Chapter 5

Phenetetic 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. schoeinooides* complex (Gordon-Gray 1988), *B. hispidula* complex (Haines and Lye 1983; Lye 1995), *B. densa* complex (Haines

*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. puberula* 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>OTU</th>
<th>State or Country</th>
<th>Collector</th>
</tr>
</thead>
<tbody>
<tr>
<td>sp. aff.</td>
<td>baffba2</td>
<td>N.T.</td>
<td>Rice B.L.</td>
</tr>
<tr>
<td></td>
<td>baffba5</td>
<td>N.T.</td>
<td>Bruhl J.J. 369A</td>
</tr>
<tr>
<td><em>Bulbostylis</em></td>
<td>bba1</td>
<td>Qld</td>
<td>Wilson K.L. 5442</td>
</tr>
<tr>
<td><em>barbata</em></td>
<td>bba2</td>
<td>N.T.</td>
<td>Beauglehole A.C. 26084</td>
</tr>
<tr>
<td></td>
<td>bba3</td>
<td>W.A.</td>
<td>Mitchell A.S. 1150</td>
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<tr>
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<td>N.S.W.</td>
<td>Tindale M.D. 2058</td>
</tr>
<tr>
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<td></td>
<td>bba6</td>
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<td></td>
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<td>N.T.</td>
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<td></td>
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<td>Clarke K.L 100, Bruhl J.J.</td>
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<td></td>
<td>bba13</td>
<td>Singapore</td>
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<tr>
<td></td>
<td>bba14</td>
<td>USA</td>
<td>Hill S.R. 24361</td>
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<td>bba15</td>
<td>Kenya</td>
<td>Napper D.M., Kanuri 2079</td>
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<td></td>
<td>bba16</td>
<td>India</td>
<td>Raizada M.B.</td>
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<td></td>
<td>bba17</td>
<td>America</td>
<td>Correll D.S. 52337</td>
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<td>bba18</td>
<td>India</td>
<td>Rajn R.R.V.</td>
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<td>bba19</td>
<td>South Africa</td>
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<td>George A.S. 820</td>
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<td>Qld</td>
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<td>bde5</td>
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<td>Code</td>
<td>Location</td>
<td>Species</td>
<td>Reference</td>
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<td>1102</td>
</tr>
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<td>bpy3</td>
<td>N.S.W.</td>
<td>Hunter J.T., Bell D.B.</td>
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<td>N.T.</td>
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<td>Sharpe P.R.</td>
<td>232</td>
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<tr>
<td>bpy8</td>
<td>Qld</td>
<td>Bean A.R.</td>
<td>4227</td>
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</table>
(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.

