (tannin cells prevalent)
31. Leaf chlorenchyma shape
    1. globular parenchyma surrounding VB
    2. elongated parenchyma near epidermal area above VB and globular around lower part of VB
    3. elongated cells surround VB
    4. obvious rectangular palisade surrounding the VB
32. Leaf anatomy mesophyll between vascular bundles, whether
    1. completely radiate (chlorenchyma arranged in a distinct ring around all major and minor vascular bundles)
    2. incompletely radiate (individual vb's partially encircled by chlorenchymatous cells that are radiately arranged - no radial vb's occur at the xylem end of the vb, radiate around the phloem end)
33. Leaf anatomy bulliform cells, whether
    1. absent
    2. present
34. Leaf anatomy epidermal cells, whether
    1. epidermal cells the same size or only slightly larger than abaxial counterparts
    2. adaxial epidermal cells about twice as large as abaxial epidermis
    3. adaxial epidermal cells mostly three to four times as large as abaxial
    4. adaxial epidermal cells about 6 times larger than abaxial cells
    5. central adaxial epidermal cells three to four times the size of abaxial epidermis
    6. central adaxial epidermis cells about six times the size of abaxial epidermis
    7. central adaxial epidermal cells about 10 times larger than abaxial epidermal cells

    Adaxial epidermal cells situated at the midrib that are much larger than the neighbouring epidermal cells - scored as present when obviously enlarged compared to abaxial epidermal cells
35. Leaf anatomy adaxial hypodermis, whether
    1. absent, as epidermal cells only present
    2. present, as 1 row often incomplete
    3. present, as 2 rows (sometimes 2nd row incomplete)
    4. present, as 3 rows (sometimes incomplete)
    5. many rows present ie greater than four rows
36. Leaf anatomy air cavities, whether
    1. absent
    2. present
37. Leaf anatomy stomata
    1. raised (protrude above cuticle layer - above leaf surface)
    2. flush (with leaf surface - discrete between epidermal cells)
    3. sunken (into leaf surface at bottom of dissecting ribs or pits etc)
38. Culm whether noded vertically
    1. not stalked (no obvious ascending nodes present)
    2. stalked (node is obvious and culms appear stalked)
39. Culm outline in transvers section, whether
    1. narrowly elliptic
    2. elliptic no dissections or wavy margins
    3. elliptical smooth dissected (deep dissections around the girth of the culm)
    4. elliptic wavy no dissections
    5. elliptical wavy or undulating with dissections evenly around the margin
    6. elliptical deeply undulating
    7. elliptic with distinct ribs (grooved)
    8. irregularly elliptic with wavy margins
    9. irregularly fusiform shaped (waves caused by protruding sclerenchyma bundles as in *Fimbristylis microcarya*)

   10. irregular quadrangle 4 sides, with the parallel sides having one shorter than the other (see *Arthrosytlis aphylla*)
   11. transversly oblong
   12. irregular no definite shape
   13. irregularly 7-ribbed
   14. irregularly 9-ribbed
   15. sub-symmetrical 6-ribbed
   16. sub-symmetrically 7 ribbed, distinct
   17. sub symmetrically 8-ribbed
   18. circular
   19. circular undulating
   20. circular with distinct ribs (see *Actinoschoenus composita*)
   21. pentagonal (having 5 sides)
   22. acutely hexagonal
   23. irregular hexagon with ribs (6 main points with 6 subpoints forming ribs)
   24. depressed triangular with convoluted margins
   25. triangular
   26. triquetrous (3-angled with concave sides (acutely triangular Metcalfe 1971)

40. Culm width (at mid third section)
   1. to 0.3 mm
   2. 0.31 to 0.8 mm
   3. 0.85 to 1.1 mm
   4. 1.15 to 1.3 mm
   5. 1.5 to 1.6 mm
   6. 1.7 to 2.4 mm
   7. 2.5 to 3.0 mm
   8. 3.2 to 4 mm
   9. greater than 4 mm
41. Culm cover
   1. glabrous (often scabrid at inflorescence junction)
   2. scabrid (minute prickle hairs isolated to sparse cover)
   3. scabrid (minute prickle hairs with dense cover)
   4. hairy not scabrid
   5. toothed ascending hairs (40–60 μm)
   6. finely pubescent (short interlocking hairs)
   7. hairs mixed (short and long ?toothed)
   8. bristly (distally)
   9. bristly along the culm length
   10. long hairs (c. 600 μm)

      dense – A<B (when A is distance between trichomes and B is trichome height);
      sparse - A=B to 5xB
      isolated – A>5xB
42. Culm anatomy, total number of vascular bundles is [41~]
   1. less than fifteen
   2. greater than fifteen less than thirty
   3. greater than thirty less than thirty-five
   4. greater than forty
43. Culm anatomy, size of vascular bundles
   1. all same size
   2. 2 sizes alternating
   3. 2 sizes not alternating
   4. varying sizes alternating evenly
   5. varying sizes not alternating evenly
44. Culm anatomy, number of rings of vascular bundles (VB's)
   1. not arranged in rings apparently 'unorganised' within the culm
   2. ring of vascular bundles around the outer culm edge and dispersed throughout the culm
   3. single ring of bundles all of similar size or alternating size
   4. one complete ring and a second semi ring (with the inner VB's being primary and pushed inward when secondary VB's form in the outer region)

5. two complete rings of vascular bundles (the inner ring formed from a lesser number of primary VB's when secondary VB's develop in the outer ring)
6. multiple rings (older VBs pushed inward while newest VBs are small and numerous near the culm margin)

