A morphological comparison between *Digitaria coenicola* and *D. divaricatissima* (Poaceae: Paniceae)

Heather Stewart[1] and Neville Walsh[2]

[1] School of Botany, University of Melbourne, Victoria 3010, email: heather.stewart@dse.vic.gov.au
[2] Royal Botanic Gardens, Private Bag 2000, South Yarra, Victoria 3141, email: Neville.Walsh@rbg.vic.gov.au

Abstract

Morphometric analysis supports the inclusion of *Digitaria coenicola* (F. Muell) Hughes within *D. divaricatissima* (R. Br.) Hughes. *Digitaria macractinia* (Benth.) Hughes, previously regarded as synonymous with *D .divaricatissima* is resurrected as a variety *D. divaricatissima* var. *macractinia*.

Keywords: taxonomy, tufted grasses, species differentiation

Introduction

Digitaria Haller, with around 218 species (Vega *et al.* 2009) is the third most speciose genera within tribe Paniceae (after *Panicum* L. c. 470 species, *Paspalum* L. c. 330 species; Clayton & Renvoize 1986). *Digitaria coenicola* (F. Muell.) Hughes and *D. divaricatissima* (R.Br.) Hughes belong to the entirely Australian section *Pennatae*, which includes those species with inflorescences having whorled branches at the lowest node and spikelets absent from the lower 1/3 of those branches. The other species of the section are *D. ammophila* (Benth.) Hughes*, D. basaltica* B.K.Simon, *D. benthamiana* Henrard, *D. hystrichoides* Vickery, *D. nematostachya* (F.M.Bailey) Henrard, *D. papposa* (R.Br.) P.Beauv., and *D. porrecta* S.T.Blake.

As currently delimited, *Digitaria coenicola* and *D. divaricatissima* are perennial, tufted grasses (Walsh & Entwisle, 1994). They occur in semi-arid, temperate and subtropical areas, mainly in central and eastern Australia. In Victoria, these species occur in grasslands and grassy woodlands of the Wimmera and Riverina regions (Conn 1992), with general localities including Dimboola, Charlton, Mitiamo, Dookie and Springhurst. They are distinguished from other *Digitaria* species in that they have relatively long (≥3.5 mm) spikelets and inflorescences of unbranched, radially arranged racemes devoid of spikelets toward their bases (Sharp & Simon 2002).

Whether these two species are clearly distinct has been a source of some conjecture. Walsh (1994) noted that the two species are separable by the width and hairiness of the space between the midrib of the lower (sterile) lemma and the adjacent longitudinal nerve. However it was further noted that some specimens have lemmas with both hairy and glabrous internerve spaces. Webster (1984) noted that the separation of the two species based on these characters is 'rather artificial in that these characters are highly correlated'. He later noted (Webster 1987) that *D. coenicola* 'is closely related to *D. divaricatissma*' but persisted in using the width and hairiness of the internerve space to separate the species, as have subsequent treatments (e.g. Harden 1993, Sharp and Simon

2002; Simon *et al. ined.*). Other characters traditionally used to separate the species include the length of the upper glume compared to lower lemma, the presence of hairs in the primary branch axil, the number of nerves on the lower lemma and the degree of hairiness of the vegetative structures (Hughes 1923; Henrard 1950).

Victorian populations have been referred to as both *Digitaria divaricatissima* and *D. coenicola*. However they are all currently recognised as *D. divaricatissima* which is regarded as a vulnerable species in the state (Walsh & Stajsic 2007). Should both taxa be accepted as occurring in Victoria, the conservation status of either is likely to be more critical, so an accurate assessment of the taxonomy is desirable before conservation plans for the populations can be developed.

This study seeks to evaluate the characters used to differentiate the two species and arrive at a practical, applicable taxonomy for the taxa.

Materials and Methods

Measurements were obtained from 39 *D. divaricatissma* and 37 *D. coenicola* specimens from the National Herbarium of Victoria (MEL), and specimens collected fresh in the course of this study. Measured specimens included types of *D. coenicola*, *Panicum divaricatissima* R.Br. var. *glaberrima* Benth, and *Panicum macractinium* Benth., the latter two taxa currently regarded as synonyms of *D. divaricatissima* (Simon *et al. ined.*). As far as possible, specimens used were those that had recent,

Figure 1. Distribution of the herbarium specimens analysed; *Digitaria coenicola* (circles) and *D. divaricatissima's* (triangles) ranges.

authoritative determinations by recognised experts (e.g. R.D. Webster or B.K. Simon). Specimens were selected to cover the geographic range of the taxa (Fig. 1).

D. coenicola and *D. divaricatissima* are not geographically disjunct although *D. coenicola* is generally regarded as having a more westerly distribution than *D. divaricatissima*, such that only the former is recognised in WA, NT and SA and only the latter in Vic.