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Description</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>char1</td>
<td>Mean aerial spikelet width in mm (spikelets with mature fruit) at the widest point</td>
<td>1</td>
</tr>
<tr>
<td>char2</td>
<td>Mean aerial nut length in mm from base of stipe to nut apex (excluding persistent style base)</td>
<td>1</td>
</tr>
<tr>
<td>char3</td>
<td>Mean aerial nut width in mm at widest point</td>
<td>1</td>
</tr>
<tr>
<td>char4</td>
<td>Aerial nut length:width (ratio 1:W/L(x) (to decimal 1/x), ratio coefficient</td>
<td>1</td>
</tr>
<tr>
<td>char5</td>
<td>Mean aerial nut ‘stipe’ length in mm</td>
<td>1</td>
</tr>
<tr>
<td>char6</td>
<td>Stipe length/nut length (proportion)</td>
<td>1</td>
</tr>
<tr>
<td>char7</td>
<td>Mean aerial anther length in mm (including appendages)</td>
<td>1</td>
</tr>
<tr>
<td>char8</td>
<td>Mean aerial style length in mm (including style base to base of style arm junction)</td>
<td>1</td>
</tr>
<tr>
<td>char9</td>
<td>Mean aerial style width in mm (at mid third)</td>
<td>1</td>
</tr>
<tr>
<td>char10</td>
<td>Style length:width (1:W/L(x) to decimal 1/x), ratio coefficient</td>
<td>1</td>
</tr>
<tr>
<td>char11</td>
<td>Mean aerial stylebase length in mm (from base to constriction at style junction)</td>
<td>1</td>
</tr>
<tr>
<td>char12</td>
<td>Mean aerial stylebase width in mm (at widest point)</td>
<td>1</td>
</tr>
<tr>
<td>char13</td>
<td>Style base length:width (1:W/L(x) to decimal 1/x); ratio coefficient</td>
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</tr>
<tr>
<td>char14</td>
<td>Mean aerial glume length in mm (from base of nerve to apical point)</td>
<td>1</td>
</tr>
<tr>
<td>char15</td>
<td>Mean aerial glume width in mm (at widest point)</td>
<td>1</td>
</tr>
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<td>char16</td>
<td>Glume length:width (1:W/L(x) to decimal 1/x); ratio coefficient</td>
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</tr>
<tr>
<td>char17</td>
<td>Mean leaf width in mm (at mid third)</td>
<td>1</td>
</tr>
<tr>
<td>char18</td>
<td>Mean culm width in mm (at mid third)</td>
<td>1</td>
</tr>
<tr>
<td>char19</td>
<td>Mean root width in mm (one cm below plant base)</td>
<td>1</td>
</tr>
<tr>
<td>char20</td>
<td>Mean inflorescence–synflorescence length in mm (from base of main bract to furthermore point of spikelets)</td>
<td>1</td>
</tr>
<tr>
<td>char21</td>
<td>Basal spikelets 0-absent: always only aerial; 1-present: basal spikelets (morphologically distinct) as well as aerial spikelets</td>
<td>0.5</td>
</tr>
<tr>
<td>char22</td>
<td>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</td>
<td>0.5</td>
</tr>
<tr>
<td>char23</td>
<td>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</td>
<td>0.2</td>
</tr>
<tr>
<td>char24</td>
<td>Nut shape in transverse section is strongly trigetrous with deeply concave faces</td>
<td>0.2</td>
</tr>
<tr>
<td>char25</td>
<td>Nut shape in transverse section is triquetrous, having 3-angles, with faces being concave</td>
<td>0.2</td>
</tr>
<tr>
<td>char26</td>
<td>Nut shape in transverse section is trigonous, 3-angles with faces somewhat flattened</td>
<td>0.2</td>
</tr>
<tr>
<td>char27</td>
<td>Nut shape in transverse section is rounded trigonously, with 3 equal sides but well rounded edges and faces (convex)</td>
<td>0.2</td>
</tr>
<tr>
<td>char28</td>
<td>Nut outline obovate (2:1 or 3:2)</td>
<td>0.125</td>
</tr>
<tr>
<td>char29</td>
<td>Nut outline widely obovate (6:5)</td>
<td>0.125</td>
</tr>
<tr>
<td>char30</td>
<td>Nut outline very widely obovate (1:1)</td>
<td>0.125</td>
</tr>
<tr>
<td>char31</td>
<td>Nut outline pyriform (pear-shaped)</td>
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</tr>
<tr>
<td>char32</td>
<td>Nut outline obtrullate</td>
<td>0.125</td>
</tr>
<tr>
<td>char33</td>
<td>Nut outline widely obtrullate (6:5)</td>
<td>0.125</td>
</tr>
<tr>
<td>char34</td>
<td>Nut outline very widely obtrullate 1:1</td>