45. Culm anatomy sclerenchyma [42^]
    1. present as strands (not in direct contact with vascular bundle)
    2. present as girders (in contact with vascular bundle)
    3. present as a cap to four cells thick above the phloem
    4. present as a cap to 9 cells thick at the base of the vascular bundle
    5. present as multiple layers around the vascular bundle
       See Metcalfe 1971
46. Culm anatomy sclerenchyma strand number per VB
    1. less than number of VB in first ring
    2. equals number of vascular bundles in first ring (or equals the number in both rings)
    3. greater than the number of vascular bundles in first ring
47. Culm anatomy sclerenchyma shape
    1. square strand
    2. rhombic (bottom wider than epidermal section)
    3. reverse rhombic (upper edge wider than inner one)
    4. low mound to dome shaped strand (wide base towards VB)
    5. high dome strand
    6. reverse high dome strand (widest part on epidermis)
    7. pulviniform strand (rounded rectangluar)
    8. elliptical strand
    9. circular strand
    10. bulbiform strand
    11. crescentiform strand
    12. rectangular strand
    13. stilted rectangular strand (edges with legs protruding into the parenchyma as in Arthrostylis planiculmis)
    14. thickly v-shaped strand (see *Actinoschoenus composita*)
    15. triangular strand (point towards VB)
    16. continuous around the culm
    17. reverse high dome girder (widest at the VB)
    18. roughly circular girder
    19. pulviniform girder
    20. rectangular girder (see *Actinoschoenus composita*)
    21. triangular girder (point to VB apex)
    22. crescentiform girder on inside of VB (as seen in *Schoenoplectus tabernaemontani* and *Eleocharis*)
    23. cap above phloem to four cells thick
    24. cap at base of vascular bundle to 9 cells thick
        follows Metcalf 1971
48. Culm anatomy sclerenchyma cap on vascular bundle
    1. absent
    2. present up to 4 cells
49. Culm anatomy photosynthetic parenchyma shape
    1. elongate rounded rectangular cells usually arranged roughly in two to four rows beneath the epidermis
    2. roughly three to four rows of rounded cells sometimes stretched and packed tightly
    3. irregularly shaped shorter parenchyma stacked like brickwork in alternating rows
    4. shorter rounded irregularly rectangular single upper row and rounded cells beside and below
    5. single row of distinct palisade upper and rounded cells beside and below
    6. rounded cells packed tightly in a single row above vascular bundle, but more may be present between the bundles (sometimes slightly stretched but not palisade)

50. Culm vascular bundles
    1. not fully immersed within the chlorenchyma tissue as all protrude into the pith (especially evident in C_3 culms)

  2. younger vascular bundles immersed within the chlorenchyma tissue while mature bundles protrude into the pith (especially evident in C_4 culms)
  3. younger vascular bundles partly immersed while mature bundles fully immersed (see Metcalfe p: 394)
  4. chlorenchyma apparently absent or highly reduced

51. Culm anatomy central clear parenchyma present as medulla [50~]
    1. absent (no pith cells visible)
    2. absent, breaks down to strands between vascular bundles only
    3. present and is distinct
    4. present but breaking down in the centre
52. Culm anatomy stomata when sunken
    1. single stomata at bottom of groove or dissection
    2. twin stomata near on side walls of groove or dissection
53. Culm anatomy stomata
    1. none apparent or at least very few
    2. raised
    3. flush (located between sclerenchyma)
    4. sunken (at base of dissection)
54. Root width [53~]
    1. to 0.13 mm
    2. 0.15 to 0.45 mm
    3. 0.46 to 0.55 mm
    4. 0.56 to 0.8 mm
    5. 0.81 to 0.85 mm
    6. 0.89 to 1.0 mm
    7. 1.1 to 2.0 mm
    8. 2.1 to 3.0 mm
55. Root colour
    1. pale cream yellow brown
    2. distinctly yellow
    3. light brown (straw coloured)
    4. orange brown
    5. mid brown
    6. red brown
    7. grey brown
    8. dark brown to black
56. Root cover
    1. glabrous
    2. few hairs
    3. villous (many long hairs not matted)
    4. tomentose (thickly matted)
57. Inflorescence~synflorescence structure
    1. spike (intraspicular prophylls indicate lateral branches with a solitary floret, as in *Nelmesia*)
    2. solitary (main florescence only)
    3. highly reduced anthelodium (main florescence plus one coflorescence either rayed or sessile)
    4. reduced anthelodium (main florescence plus multiple 'rayed' coflorescences - usually 2 to 3)
    5. sessile reduced anthelodium (main florescence plus sessile coflorescences - usually 2 giving 3 spikelets)
    6. compressed reduced paniculodium forming a 'head' (compressed spike ie main florescence plus multiple lateral primary coflorescences ie reduced paniculodium as in *Fimbristylis schultzii*)
    7. highly reduced secondary anthelodium (with one second order main florescence (HF2), either sessile or on lengthened epipodia (ray)
    8. ramified reduced anthelodium (spikelets of second order or higher branching that are mostly 'rayed' or sometimes sessile)
    9. many spikeleted ‘head’ of sessile spikelets formed by primary secondary growth and their secondary lateral growth i.e. HF1, Cofl + Cofl2 (anthela type florescences with reduced epipodia as seen in *Crosslandia* WA)
    10. lateral hemispherical ‘head’ on long mesopodia (one or two primary 'rays' supporting lateral ‘heads’ formed from secondary main florescence (HF2) plus sessile secondary coflorescences (Cofl2) and their sessile lateral branches (Cofl3)

  11. terminal ‘head’ from many sessile spikelets formed from lateral rays (Cofl) and ramification from intraprophyllar growth (as in *Bulbostylis barbata*)
  12. pseudolateral digitate sessile or on lengthened epipodia (reduced paniculodium)
  13. second order pseudolateral digitate lateral and intraprophyllar growth (paniculodium)

  Synflorescence structures in this study are based on the premise of consistent reduction ie paracladia are absent from the main florescence therefore are also absent from the coflorescences; branches arising are considered as secondary lateral branches (ie ramification)

58. Inflorescence–synflorescence number of usual primary coflorescence branches 'rayed' or sessile [57~; 54^]
  1. absent
  2. one
  3. two to four
  4. five to eight
  5. eight to fourteen
  6. greater than fifteen
59. Inflorescence (maximum number of orders consistently present)
  1. primary (HF1 and Cofl1 includes solitary and simple anthelas)
  2. secondary (HF2 lateral florescence growth arising from primary florescence parts with its own lateral growth)
  3. secondary intraprophyllar (growth from within primary prophylls)
  4. tertiary (HF3 lateral florescence growth arising from secondary florescence parts with its own lateral growth)
  5. tertiary intraprophyllar (growth arising from with secondary prophylls)
  6. fourth (HF4 lateral florescence growth arising from tertiary florescence parts)

  Orders were determined using compound rayed specimens and then extrapolated to taxa with congested ‘heads’. Orders were determined using the terminal spikelets on each culm or ray. For example if a rayed spikelet (i.e. Cofl) developed lateral spikelets (either sessile or on rays) then that spikelet became the terminal spikelet (HF2) for that ray and the lateral spikelets are Cof3. Care is required when assessing congested 'heads' of spikelets to ensure that congestion is from the same florescence order. See *Crosslandia* Figures 3.12-3.17 and *Bulbostylis* Figure 5.15 for synflorescence type detail.

60. Inflorescence–synflorescence position whether [56^]
  1. terminal (and ascending on the culm)
  2. pseudolateral (pushed laterally by the main bracts that usually continue to ascend in line with the culm, although when large spikelet numbers present (as in Schoenoplectus) the main bract is reflexed. In *Trachystylis* the coflorescence appears in the terminal growing position and the main florescence is pushed sideways)
61. Inflorescence synflorescence, whether open or contracted due to ray length
  1. consistently open (solitary spikelet or spikelet 'rays' long and spreading - looks gangly)
  2. open (rays lengthened, but not extremely long - as in *Bulbostylis turbinata*)
  3. consistently contracted (spikelets on short rays that can be easily seen giving shortened appearance but not capitate; as in *Fimbristylis complanata*)
  4. mixed (some single spikelets on 'rays' while others may be sessile or on shortened rays)
  5. congested (multiple sessile spikelets on severly restricted epipodia, forming heads or finger clusters; see inflorescence–synflorescence structure for different types)
62. Inflorescence–synflorescence length
  1. to 35 mm
  2. 38 to 60 mm
  3. greater 60 to 75 mm
  4. 80 to 100 mm
  5. 105 to 120 mm
  6. 125 to 170 mm
64. Inflorescence–synflorescence bracts whether [60^]
  1. absent
  2. present
65. Inflorescence–synflorescence bracts (when present)
  1. glume-like and clearly associated with inflorescence when not solitary (may have an apiculate extension as seen in some lower glumes on spikelets)
  2. leaf-like and ascending (growing upright at roughly 45 degrees or sometimes loosely erect)
  3. leaf-like and spreading (between 45 and 90 degrees separation from culm)

    4. leaf-like and distinctly erect
    5. leaf-like and reflexed downwards due to many aggregated spikelets (as in *Fimbristylis schultzii*)
    6. culm-like and continuing in line with the culm (or sometimes obviously bent backwards due to many aggregate spikelets)
66. Inflorescence–synflorescence bracts length
    1. shorter than inflorescence
    2. equals inflorescence
    3. longer than inflorescence
    4. much longer than inflorescence
67. Inflorescence–synflorescence primary bract number [63^]
    1. one
    2. two (closely alternately opposite)
    3. three (ascending alternately of roughly equal length)
    4. many (of roughly equal length)
68. Spikelet axis whether
    1. monopodial (rachilla of spikelet has one axis ie growth continuous from one growing point)
    2. sympodial (rachilla formed from multiple reduced axes)

    Crosslandia with sympodial growth has distichous glumes which when glume pulled away breaks the section of rachilla away as well. The nut is partly surrounded by the glume margins of the opposite (lower) glume. The nutlet is buried deep within the rachilla section. Basal and aerial spikelets show the same pattern even though the spikelets are morphologically different.
69. Aerial spikelet prophylls whether
    1. present (distinct bract-like extension between nut and rachilla)
    2. absent
70. Aerial spikelet rachilla shape of wings [64^]
    1. wingless or minute
    2. reduced and rounded (due to compaction of the rachilla)
    3. reduced and truncate (due to compaction of the rachilla)
    4. reduced and tapered to a point
    5. distinct (elongated) rounded - broad with rounded apex (rachilla expanded where fertile)
    6. distinct oblong - narrow with curved apex (rachilla expanded where fertile)
    7. distinct truncate (apex terminates abrubtly)
    8. distinct narrowly triangular - narrow with pointed apex
71. Spikelet sex in aerial spikelets (excluding lowest empty glumes)
    1. hermaphrodagamous (bisexual florets only spikelet)
    2. hermaphrodandrous (male florets proximal, bisexual florets distal in spikelet)
    3. gynehermaphroditic (bisexual florets proximal, female florets distal in the spikelet)
    4. gynagamous (female florets only in spikelet)
    5. gynecandrous (male florets proximal, female florets distal in spikelet)
    6. androgynous (male florets only in spikelet)
    7. gynehermaphrodandrous (male, bisexual mid, female distal)
72. Aerial spikelet outline
    1. glumes angular - widely dome shaped (truncated proximally and broadly rounded at the apex)
    2. elliptic (2:1 to 3:2 widest point at centre)
    3. loosely narrowly elliptic (6:1 to 3:1 narrow at base and apex widest point at centre - glumes not tightly imbricate or angular)
    4. angularly narrrowly elliptic (6:1 - glumes somewhat reflexed)
    5. obliquely ovate (curving on one side of spikelet due to rachilla twisting)
    6. smoothly ovate (2:1 to 3:2 wider at the base narrowing towards apex)
    7. loosely ovate
    8. angularly ovate (glumes apex reflexed)
    9. cylindrical (as in *Schoenoplectiella laevis*)
    10. smoothly narrowly cylindrical (glumes tightly imbricate - 6:1 as in *Nelmesia melanostachya*)
    11. loosely narrowly cylindrical
    12. loosely lanceolate (glumes not tightly imbricate 3:1 to 6:1 wider at the base narrowing towards the apex)
    13. loosely obliquely lanceolate (curving on one side due to twisting rachilla)
    14. angularly lanceolate
    15. narrowly oblong (3:1 to 6:1 base and apex same width)
    16. triangular (2:1 to 3:2 wide at base to pointed apex)

17. narrowly triangular (6:1 to 3:1 wide at base to pointed apex)
18. smoothly linear (glumes tightly imbricate - 12:1 narrower than narrowly oblong sides even)
19. angularly linear (glume nerves long and recurved)

73. Number of fertile florets (male or female) per aerial spikelet [72~]
    1. 1 to 2 (as in *Actinoschoenus*, *Arthrostylis*, *Trachystylis*)
    2. greater than 2 to 4
    3. many (greater than 4 up to 25 sometimes many glumes but few nuts as in *Abildgaardia*)
    4. numerous greater than 25 (as in *Nemum*)
74. Spikelets whether morphologically different to aerial spikelets [73~; 66!]
    1. aerial only (always on lengthened culms)
    2. aerial plus subradical (subradical culms distinctly shortened and spikelets near base, but spikelets otherwise identical to aerial counterparts)
    3. Aerial plus basal (basal spikelets absent or very highly reduced and with different morphology and floret sex to aerial counterparts)
    4. aerial plus subterranean (spikelets reduced to one or two nuts close to or below ground level - amphicarpy)