<td>0.125</td>
</tr>
<tr>
<td>char35</td>
<td>Nut outline napiform</td>
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</tr>
<tr>
<td>char36</td>
<td>Nut epidermis without protuberances (apparent at 50x magnification under a dissecting microscope)</td>
<td>0.125</td>
</tr>
<tr>
<td>char37</td>
<td>Nut epidermis rugulose (minutely rugose)</td>
<td>0.125</td>
</tr>
<tr>
<td>char38</td>
<td>Nut epidermis rugose with rounded waves</td>
<td>0.125</td>
</tr>
<tr>
<td>char39</td>
<td>Nut epidermis rugose with acute waves (apex acute from a central raised silica body)</td>
<td>0.125</td>
</tr>
<tr>
<td>char40</td>
<td>Nut epidermis sub-puncticulate, from single raised cells that are not prominent and are scattered over the surface</td>
<td>0.125</td>
</tr>
<tr>
<td>char41</td>
<td>Nut epidermis puncticulate, from prominent single cells raised evenly over surface</td>
<td>0.125</td>
</tr>
<tr>
<td>char42</td>
<td>Nut epidermis with rows of warts on face, usually 2 vertical rows on each face</td>
<td>0.125</td>
</tr>
<tr>
<td>char43</td>
<td>Nut epidermis reticulate, from distinct and raised cell walls</td>
<td>0.125</td>
</tr>
<tr>
<td>char44</td>
<td>Nut epidermis finely hexagonal, giving a honeycomb appearance, obvious at 10x magnification under a dissecting microscope</td>
<td>0.2</td>
</tr>
<tr>
<td>char46</td>
<td>Nut epidermal cells isodiametric; almost square to just rectangular</td>
<td>0.2</td>
</tr>
<tr>
<td>char47</td>
<td>Nut epidermal cells oblong longitudinally (2:1)</td>
<td>0.2</td>
</tr>
<tr>
<td>char48</td>
<td>Nut epidermal cells narrowly oblong longitudinally (6:1;3:1)</td>
<td>0.2</td>
</tr>
<tr>
<td>char49</td>
<td>Stamen number: 1</td>
<td>0.33</td>
</tr>
<tr>
<td>char50</td>
<td>Stamen number: 2</td>
<td>0.33</td>
</tr>
<tr>
<td>char51</td>
<td>Stamen number: 3</td>
<td>0.33</td>
</tr>
<tr>
<td>char52</td>
<td>Sheath glabrous (hairs absent)</td>
<td>0.33</td>
</tr>
<tr>
<td>char53</td>
<td>Sheath with short to medium hairs (60-100 μm)</td>
<td>0.33</td>
</tr>
<tr>
<td>char54</td>
<td>Sheath with bristly hairs almost erect from surface (&gt; 100-1000 μm)</td>
<td>0.33</td>
</tr>
<tr>
<td>char55</td>
<td>Glume margins entire</td>
<td>0.25</td>
</tr>
<tr>
<td>char56</td>
<td>Glume margins ciliolate; small fine hair-like projections from the margins, sometimes only distally (5 div @ 50x - sometimes only distally)</td>
<td>0.25</td>
</tr>
<tr>
<td>char57</td>
<td>Glume margins fimbriolate; small, flattened projections from margins, sometimes only distally (100 μm)</td>
<td>0.25</td>
</tr>
<tr>
<td>char58</td>
<td>Glume margins piliferous; fine, long, loose hairs arising from the margins (1000 μm)</td>
<td>0.25</td>
</tr>
<tr>
<td>char59</td>
<td>Glume apex rounded</td>
<td>0.143</td>
</tr>
<tr>
<td>char60</td>
<td>Glume apex acute (muticous)</td>
<td>0.143</td>
</tr>
<tr>
<td>char61</td>
<td>Glume apex sub-mucronulate</td>
<td>0.143</td>
</tr>
<tr>
<td>char62</td>
<td>Glume apex mucronulate</td>
<td>0.143</td>
</tr>
<tr>
<td>char63</td>
<td>Glume apex mucronate</td>
<td>0.143</td>
</tr>
<tr>
<td>char64</td>
<td>Glume apex acuminate</td>
<td>0.143</td>
</tr>
<tr>
<td>char65</td>
<td>Glume apex aristate</td>
<td>0.143</td>
</tr>
<tr>
<td>char66</td>
<td>Glume outline ovate</td>
<td>0.25</td>
</tr>
<tr>
<td>char67</td>
<td>Glume outline trullate (kite-shaped)</td>
<td>0.25</td>
</tr>
<tr>
<td>char68</td>
<td>Glume outline narrowly triangular</td>
<td>0.25</td>
</tr>
<tr>
<td>char69</td>
<td>Glume outline linearly triangular</td>
<td>0.25</td>
</tr>
<tr>
<td>char70</td>
<td>Glume apex reflexed at maturity</td>
<td>0.5</td>
</tr>
<tr>
<td>char71</td>
<td>Glume apex not reflexed at maturity</td>
<td>0.5</td>
</tr>
<tr>
<td>char72</td>
<td>Glume nerve muticous</td>
<td>0.33</td>
</tr>
<tr>
<td>char73</td>
<td>Glume nerve to a mucro point</td>
<td>0.33</td>
</tr>
<tr>
<td>char74</td>
<td>Glume nerve excurrent (greater than 0.5 mm)</td>
<td>0.33</td>
</tr>
<tr>
<td>char75</td>