    Basal spikelets are those that differ in morphology and frequently sexuality, from aerial spikelets, usually maturing before their aerial counterparts i.e. amphicarpic. As seen in *Crosslandia*, *Fimbristylis spiralis* and occasionally in *Abildgaardia vaginata*, plus some species of *Bulbostylis* and *Schoenoplectiella*.
75. Basal spikelet sex (excluding lowest empty glumes whether)
    1. hermaphrodagamous (bisexual [perfect] florets only in spikelet)
    2. gynehermaphroditic (bisexual florets [perfect] proximal, female florets distal in the spikelet)
    3. gynagamous (female florets only in spikelet)
76. Basal spikelet (shape)
    1. irregularly widely ovate (due to extreme reduction of number of florets - usually one to two)
    2. narrowly elliptic (6:1 to 3:1 narrow at base and apex widest point at centre)
    3. lanceolate (3:1 to 6:1 wider at the base narrowing towards the apex)
    4. narrowly oblong (3:1 to 6:1 base and apex same width)
    5. oblanceolate (6:1 to 3:1 narrow at base and wider at apex due to spreading glumes)
    6. narrowly triangular (6:1 to 3:1 wide at base to pointed apex)
    7. linear triangular (12:1 wider at base than the tapered apex)
    8. linear (12:1 narrower than narrowly oblong with sides even)
77. Basal spikelet (floret numbers)
    1. one to two
    2. greater than two but less than four
    3. greater than four to many
78. Basal spikelets whether
    1. Basal spikelets always sessile (no culm present)
    2. Basal spikelets mostly sessile although some with very short culms present (less than 3 mm long)
    3. Basal spikelets mostly on reduced culms (at first appearing sessile and clumped at plant base although rarely some longer culms with gynagamous spikelets present)
    4. Basal spikelets mostly on shortened culms greater than 5mm long (often c. 15 mm) and restricted to plant base
79. Spikelet glumes whether
    1. always falls with mature nuts
    2. persists on the spikelet after nuts mature
80. Aerial glume length
    1. to 2.12 mm
    2. 2.2mm to 3.5 mm
    3. 3.6 to 3.8 mm
    4. 3.9 to 4.1 mm
    5. 4.2 to 4.55 mm
    6. 4.6 to 4.85 mm
    7. 4.9 to 5.1 mm
    8. 5.2 to 5.75 mm
    9. 5.8 to 5.95 mm
    10. 6.0 to 6.25 mm
    11. 6.3 to 6.55 mm
    12. 6.6 to 6.8 mm

    13. 6.9 to 7.1 mm
    14. 7.2 to 8.4 mm
    15. 8.5 to 10.1 mm
    16. 10.2 to 11.6 mm
    17. 12 to 13.7 mm
    18. 14 to 15 mm

81. Aerial glume width [74^]
    1. to 0.7 mm
    2. 0.75 to 0.9 mm
    3. greater than 0.9 to 1.46 mm
    4. 1.5 mm to 1.7 mm
    5. greater than 1.7 mm to 1.85 mm
    6. greater than 1.85 mm to 2.05 mm
    7. 2.05 mm to 2.4 mm
    8. 2.45 mm to 2.55 mm
    9. 2.6 mm to 2.9 mm
    10. greater than 2.9 mm
82. Aerial glume back colour (excluding tannins)
    1. no real colour as is translucent (some tannin may be present mainly near the glume base)
    2. cream
    3. straw
    4. yellow brown
    5. pale orange brown
    6. orange brown
    7. light brown
    8. pink-brown
    9. mid brown
    10. red brown
    11. deep burgundy (as in *Nemum*)
    12. burgundy black (very dark burgundy appearing almost black)
83. Aerial glume margin colour whether
    1. darker than gume back
    2. same colour as glume back and sides
    3. colour lighter than glume back
    4. consistantly colourless and distinct
84. Aerial glume margins [83~]
    1. entire (without indentations, incisions, or trichomes along margins)
    2. lacerate (margins irregularly cut, appearing torn)
    3. with antrorse prickle hairs pointing towards apex
    4. minutely ciliolate (<20 µm)
    5. ciliolate (with tiny or small trichomes protruding from margins c. 20 µm)
    6. short hairs
    7. hispid or almost so (as a continuation of glume back indumentum)
    8. fimbriolate (minutely fimbriate flattened projections)
    9. fimbriate (fringed margins with flattened processes)
    10. ciliate at apex only
    11. loosely ciliate (long lax hairs that look mishappen)
    12. piliferous (with long conspicuous trichomes c. 200 µm, that are lax or flexuose, and protruding from margins)
85. Aerial glume whether margin in transverse section
    1. is continuing in line with the glume sides, not inrolled or splayed
    2. is inrolled between 1/2 and upper 1/3 of glume
    3. margins only slightly curved backwards or flattened with glume still generally boat shaped
    4. is splayed so that the margin is between 45 and 90 degrees - flattening out giving a narrow keel with splayed sides
    5. is almost flattened (only the nerve is raised; the glume sides are flattened against the glume below, although the basal area around the nutlet may be boat shaped)
    6. is revolute (margin strongly recurved and bending backwards)
86. Glume texture whether [77!]
    1. hyaline (thinner than membranous and very delicate, usually colour is absent)

    2. membranous (almost transparent and usually colourless nut can be seen through the glume as in *Bulbostylis* sp. aff *barbata*)
    3. finely chartaceous (thicker than membranous light may be seen but is dulled and papery, has some flexibility but easily damaged with forceps, as in *Fimbristylis blakei*)
    4. tougher than chartaceaous as is more flexible but damaged with forceps (as in *Actinoschoenus*)
    5. chartaceous (thicker than finely chartaceous as light does not pass through but may still be damaged, as in *Crosslandia anthelata*)
    6. fine leathery (not overly thickened but is quite tough and flexible not easily damaged unless pulled, as in some *Fimbristylis*)
    7. subcoriaceous (quite tough and hard to bend, thick and not at all transparent, as in species of *Abildgaardia*)

87. Aerial glume margins [86~; 80^]]
    1. margins hyaline (light passes directly through)
    2. membranous (light is opaque)
    3. finely chartaceous and indistinct, or almost so, from rest of glume
    4. indistinct from rest of glume (with same texture as glume backs which are subcoriaceous as in *Abildgaardia*)
88. Aerial glume apex outline
    1. rounded (margins and apex forming a smooth arc)
    2. retuse (lobe rounded; sinus depth to 1/16 distance to midpoint of blade; margins convex)
    3. emarginate (lobe rounded; sinus depth 1/16 to 1/8 distance to midpoint of blade;margins straight or convex)
    4. obtuse (margins straight to convex, forming a terminal angle more than 90 degrees)
    5. acute (base cuneate - margins straight to convex forming a terminal angle 45–90 degrees; muticous)
    6. acuminate (base narrowly cuneate - margins straight to convex forming a terminal angle of less than 45 degrees; muticous)
    7. sub-mucronate (nerve less than 0.1 mm, but not muticous)
    8. mucronulate (1:1 l w nerve 0.1 mm)
    9. mucronate (with nerve less than 3:1 length/width, straight and stiff between 0.1 and 0.3 mm)
    10. apiculate (more than 3:1 length/width, usually slightly curled and flexuous; used for nerve extension greater than 0.3mm but equals or less than 0.7 mm)
    11. aristate (more than 3:1 length/width, usually prolonged, straight and stiff; used here for excurrent nerve forming awn-like projection greater than 0.7 mm long)
89. Aerial glume general shape [80!]
    1. oblong (2:1 to 3:2 with widest axis at midpoint of structure and with margins essentially parallel)
    2. narrowly oblong (6:1 to 3:1 with widest axis at midpoint of structure and with margins essentially parallel)
    3. spathulate
    4. linear (more than 12:1 with widest axis at midpoint of structure and with margins essentially parallel)
    5. ovate
    6. widely ovate
    7. very widely obovate (1:1 with apex curving in a wide arc)
    8. narrowly emarginate glume apex narrowing but often rounded at end with nerve extending and is usually reflexed (see *Fimbristylis schultzii*)
    9. emarginate (glume apex almost as wide as base and rounded, dipping into but not attached to nerve)
    10. obtuse (nerve terminates below glume apex and apex is broad and round)
    11. trullate (2:1 to 3:2 kite shaped with widest point near base)
    12. lanceolate (more than 6:1 to 3:1 with widest axis below middle and with margins symmetrically curved)
    13. oblanceolate (more than 6:1 to 3:1 reverse of lanceolate)
    14. narrowly trullate (6:1 to 3:1 with widest axis below middle and with straight margins, trowel shaped)
    15. triangular (2:1 to 3:2 with 3 sides and 3 angles)
    16. narrowly triangular (6:1 to 3:1 with 3 sides and 3 angles)
    17. linear triangular (more than 12:1 with 3 sides and 3 angles)
90. Aerial glume apex whether
    1. not recurved at maturity (usually looks quite sleek and neat)