<td>Glume abaxial surface glabrous</td>
<td>0.167</td>
</tr>
<tr>
<td>Character</td>
<td>Description</td>
<td>Value</td>
</tr>
<tr>
<td>-----------</td>
<td>------------------------------------------------------------------------------</td>
<td>-------</td>
</tr>
<tr>
<td>char76</td>
<td>Glume abaxial surface with nerve only scabrid</td>
<td>0.167</td>
</tr>
<tr>
<td>char77</td>
<td>Glume abaxial surface scabrid over lower half of glume (even - isolated, sparse, dense toothed hairs)</td>
<td>0.167</td>
</tr>
<tr>
<td>char78</td>
<td>Glume abaxial surface scabrid over most of the glume back (20-40 μm)</td>
<td>0.167</td>
</tr>
<tr>
<td>char79</td>
<td>Glume abaxial surface with short hairs (100 μm)</td>
<td>0.167</td>
</tr>
<tr>
<td>char80</td>
<td>Glume abaxial surface bristly, with erect hairs (&gt; 1000 μm)</td>
<td>0.167</td>
</tr>
<tr>
<td>char81</td>
<td>Glume arrangement on the rachilla distichously spiral (glumes opposite each other and glume pairs ascending arranged spirally)</td>
<td>0.5</td>
</tr>
<tr>
<td>char82</td>
<td>Glume arrangement on the rachilla tristichous</td>
<td>0.5</td>
</tr>
<tr>
<td>char83</td>
<td>Non fertile glume number at the base of each spikelet: 0</td>
<td>0.5</td>
</tr>
<tr>
<td>char84</td>
<td>Non fertile glume number at the base of each spikelet: 1</td>
<td>0.5</td>
</tr>
<tr>
<td>char85</td>
<td>Leaf to culm ratio: 1:1</td>
<td>0.2</td>
</tr>
<tr>
<td>char86</td>
<td>Leaf to culm ratio: 2:3</td>
<td>0.2</td>
</tr>
<tr>
<td>char87</td>
<td>Leaf to culm ratio: 1:2</td>
<td>0.2</td>
</tr>
<tr>
<td>char88</td>
<td>Leaf to culm ratio: 1:3</td>
<td>0.2</td>
</tr>
<tr>
<td>char89</td>
<td>Leaf to culm ratio: 1 to 4</td>
<td>0.2</td>
</tr>
<tr>
<td>char90</td>
<td>Culm surface glabrous</td>
<td>0.25</td>
</tr>
<tr>
<td>char91</td>
<td>Culm surface scabrid (includes distally)</td>
<td>0.25</td>
</tr>
<tr>
<td>char92</td>
<td>Culm surface with short hairs that are almost erect (c. 100 μm)</td>
<td>0.25</td>
</tr>
<tr>
<td>char93</td>
<td>Culm surface bristly with stiff erect hairs (includes distally)</td>
<td>0.25</td>
</tr>
<tr>
<td>char94</td>
<td>Leaf abaxial surface glabrous</td>
<td>0.2</td>
</tr>
<tr>
<td>char95</td>
<td>Leaf abaxial surface with scabrid margins</td>
<td>0.2</td>
</tr>
<tr>
<td>char96</td>
<td>Leaf abaxial surface scabrid over the abaxial surface</td>
<td>0.2</td>
</tr>
<tr>
<td>char97</td>
<td>Leaf abaxial surface with erect to ascending hairs (c. 100 μm)</td>
<td>0.2</td>
</tr>
<tr>
<td>char98</td>
<td>Leaf abaxial surface bristly/hispid (1000 μm – erect to outwardly ascending)</td>
<td>0.2</td>
</tr>
<tr>
<td>char99</td>
<td>Inflorescence-synflorescence mostly solitary (HF1), or 1–2 coflorescences (Cof1)</td>
<td>0.2</td>
</tr>
<tr>
<td>char100</td>
<td>Inflorescence-synflorescence as anthemodia, main florescence (HF1) plus multiple primary coflorescences (Cof1) on lengthened epipodia (rays); some coflorescences may be sessile, but not all</td>
<td>0.2</td>
</tr>
<tr>
<td>char101</td>
<td>Inflorescence-synflorescence as ramified (compound) anthemodia</td>
<td>0.2</td>
</tr>
<tr>
<td>char102</td>
<td>Inflorescence-synflorescence as ‘heads’ of 3-7 sessile spikelets</td>
<td>0.2</td>
</tr>
<tr>
<td>char103</td>
<td>Inflorescence-synflorescence hemispherical ‘head’ of &gt; 7 sessile spikelets</td>
<td>0.2</td>
</tr>
<tr>
<td>char104</td>
<td>Inflorescence-synflorescence bracts present and glume-like</td>
<td>0.5</td>
</tr>
<tr>
<td>char105</td>
<td>Inflorescence-synflorescence bracts present and leaf-like</td>
<td>0.5</td>
</tr>
<tr>
<td>char106</td>
<td>Inflorescence-synflorescence bracts shorter than inflorescence-synflorescence length</td>
<td>0.33</td>
</tr>
<tr>
<td>char107</td>
<td>Inflorescence-synflorescence bracts equals the inflorescence-synflorescence length</td>
<td>0.33</td>
</tr>
<tr>
<td>char108</td>
<td>Inflorescence-synflorescence bracts longer than the inflorescence-synflorescence length</td>
<td>0.33</td>
</tr>
<tr>
<td>char109</td>
<td>Inflorescence-synflorescence prophyllar buds or spikelets present</td>
<td>0.5</td>
</tr>
<tr>
<td>char110</td>
<td>Inflorescence-synflorescence prophyllar buds or spikelets absent</td>
<td>0.5</td>
</tr>
</tbody>
</table>
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 prophyls 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.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>No. specimens sampled</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Ingroup</strong></td>
<td></td>
</tr>
<tr>
<td><em>Abildgaardia macrantha</em> (provisional)</td>
<td>10</td>
</tr>
<tr>
<td><em>Abildgaardia mexicana</em></td>
<td>5</td>
</tr>
<tr>
<td><em>Abildgaardia odontocarpa</em> (provisional)</td>
<td>2</td>
</tr>
<tr>
<td><em>Abildgaardia ovata</em></td>
<td>13</td>
</tr>
<tr>
<td><em>Abildgaardia oxystachya</em> (provisional)</td>
<td>13</td>
</tr>
<tr>
<td><em>Abildgaardia pachyptera</em> (provisional)</td>
<td>11</td>
</tr>
<tr>
<td><em>Abildgaardia schoenoides</em></td>
<td>12</td>
</tr>
<tr>
<td><em>Abildgaardia triflora</em></td>
<td>4</td>
</tr>
<tr>
<td><em>Bulbostylis barbata</em></td>
<td>20</td>
</tr>
<tr>
<td><em>Bulbostylis burdigeae</em></td>
<td>5</td>
</tr>
<tr>
<td><em>Bulbostylis capillaris</em></td>
<td>4</td>
</tr>
<tr>
<td><em>Bulbostylis densa</em></td>
<td>15</td>
</tr>
<tr>
<td><em>Bulbostylis hispidula subsp. pyriformis</em></td>
<td>3</td>
</tr>
<tr>
<td><em>Bulbostylis hispidula subsp. senegalensis</em></td>
<td>2</td>
</tr>
<tr>
<td><em>Bulbostylis puberula</em></td>
<td>7</td>
</tr>
<tr>
<td><em>Bulbostylis pyriformis</em></td>
<td>8</td>
</tr>
<tr>
<td><em>Bulbostylis humilis</em></td>
<td>3</td>
</tr>
<tr>
<td><em>Bulbostylis turbinata</em></td>
<td>8</td>
</tr>
<tr>
<td><em>Bulbostylis sp. aff. barbata</em></td>
<td>7</td>
</tr>
<tr>
<td><em>Bulbostylis sp. aff. burdigeae</em></td>
<td>1</td>
</tr>
<tr>
<td><em>Bulbostylis sp. aff. densa 1</em></td>
<td>2</td>
</tr>
<tr>
<td><em>Bulbostylis sp. aff. densa 2</em></td>
<td>3</td>
</tr>
<tr>
<td><em>Bulbostylis sp. aff. turbinata 1</em></td>
<td>1</td>
</tr>
<tr>
<td><em>Bulbostylis sp. aff. turbinata 2</em></td>
<td>1</td>
</tr>
<tr>
<td><em>Bulbostylis sp. aff. puberula</em></td>
<td>1</td>
</tr>
<tr>
<td><em>Crosslandia anthelata</em> (provisional)</td>
<td>5</td>
</tr>
<tr>
<td><em>Crosslandia setifolia</em></td>
<td>18</td>
</tr>
<tr>
<td><em>Crosslandia spiralis</em> (provisional)</td>
<td>3</td>
</tr>
<tr>
<td><em>Crosslandia vaginata</em> (provisional)</td>
<td>14</td>
</tr>
<tr>
<td><em>Fimbristylis bahiensis</em></td>
<td>4</td>
</tr>
<tr>
<td><em>Fimbristylis blakei</em></td>
<td>2</td>
</tr>
<tr>
<td><em>Fimbristylis cinnamometorum</em></td>
<td>5</td>
</tr>
<tr>
<td><em>Fimbristylis depauperata</em></td>
<td>2</td>
</tr>
<tr>
<td><em>Fimbristylis fimbristyloides</em></td>
<td>4</td>
</tr>
<tr>
<td><em>Fimbristylis furva</em></td>
<td>2</td>
</tr>
<tr>
<td><em>Fimbristylis hygrophila</em></td>
<td>2</td>
</tr>
<tr>
<td><em>Fimbristylis microcarya</em></td>
<td>2</td>
</tr>
<tr>
<td><em>Fimbristylis schultzii</em></td>
<td>2</td>
</tr>
<tr>
<td><em>Fimbristylis sp L.</em></td>
<td>2</td>
</tr>
<tr>
<td><em>Fimbristylis variegata</em></td>
<td>1</td>
</tr>
<tr>
<td><strong>Outgroup</strong></td>
<td></td>
</tr>
<tr>
<td><em>Actinoschoenus compositus</em> (provisional)</td>
<td>4</td>
</tr>
<tr>
<td><em>Arthrostyles aphylla</em></td>
<td>4</td>
</tr>
<tr>
<td><em>Schoenoplectiella laevis</em></td>
<td>5</td>
</tr>
<tr>
<td><em>Schoenoplectiella lateriflora</em></td>
<td>5</td>
</tr>
<tr>
<td><em>Schoenoplectus tabernaemontani</em></td>
<td>3</td>
</tr>
<tr>
<td><em>Trachystylis stradbroakensis</em></td>
<td>7</td>
</tr>
</tbody>
</table>
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.
*bobata*, *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.
*bobata* 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.
Stipe length/nut length
Inflorescence: primary ‘anthela’
Glume shape: ovate
Nut width