   2. distinctly straight – not bent backwards or curving forwards
   3. slightly reflexed backwards, but not strongly recurved
   4. strongly and consistently recurved at maturity (as in *Abildgaardia schoenoides*)
91. Aerial glume nerve whether
   1. muticous (nerve does not extend pass glume apex, frequently finishes abrubtly beneath glume apex)
   2. submruco point (c.0.05 to 0.1 mm)
   3. nerve to mucro point (to 0.1 to 0.5 mm)
   4. nerve excurrent (greater than 0.5 mm)
92. Aerial glume abaxial surface
   1. glabrous
   2. nerve only scabrid
   3. sparsely scabrid
   4. scabrid over most of the surface
   5. short antrorse appressed hairs
   6. antrorse hairs (c. 100um long at 45 degrees to glume back)
   7. bristly
   8. tomentose
93. Glume epidermal cells shape in glume sides (at 50 x magnification)
   1. indistinct
   2. rectangular 1:2 to 1:3 longitudinally lengthwise with strongly sinuose walls
   3. rectangular 1:2 to 1:3 longitudinally lengthwise with straight walls
   4. linearly rectangular 1:6 longitudinally
   5. linear longitudinally
   6. irregularly elongate
94. Glume epidermal cells whether
   1. tanin idioblasts absent
   2. tanin idioblasts present (cells filled with tanins but not raised)
95. Glume epidermal tanins shape
   1. present as cellular 'dots'
   2. present as squares
   3. present as rectangular c. 3:1
   4. minute striations which are very faint
   5. present as long striations (vertical lines along length of glume)
   6. present as joined striations forming almost continuous lines
   7. forming continuous 'colour'
96. Aerial glumes tanin cover
   1. restricted mainly to apex
   2. sparse and restricted mainly to glume base
   3. sparse and restricted to glume backs and sides, not on margins
   4. sparse mostly occurring near outer margins only
   5. sparse mostly occurring on glume sides and margins (rarely in nerve area)
   6. evenly over glume but not all cells gives speckled appearance
   7. dense over glume sides and margins
   8. dense and continuous over glume back and thinning on sides
97. Glume epidermal cells whether
   1. raised 'gland' cells (as seen in *Fimbristylis cinnamometorum*)
   2. devoid of any obvious raised gland-like cells
98. Aerial glume shape in cross-section [91^]
   1. single highly thickened nerve giving distinct keel (see *Fimbristylis schultzii*)
   2. narrowly keeled (as in *Bulbostylis barbata*, narrow V of 3-nerves forming a keel)
   3. narrow U of 3 to 5 nerves
   4. broad V (from multiple nerves but forming a distinct V as in *Abildgaardia vaginata*)
   5. nerve area broad 5 to 7 nerves forming U but margins continuous texture with sides (sometimes glume flattened but nerves distinct)
   6. nerve area broad (forming U with distinct margins from glume sides, usually consists of 5 to 7 nerves forming rounded U-bottom)
   7. nerves indistinct (glume forms wide, shallow U with margins not flattened as in 2; nerves usually indistinct or only 1 fine nerve visible)
   8. nerve distinct and broad with glume broad and shallow curved or almost flat

  9. nerve area often indistinct or as apparent single slim nerve glume relatively flat at least above

99. Aerial glumes glandular cover
  1. mostly restricted to apex
  2. mostly restricted to margins
  3. over most of surface

100. Aerial glume arrangement
  1. distichous (attached directly oppositely ascending, sometimes rachilla twists to give spiral-distichous impression but glumes in definite rows)
  2. sub-distichous (glumes at least distichous at first then twisting, but not fully spiral - spirodistichous) glumes appear spirally arranged and not in rows but spikelet is slightly depressed in cross section
  3. almost alternately opposite (decussuate but ascending minutely acropetally as seen in *Bulbostylis barbata*)
  4. opposite decussate (as in *Trachystylis* where empty glumes are paired and 90 degrees from distal fertile pair)
  5. tristichous where glumes attached ascending in a tristichous spiral
  6. spiral (glumes attached in a close ascending spiral acropetally)

101. Aerial glumes (number neutral (empty) per spikelet)
  1. none
  2. one
  3. two
  4. three
  5. four
  6. five
  7. six or seven

102. Basal glume (length)
  1. less than 2 mm
  2. greater than 4 mm

103. Basal glumes (margins)
  1. entire
  2. ciliate
  3. ciliolate
  4. fimbriate
  5. fimbriolate
  6. involute
  7. lacerate

104. Basal glumes (general outline)
  1. linear (12:1 - widest axis at midpint of structure and margins essentially parallel)
  2. narrowly oblong (6:1 to 3:1)
  3. lanceolate (more than 6:1 to 3:1 - widest axis below middle and margins symmetrically curved)
  4. ovate (2:1 to 3:2 - see lanceolate)
  5. widely obliquely ovate
  6. narrowly trullate (more than 6:1 to 3:1 - with widest axis below middle and with straight margins)
  7. triangular (2:1 to 3:2 - with 3 angles and 3 sides)
  8. narrowly triangular (6:1 to 3:1 - with 3 sides and 3 angles)
  9. linear-triangular (more than 12:1 - with 3 sides and 3 angles)

105. Basal glumes abaxial surface
  1. glabrous
  2. nerve scabrid
  3. back scabrid

106. Basal glume epidermal cells whether
  1. tanin idioblasts absent
  2. tanin idioblasts present

107. Basal glume epidermal cells tanin cover
  1. restricted to glume base
  2. sides of glumes
  3. over entire glume (giving striated appearance)

108. Perianth whether present
  1. absent

2. present as bristles

Hypogynous bristles or scales are absent in members of the Abildgaardieae, however, there is one specimen of *Abildgaardia schoenoides* collected from Kakadu NP that has perianth present.