Culm glabrous
Glume back glabrous

Stamens: 3

Inflorescence: hemispherical
Glume shape: trullate
Nut epidermis: reticulate
Nut cell outline: isodiametric

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 Bulboystis 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. burbridgeae 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 Bulbostyliis. OTUs form six groups, the putative species $B$. sp. aff. $b$.barbata is clearly separated from $B$. $b$.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. burbridgeae), 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. burbridgeae OTU group. However, the dissimilarity of baffpu to OTUs of B. burbridgeae is present in the phenogram.

Discrete groups of OTUs were retrieved as the species groups B. sp. aff. barbata, B. barbata, B. pyriformis, B. burbridgeae 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).

Bulboystis 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 ($\beta = -0.1$) 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. burbridgeae group

Subset analysis of the B. turbinata–B. sp. aff. burbridgeae group of OTUs indicates that B. sp. aff. burbridgeae 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. burbridgeae, B. densa, B. sp. aff. densa 1, B. sp. aff. densa 2 (African amphicarpic), B. sp. aff. burbridgeae, 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. burbridgeae* (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. burbridgeae* (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. burbridgeae–B. hispida 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. burbridgeae–B. sp. aff. burbridgeae* 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.
Bootstrap support (73%) for the terminal branch *B. aff. burbridgeae* and *B. burbridgeae* 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. burbridgeae*; these spikelets have similar morphology to the aerial spikelets. Scale=10 mm. See Table 5.1 and Appendix 1 for OTU and specimen details.
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 burbridgeae 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 burbridgeae* group. A. *B. burbridgeae* (bbu5) with *B.* epidermis at higher magnification; C. *B.* sp. aff. *burbridgeae* (baffbu); with D. epidermis at higher magnification; E. *B.* sp. aff. *puberula* 1 (baflipu) 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. burbridgeae* (baflbu) 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. burridgeae* (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 bbal. 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 C₄ 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 *Fimbristyli*s 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 *Fimbristyli*s 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 synonymy 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. burbridgeae*, *B. sp. aff. puberula* and *B. burbridgeae*, 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 Guaglione (1970), have also been described for some species of *Schoenoplectus* (e.g. *S. californicus*) 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* Cherms. (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. funkii* (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.), *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* (bafid2: 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. burbridgeae*, 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* (Rotb.) C.B.Clarke
Basionym: *Scirpus barbatus* Rotb.
*B. eustachyi* Eardley

2. *Bulbostylis burbridgeae* K.L.Wilson

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) Lyne
*Abildgaardia striatella* (C.B.Clarke) Lyne


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. burbridgeae*, 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 Lyé (in Haines and Lyé 1983) placed *Bulbostylis* as a subgenus within *Abildgaardia*, although both authors have since reverted to using *Bulbostylis* at the generic rank (Lyé 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.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>No. specimens sampled</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Ingroup</strong></td>
<td></td>
</tr>
<tr>
<td><em>Abildgaardia macrantha</em> (provisional)</td>
<td>10</td>
</tr>
<tr>
<td><em>Abildgaardia mexicana</em></td>
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</tr>
<tr>
<td><em>Abildgaardia odontocarpa</em> (provisional)</td>
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</tr>
<tr>
<td><em>Abildgaardia ovata</em></td>
<td>13</td>
</tr>
<tr>
<td><em>Abildgaardia oxytachya</em> (provisional)</td>
<td>13</td>
</tr>
<tr>
<td><em>Abildgaardia pachyptera</em> (provisional)</td>
<td>11</td>
</tr>
<tr>
<td><em>Abildgaardia schoenoides</em></td>
<td>12</td>
</tr>
<tr>
<td><em>Abildgaardia triflora</em></td>
<td>4</td>
</tr>
<tr>
<td><em>Bulbostylis barbata</em></td>
<td>20</td>
</tr>
<tr>
<td><em>Bulbostylis sp. aff. barbata</em></td>
<td>7</td>
</tr>
<tr>
<td><em>Bulbostylis burdigeae</em></td>
<td>5</td>
</tr>
<tr>
<td><em>Bulbostylis sp. aff. burdigeae</em></td>
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</tr>
<tr>
<td><em>Bulbostylis capillaris</em></td>
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</tr>
<tr>
<td><em>Bulbostylis densa</em></td>
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</tr>
<tr>
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<td>2</td>
</tr>
<tr>
<td><em>Bulbostylis sp. aff. densa 2</em></td>
<td>3</td>
</tr>
<tr>
<td><em>Bulbostylis hispidula subsp. pyriformis</em></td>
<td>3</td>
</tr>
<tr>
<td><em>Bulbostylis hispidula subsp. senegalensis</em></td>
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</tr>
<tr>
<td><em>Bulbostylis humilis</em></td>
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<tr>
<td><em>Bulbostylis puberula</em></td>
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</tr>
<tr>
<td><em>Bulbostylis sp. aff. puberula</em></td>
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</tr>
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<td><em>Bulbostylis pyriformis</em></td>
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<tr>
<td><em>Bulbostylis turbinata</em></td>
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</tr>
<tr>
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</tr>
<tr>
<td><em>Bulbostylis sp. aff. turbinata 2</em></td>
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</tr>
<tr>
<td><em>Crosslandia anthelata</em> (provisional)</td>
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<tr>
<td><em>Crosslandia setifolia</em></td>
<td>18</td>
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<tr>
<td><em>Crosslandia spiralis</em> (provisional)</td>
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</tr>
<tr>
<td><em>Crosslandia vaginata</em> (provisional)</td>
<td>14</td>
</tr>
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<td><em>Fimbristylis bahiensis</em></td>
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<tr>
<td><em>Fimbristylis blakei</em></td>
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<tr>
<td><em>Fimbristylis cinnamometorum</em></td>
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<tr>
<td><em>Fimbristylis depauperata</em></td>
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<td><em>Fimbristylis fimbristyloides</em></td>
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</tr>
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<td><em>Fimbristylis furva</em></td>
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<tr>
<td><em>Fimbristylis hygrophila</em></td>
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</tr>
<tr>
<td><em>Fimbristylis microcarya</em></td>
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</tr>
<tr>
<td><em>Fimbristylis schultzii</em></td>
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<td><em>Fimbristylis variegata</em></td>
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</tr>
<tr>
<td><em>Nelmesia melanostachya</em></td>
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</tr>
<tr>
<td><em>Nemum equitans</em></td>
<td>2</td>
</tr>
<tr>
<td><em>Nemum megastachyum</em></td>
<td>2</td>
</tr>
<tr>
<td><em>Nemum spadiceum</em></td>
<td>4</td>
</tr>
<tr>
<td><em>Tylocarya cylindrostachya</em></td>
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</tr>
<tr>
<td><strong>Outgroup</strong></td>
<td></td>
</tr>
<tr>
<td><em>Actinoschoenus compositus</em> (provisional)</td>
<td>4</td>
</tr>
<tr>
<td><em>Arthrostylis aphylla</em></td>
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</tr>
<tr>
<td><em>Schoenoplectilla laevis</em></td>
<td>5</td>
</tr>
<tr>
<td><em>Schoenoplectilla lateriflora</em></td>
<td>5</td>
</tr>
<tr>
<td><em>Schoenoplectus tabernaemontani</em></td>
<td>3</td>
</tr>
<tr>
<td><em>Trachystylis stradbroakensis</em></td>
<td>7</td>
</tr>
</tbody>
</table>
(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 analysis 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 ‘Arthrostylelidae’, 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 Arthrostylelidae, formed a broad clade sister to the outgroup species of *Schoenoplectus*, with strong branch support indicated (Bootstrap=87%) (Figure 6.1). *Arthrostyles aphylla* and *Actinoschoenus compositus*...
were nested with the species *F. variegata* and the C₄ *Fimbristylis bahiensis*, and were sister to the F3–*Abildgaardia–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 synapomorphies 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 prophyll 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 (tubercules), 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 (*Arthrotylis*, *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* (fl2) 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. schultzei* (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 surface 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 homoplasic 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 *Tylocarya* 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 Goetghhebeur (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 C₄ fimbristyloid photosynthetic pathway. The C₃ photosynthetic pathway arises several times amid the ingroup in the tribal analysis, and taxa with C₃ anatomy (Arthrostylis aphylla, Actinoschoenus compositus, Fimbristylis variegata and Trachystylis stradbrokensis (Figure 6.11) are placed with C₄ 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 C₄ 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 Metcalf 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 ‘Arthrostyliadeae’ selected as outgroup taxa for use in cladistic analysis, showing the typical outlines, arrangement of sclerenchyma strands per vascular bundle, and C₃ 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 *Arthrostyle*, and the species of *Fimbrystylis* (see Figures 6.9-10 and 6.11-12). Clearly, *Arthrostyle*, *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 *Fimbrystylis*.

Species of *Bulbostylis* and *Fimbrystylis* in clade A of this study are all C₄ 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 C₃ taxa that occur within the predominantly C₄ 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 C₃ and C₄ species in the genus (Stock et al. 2004), however, Bruhl and Wilson (2005, in press) suggest that the C₄ *S. pulchella* sampled by Stock et al. may be misidentified, as all other species of *Schoenoplectus* are reportedly C₃. The species of *Shoenoplectus* and *Schoenoplectiella* sampled in this study i.e. *Schoenoplectus tabernaemontani* (= *S. validus*), *Schoenoplectiella lateriflora* (= *Schoenoplectus lateriflorus*) and *Schoneoplectiella laevis* (= *Schoenoplectus laevis*) are all C₃ taxa. Alternatively, *Schoenoplectus pulchella* may be misplaced. The study by Bruhl and Wilson (2005, in press) reports the presence of C₃ and C₄ species in *Abildgaardia*. However, *A. hygropyhila* is the only C₃ species currently accepted in the genus, and is misplaced in *Abildgaardia* (see Chapter 4). Future studies in *Fimbrystylis* could determine if C₃ species such as *Fimbrystylis variegata* (with a Schoenus-type embryo and a prior history with *Abildgaardia*) should be removed
from *Fimbristylis* that is currently accepted as containing both C₃ and C₄ 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 trnL-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 intraprophylar 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 *Nelmesia*, 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 C₃ 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 *Nenum 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 *Nenum* 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. *Nelmiesia* 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 C₃ 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 squarrulosana* (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 Fimbrystylideae 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.
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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.

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**Fimbristylis spiralis R.Br.**

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**Abildgaardia Vahl**

**Abildgaardia baeothryon A.St.-Hil.**

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(all as *Fimbristylis bahiensis* #+ Steud.)