109. Bristle hairs, whether
    1. antrorse
    2. retrorse
110. Perianth number when present
111. Stamen number in aerial male or bisexual florets
    1. one
    2. two
    3. three
    4. four
    5. five
    6. six
112. Anther length, including apiculum
    1. to 0.15 mm
    2. 0.2 to 0.75 mm
    3. 0.8 to 0.9
    4. 0.95 to 1.50 mm
    5. 1.55 mm to 1.65
    6. 1.70 to 1.85
    7. 1.9 to 3.0
    8. 3.0 to 3.50
    9. 3.60 to 4.2
    10. 4.3 to 6.7 mm
113. Anther apiculum, whether connective tissue extends past the antheridium
    1. indistinct (either absent or to 0.05 mm in length)
    2. distinct (greater than 0.05 mm to 0.2mm)
    3. prominent (greater than 0.2 mm)
114. Aerial style length (measured from base of stylebase to base of stigmas)
    1. to 1.25 mm
    2. 1.30 to 2.75 mm
    3. 2.80 to 3.35 mm
    4. 3.4 to 3.8 mm
    5. 3.9 to 4.30
    6. 4.40 to 4.9
    7. 5.0 to 5.50 mm
    8. 5.6 to 6.2 mm
    9. 6.5 to 7.9 mm
    10. 8.0 to 12.60 mm
115. Aerial style width [106!]
    1. to 0.1 mm maximum measurement
    2. greater than 0.1 to 0.15 mm (0.1 is minimum measurement)
    3. greater than 0.15 mm to 0.2 mm
    4. greater than 0.2 mm to 0.25 mm
    5. greater than 0.25 mm to 0.30 mm
    6. greater than 0.30 mm to 0.34 mm
    7. 0.35 mm to 0.45 mm
116. Aerial style surface cover, (excludes style-base)
    1. glabrous
    2. isolated fimbriola 40–80um
    3. sparse fimbriola 40–80um
    4. dense fimbriola 40–80um
    5. isolated fimbria 100–140um, scattered along style often nearer the base and missing from apex
    6. sparse fimbria 100–140um, with the distance between each process greater than the length of each process
    7. dense fimbria 100–140um, with the distance between each process less than the length of the process
    8. coarsly fimbriate 220 μm long and 100 μm apart dense becoming very dense towards base
    9. ciliate

10. densely matted with long hairs excluding style-base

117. Aerial style outline in transverse section
    1. flattened and broad
    2. distinctly flattened (strap-like, as seen in many *Fimbristylis* species)
    3. terete (apparantly, as seen in *Trachystylis*)
    4. finely triangular (as seen in *Crosslandia*)
    5. minutely triangular (as seen in *Bulbostylis barbata*)
    6. distinctly triangular (sometimes slightly flattened but with 3rd angle distinct)
    7. broadly triangular with distinct flattened face giving flat appearance
118. Aerial style base length (in millimetres)
    1. from 0.05 to 0.2 mm
    2. to 0.5 mm
    3. greater than 0.5 and less than 1.5 mm
    4. greater than 1.5 to 3.5 mm
119. Aerial style base width (in millimetres)
    1. to 0.15 mm
    2. 0.2 to 0.5 mm
    3. greater than 0.5 to 1.0 mm
    4. greater than 1.0 mm
120. Style-base shape
    1. not widened or distinct
    2. globular (as seen in *Bulbostylis barbata*)
    3. bulbous
    4. narrowly triangular (as in *Crosslandia* and *Abildgaardia vaginata*)
    5. regularly triangular (no face distinctly concave or convex)
    6. triangular (with adaxial faces concave and abaxial face flat as in *Abildgaardia macrantha*)
    7. conical
    8. broadly triangular (somewhat rounded not with distinct triangular edges)
    9. broad and convex (on abaxial side away from rachilla giving a depressed appearance)
    10. squarish to barely triangular and depressed (as seen in *Fimbristylis depauperata* continues in line with style but is distinct)
121. Aerial style-base surface cover [110!]
    1. glabrous
    2. sparse rounded fimbriola (20 μm in length)
    3. isolated to sparse fimbriola (40–60 μm)
    4. dense fimbriola (40–60 μm)
    5. fimbriate (100–140 μm)
    6. coarsely fimbriate (c. 220 μm and 100 μm apart thick coarse looking very dense on style base)
122. Aerial or basal style-base, whether persistent or deciduous [116^]
    1. persistant (style-base always separates from style and often persists on nut apex, but not always)
    2. deciduous (style-base remains connected to style when abscissed from nut apex)
123. Aerial style stigma number
    1. two
    2. three
124. Aerial style stigmas relative length, when compared with style length
    1. stigmas (less than length of style)
    2. approximately equals (stigmas=style L)
    3. stigmas greater than style length
125. Aerial style stigmatic processes observed at 10x magnification
    1. minute papillae
    2. small fine papillae
    3. fimbriolate
    4. fimbriate
    5. woolly (distinctly)
126. Aerial style stigma colour
    1. white
    2. golden brown
    3. red brown
    4. deep red-brown
127. style (surface cover, excludes style-base)

   1. glabrous
   2. occasional fimbriola
   3. sparse
   4. hairs denser at base and sparse or absent towards style apex

128. Basal style (shape in transverse section)
   1. ligulate
   2. terete
   3. narrowly triangular
   4. minutely triangular
129. Basal stylebase (indumentum cover) whether
   1. absent as stylebase is glabrous (at least appearing so)
   2. occasional fimbriola
   3. sparse fimbriola occuring near style base to nut abscission zone
   4. dense fimbriola 40–120 µm
130. Aerial nutlet length [124^]
   1. less than 0.65mm
   2. 0.65 to 1.3mm
   3. 1.35 to 2.0mm
   4. greater than 2 and less than 3mm
   5. greater than 3 less than 4.5mm
131. Aerial nutlet width [125^]
   1. to 0.60 mm
   2. 0.61 to 1.15 mm
   3. greater than 1.15 mm to 1.34 mm
   4. 1.35 mm to 1.50 mm
   5. greater than 1.50 mm to 1.75 mm
   6. greater than 1.75 mm less than 1.90 mm
   7. 1.90 mm to 2.50 mm
132. Aerial nutlet stipe length
   1. zero as no constriction observed
   2. to 0.2 mm
   3. greater than 0.2 to 0.28
   4. 0.3 to 0.4
   5. greater than 0.4 to 0.8
   6. greater 0.8 to 1.0 mm
   7. greater than 1.0 to 1.10
133. Aerial nut hypogynophore [127^]
   1. apparently absent or highly reduced enclosed within the fruit wall (may appear as a 'button')
   2. distinct as a stalk not enclosed by the fruit wall of the nut (usually brownish) with filaments attached at the base
   3. completely enclosed within the 'stipe' of the nut fruit wall and not apparent from the outside (with filaments attached at the base of the stipe)

   Hypogynophore is a stalk directly below the ovary and may be apparent as separate from the nut proper or enclosed within the stipe of the nut. On some nuts the hypogynophore may be highly reduced or appear absent. Stamens and perianth parts are attached at the base of the hypogynophore.