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**Abildgaardia mexicana**  
(Palla) Kral

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S.T.Blake

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**Abildgaardia ovata**  
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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 (papyry, 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 (papyry, 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 abruptly 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 (banseniform)
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 than 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 midrib

28. Leaf and culm anatomy type of vascularisation [27; 26]
   1. C₄ fimbristyloid (primary and secondary bundles have PCR tissue interrupted laterally by the metaxylem vessel elements, the mestome sheath complete and surrounded by PBS)
   2. C₄ 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 C₄ 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. C₄ has either fimbristyloid, chlorocyperoid, eleocharoid, or rhynchosporoid type

   Fimbristyloid C₄ 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 C₄ 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 C₄ 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 C₄ 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 <i>Schoenoplectus</i> and <i>Arthrostyle</i>
      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 around 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
       <i>Fimbristylis microcarya</i>)
10. irregular quadrangle 4 sides, with the parallel sides having one shorter than the other (see *Arthrostylis aphylla*)
11. transversely 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 rectangular)
   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)

   follows Metcalf 1971

50. Culm vascular bundles
   1. not fully immersed within the chlorenchyma tissue as all protrude into the pith (especially evident in C3 culms)
2. younger vascular bundles immersed within the chlorenchyma tissue while mature bundles protrude into the pith (especially evident in C₄ 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 indicates 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 *Fimbristyris 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, Cof1 + Cof2 (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 (Cof2) and their sessile lateral branches (Cof13)}
11. terminal 'head' from many sessile spikelets formed from lateral rays (Cof1) and ramification from intraprophylar growth (as in Bulbostylis barbata)
12. pseudolateral digitate sessile or on lengthened epipodia (reduced paniculodium)
13. second order pseudolateral digitate lateral and intraprophylar growth (paniculodium)

Synflorescence structures in this study are based on the premise of consistent reduction ie paracaldia 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 Cof1 includes solitary and simple anthelas)
2. secondary (HF2 lateral florescence growth arising from primary florescence parts with its own lateral growth)
3. secondary intraprophylar (growth from within primary prophylls)
4. tertiary (HF3 lateral florescence growth arising from secondary florescence parts with its own lateral growth)
5. tertiary intraprophylar (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. Cof1) 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 severely 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 *Fimbristyliis 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 abruptly)
   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 narrowly 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)
1. narrowly triangular (6:1 to 3:1 wide at base to pointed apex)
2. smoothly linear (glumes tightly imbricate - 12:1 narrower than narrowly oblong sides even)
3. 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, Arthroystis, 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 Bulbosyris and Schoenoplectiella.

75. Basal spikelet sex (excluding lowest empty glumes whether) 
1. hermaphrodagamous (bisexual [perfect] florets only in spikelet)
2. gynohermaphroditic (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 glume 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 antorse 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 (thinner 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 chartaceous as is more flexible but damaged with forceps (as in *Actinoschoenus*)

5. chartaceous (thinner 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. mucromulate (1:1 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 0.3 mm 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. spatulate

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 abruptly 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 (decussate but ascending minutely acropetally as seen in Bulboystylis
      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 0.2 mm)
   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 (apparently, 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
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
1. persistent (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 style base (indumentum cover) whether
1. absent as style base is glabrous (at least appearing so)
2. occasional fimbriola
3. sparse fimbriola occurring near style base to nut abscission zone
4. dense fimbriola 40–120 μm

130. Aerial nutlet length [124°]
1. less than 0.65 mm
2. 0.65 to 1.3 mm
3. 1.35 to 2.0 mm
4. greater than 2 and less than 3 mm
5. greater than 3 less than 4.5 mm

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 umbo-bonate)
8. obamulliformis (compressed in 3-dimensions - apex somewhat elliptic with slight contraction 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. obtullate (3:2)
11. widely obtullate (6:5)
12. very widely obtullate (1:1)
13. napiform (more tapered than obtullate 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. capitata (head like as in A ovata as stipe forms neck)
17. strongly capitata (where nut severely 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 transversely 1 by 1 (or 1 by 2)
7. transversely narrowly oblong (20 x 60 \(\mu\)m to 20 x 120 \(\mu\)m)
8. transversely rectangular 40 x 60 \(\mu\)m (in distinct longitudinal rows)
9. transversely rod-shaped having tapered ends (walls straight)
10. longitudinally oblong (40 x 20\(\mu\)m)
11. longitudinally narrowly oblong 6:1 (120 x 20 \(\mu\)m), 3:1 (60 x 20 \(\mu\)m)
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 \(\mu\)m 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 \(\mu\)m 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. transversely oblong cells in indistinct longitudinal rows
16. transversely 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. subpuncticulate (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. Nenum-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 Nenum 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).

<table>
<thead>
<tr>
<th>Ingredients</th>
<th>Quantities</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distilled water</td>
<td>35 mL</td>
</tr>
<tr>
<td>Glycerin</td>
<td>30 mL</td>
</tr>
<tr>
<td>Gelatin</td>
<td>10 g</td>
</tr>
<tr>
<td>Phenol – crystalline (preservative)</td>
<td>1 g</td>
</tr>
</tbody>
</table>

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.