   In *Abildgaardia odontocarpa* the hypogynophore is present in the stipe of the nut and not evident from the outside - separating from the seed proper when the wet nut is opened. The hypogynophore adheres to the inner area of the nut that encased it.
134. Aerial nutlet shape in transverse section (at mid-third of organ) [123!]
   1. biconvex (lenticular depressed due to two faces)
   2. cylindrical (without distinct sides appearing rounded - ribs not evident)
   3. rounded trigonous
   4. distinctly plano-convex (distinct dorsal ventral sides in 3-sided fruit ie has definite face where fruit sits against the rachilla evenly-flatly - usually slightly larger than the other 2 faces that form an almost single convex face eg *A macrantha*)
   5. sub-trigonous
   6. trigonous (3-sided, of roughly equal size, faces not concave)
   7. triquetrous
   8. strongly triquetrous

135. Aerial nutlet nut apex (excluding any persistent stylebase)
    1. nut apex with a distinct extension or point formed from style base (as in *Schoenoplectus*)
    2. nut apex umbonata (sometimes nut apex may have a small point but it is not formed from the stylebase and is usually no more than 0.1 mm in length)
    3. nut apex generally rounded
136. Aerial nutlet outline excluding external gynophore
    1. ovate
    2. elliptic (2:1 to 3:2 as in *Crosslandia*)
    3. widely elliptic (6:5)
    4. obovate (2:1 to 3:2)
    5. widely obovate (6:5 as in *Bulbostylis barbata*)
    6. very widely obovate (1:1 as seen in *Schoenoplectus*)
    7. pyriformis (pear shape - nut with truncate base with style-base protruding, apex umbonate)
    8. obampulliformis (compressed in 3-dimensions - apex somewhat elliptic with slight contriction near base but not like stipe in *Abildgaardia*)
    9. obcordate (as in *Abildgaardia pachyptera* nut wings give the distinct shape with wings pronounced or not, sometimes entire or with notches)
    10. obtrullate (3:2)
    11. widely obtrullate (6:5)
    12. very widely obtrullate (1:1)
    13. napiform (more tapered than obtrullate with smoother lines)
    14. widely napiform (starting as widley obovate but with tapered base)
    15. clavate (club shaped as in A macrantha as stipe forms club handle)
    16. capitate (head like as in A ovata as stipe forms neck)
    17. strongly capitate (where nut severly restricted half way forming tight head at apex on a long narrow stalk or stipe)
    18. mace shaped (from pronounced horns from deep notches on strongly constricted head with extended stipe)
137. Aerial nutlet wings, whether present or absent on the nut (see Lye 2000 p:625)
    1. absent as there are no pronounced projections from face edges
    2. present (in the horizontal plane ie not on the convex face sometimes greatly reduced and notched)
    3. as three distinctly broad notched protusions from the face edges and top (looks mace-like)
138. Aerial nutlet colour
    1. white
    2. pale pink, with white 'bloom' on outer surface
    3. cream
    4. straw
    5. yellow
    6. dark golden brown
    7. port wine (may have cream-pink face and port wine ribs as seen in *Bulbostylis barbata*)
    8. light grey
    9. dark grey
    10. light brown
    11. grey brown
    12. dark brown
    13. black
139. Aerial nutlet surface whether (follows Radford et al. 1974)
    1. glaucous (covered with a bloom or smooth waxy coating)
    2. glaucescent (sparingly or slightly glaucous; does not include waxy coating removed or damaged)
    3. dull (light not reflected back; surface not coating with wax but not highly lustrous)
    4. lacquered (nut appearing as if lacquered; some light reflected but not lustrous)
    5. glistening (especially evident in white nuts)
    6. shining (nitid or laevigate; appears lustrous or polished)
140. Aerial nutlet epidermal cell outline (at 50x magnification)
    1. indistinct
    2. minutely ovate (need measurements)
    3. appearing circular to hexagonal (c. 20 µm in size and at 500x are actually hexagonal)
    4. widely elliptic to roughly circular (40–80 µm sometimes squarish, at 500x are actually hexagonal)

    5. distinctly hexagonal (giving nut surface a honecombe appearance)
    6. cells almost square to just rectangular transverely 1 by 1(or 1 by 2)
    7. transversly narrowly oblong (20 x 60 μm to 20 x 120 μm)
    8. transversely rectangular 40 x 60 μm (in distinct longitudinal rows)
    9. transversly rod-shaped having tapered ends (walls straight)
    10. longitudinally oblong (40 x 20μm)
    11. longitudinally narrowly oblong 6:1 (120 x 20 μm), 3:1 (60 x 20 μm)
    12. aciculated (marked with very fine longitudinal irregular streaks, as if produced by the point of a needle)

141. Aerial nutlet surface patterning (including protuberances follows Lye 2000)
    1. smooth (no apparent pattern on nutlet surface, epidermal cells indistinct at 10x magnification)
    2. subpuncticulate (some single papillae raised but not over all of surface or not prominent)
    3. puncticulate (single papilla 5–15 um diameter raised to form minute bumps prominent in cells over the surface of the nutlet)
    4. subpusticulate (1–3 cells raised in groups forming low mounds and are not prominent)
    5. small tubercules (from 1–3 cells prominent)
    6. pusticulate (large rounded tubercules)
    7. tuberculate (from multiple cells - prominent greater than 4, protruding conical outgrowths or papillae formed over more than one epidermal cell, usually 20–100 um diameter)
    8. verrucate (usually flat topped and very distinct and upright)
    9. continuously rugulose
    10. discontinuously mildly rugose
    11. continuously mildly rugose over nut excluding stipe
    12. rugose (longitudinally elongate epidermal cells that are raised to form prominent undulating transverse wrinkles)
    13. continuously acutely rugose
    14. longitudinally grooved striated (grooves in prominent longitudinal rows)
    15. transversly oblong cells in indistinct longitudinal rows
    16. transversly interlocking rod-shaped in roughly longitudinal rows
    17. reticulate ('netted' epidermal cells with defined walls but not in distinct rows)
    18. scalariform (ladderlike and almost in rows)
    19 mostly individual cells sunken
    20. individual epidermal cells raised (not forming tubercules and not puncticulate)
    21. reticulate-foveate (cell walls raised and thickened)
    22. alveolate (cell depression but cell walls not raised and distinct)

142. Aerial nutlet protuberance or pattern distribution
    1. absent
    2. occasional
    3. uneven distribution (sparse)
    4. restricted to vertical rows (usually two) down the fruit wall face and nut trigonous ribs
    5. bordering margins of nutlet (i.e. along face ribs)
    6. sparse distribution even over upper three quarters of area of nutlet (no constriction)
    7. sparse distribution spread evenly over all of nutlet (no constriction)
    8. sparse distribution over nutlet surface excluding stipe (constriction)
    9. dense distribution over upper three quarters of nutlet (not constricted towards base)
    10. dense distribution spread evenly over nutlet surface excluding stipe (constriction)
    11. dense distribution evenly of nutlet surface (constriction not present or at least minimal)

143. Basal nut length
    1. to 1.2 mm
    2. from 1.3 to 2.1 mm

144. Basal nut width
    1. from 0.75 to 1.25 mm

145. Basal nutlet, whether distinctly beaked at nut apex
    1. nut with a distinct beak formed from style base (as in *Schoenoplectus*)
    2. distinct beak absent (sometimes nut apex may have a small point but it is not formed from the stylebase and is usually no more than 0.1 mm in length)

146. Basal nutlet shape in transverse section
    1. cylindrical (dorsal ventral sides not easily determined)
    2. plano convex (dorsal ventral sides obvious in fruit)
    3. sub trigonous to trigonous

147. Basal nutlet outline shape
    1. elliptic (2:1 to 3:2)
    2. narrowly elliptic (3:1)
    3. widely elliptic (6:5)
    4. obovate (2:1 to 3:1)
    5. widely obovate
148. Basal nutlet colour
    1. cream
    2. golden
    3. dark golden brown
    4. dark grey
    5. dark brown
    6. black
149. Basal nutlet surface protuberances (follows Lye 2000) [138!]
    1. absent
    2. rugose
    3. puncticulate (each cell with a raised silica body)
    4. subpusticulate (individual epidermal cells raised -not forming tubercules and not puncticulate - as seen in *Crosslandia* nutlets)
    5. groups of 1–3 cells raised but not prominent (giving 'chequered appearance of raised areas over entire nut surface)
    6. cells walls raised and thickened over nut surface
    7. small tubercules (from 1–3 cells) raised evenly over nutlet surface
150. Basal nutlet surface, whether [139!]
    1. glaucous (covered with a bloom or smooth waxy coating)
    2. glaucescent (sparingly or slightly glaucous)
    3. dull
    4. lacquered
    5. shining (nitid, laevigate, lustrous or polished)
151. Embryo, general type [150~; 145^]
    1. Fimbristylis-type (root orientation lateral and smaller than basal orientated shoot)
    2. Abildgaardia-type (root orientation basal and smaller than basal orientated shoot, but larger than Fimbristylis-type)
    3. Bulbostylis-type (root orientation basal and the same size or larger than the basal orientated shoot)
    4. Nemum-type (root orientation basal and smaller in size to the basal orientated shoot)
    5. Schoenoplectus-type (root orientation lateral distal (apical) beneath mushroom shaped cotyledon and and smaller than basally pointing shoot but midway along cotyledon apical extension)
    6. Carex-type (root terminal and larger than the inconspicuous lateral shoot)
    7. Schoenus-type (shoot and root distinctly sub basal)
152. Embryo cotyledon outline
    1. narrowly top-shaped (wide at the apex and gradually narrowing to a 'point' as in Fimbristylis A-type embryo)
    2. reverse dome shaped (with base rounded and almost parallel sides as in *Fimbristylis cinnamometorum* Fimb B type)
    3. roughly reverse dome shaped with cotyledon having a saddle (as in *Fimbristylis disticha* Fimb C type)
    4. broadly top-shaped with base widely rounded due to shoot and root size (as in Bulbostylis-type embryo)
    5. very widely top shaped with base wide due to shoot root (as in *Nemum megastachyum*)
    6. inversely bell shaped (as in *Crosslandia* type embryo Fimb D type embryo)
    7. broadly inverse bell-shaped (as in Abildgaardia-type embryo)
    8. very broadly inversely bell shaped (cotyledon very wide brimmed and not deep almost hat-like as in *Abildgaardia oxystachya* base rounded)
    9. saucer shaped (as in *Actinoschoenus* broad and compressed at poles)
    10. ellipsoid (as in Carex-type embryo - seen in *Actinoschoenus*, see Kern 1974)
    11. subpyramidal (distinctly 3-sided not rounded and sharply pointed at the base as in *Abildgaardia mexicana*)
    12. mushroom shaped with cotyledon distal extension (as in Schoenoplectus-type embryo)

The outline of the embryo can depend on the view i.e. from the side the embryo may look inversely bell shaped but from the front position may look ellipsoid.

153. Cotyledon shape from distal or proximal view
    1. narrowly elliptic (cotyledon appearing somewhat flattened on the sides)
    2. elliptic
    3. circular
    4. cotyledon almost triangular-trigonous
    5. triangular
154. Embryo morphology, orientation of the germ pore compared to the first leaf primordia [153~]
    1. parallel with the first leaf primordia
    2. perpendicular
    3. distinctly open and circular in the centre (as seen in *Fimbristylis schultzii*)

Appendix 3 Glycerin jelly for semi-permanent slides (Kearns and Inouye 1993).

Ingredients	Quantities
Distilled water	35 mL
Glycerin	30 mL
Gelatin	10 g
Phenol – crystalline (preservative)	1 g

N.B. phenol is a known carcinogen.

Method: In a beaker, dissolve the gelatin in distilled water by heating gently. Add the glycerin and phenol, stirring while on low heat. Avoid creating bubbles in the mixture. When dissolved pour slowly into two new Petri dishes and allow to cool. If preferred the phenol can be omitted, but the jelly will need to be kept refrigerated to prevent mould growing.

Preparing semi-permanent slides: Take a cleaned microscope slide and place onto it a small cube of glycerin jelly c. 5 x 5 mm. Place the prepared sections onto the top of the jelly in a small amount of distilled water. Gently place a cover slip so that it balances on top of the jelly. Heat the slide simply by placing onto a dissecting microscope slide that has under lighting and heat until melted and the coverslip is sitting flat on the slide. Allow to cool before storing in slide boxes.