A list of the most definitive quantitative and qualitative traits used in published treatments (e.g. Wheeler *et al.* 1982; Harden 1993; Webster 1987; Sharp & Simon 2002; Simon *et al. ined.*) to separate the species was compiled (appendix 1). Initially, 29 characters were measured. Once these characters were analysed in PATN software, 11 were excluded because they did not contribute to the separation of the data between the species. Measurements were taken using either a Leica M80 dissecting microscope or Olympus SZX16 microscope with measurement accuracy to 0.01 mm. Detailed images of spikelet features were captured electronically via an Olympus DP71 camera.

Analysis

All quantitative data were entered into a data matrix in PATN v3 (Belbin 2004). PATN software employs a Gower's (1971) association co-efficient to unite most similar elements into groups. Utilising these groupings, a dendrogram was produced to determine the groups' statistical support. An ordination illustration was compiled to represent the relationship between the two species. From this, Kruskal Wallis values were obtained for every character to identify those that were most useful in discriminating groups.

All qualitative traits were entered into Microsoft Excel and a series of graphs comparing these characters was compiled.

Results

Quantitative characters

PATN software separated the specimens into three groups in the dendrogram (Fig 2). One group comprised *D. divaricatissima* specimens only and the other two groups comprised of both *D. coenicola* and *D. divaricatissima* specimens. PATN based these three groupings on characters predominantly (in order of weight) primary branch length (Kruskal Wallis value 38.57), maximum leaf
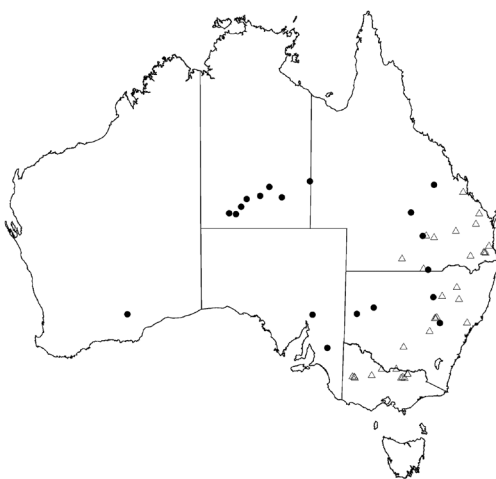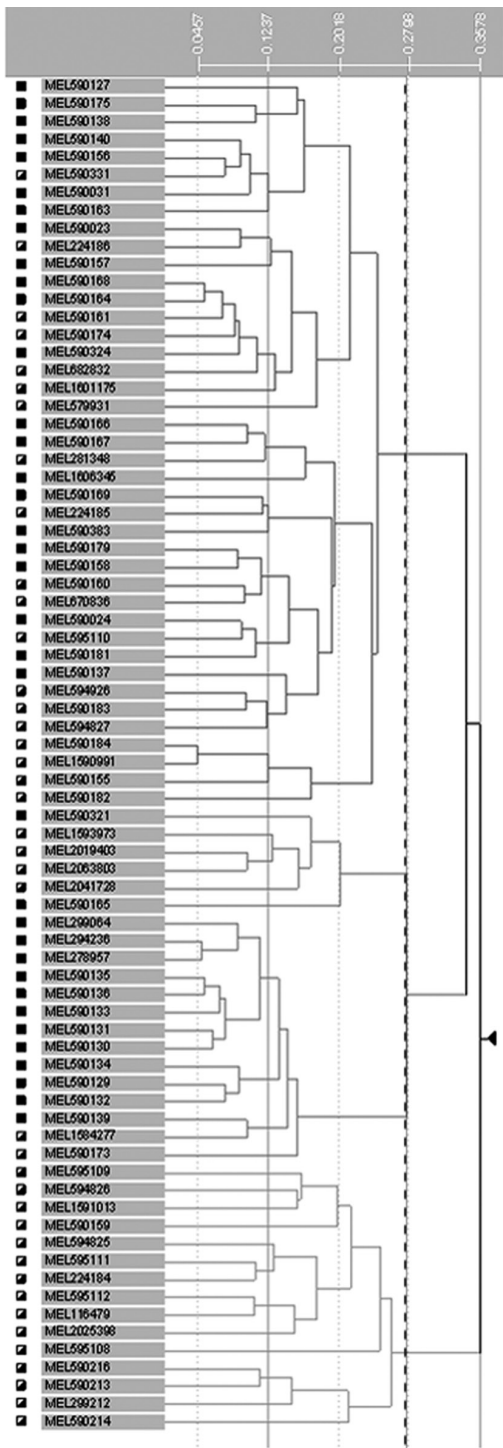
width (Kruskal Wallis value 37.42), anther length (Kruskal Wallis value 33.83), ratio of first to second lemmatal internerve width (Kruskal Wallis value 25.88) and first internerve width (Kruskal Wallis value 23.87).

As shown in Fig 3, the PATN ordination (stress value 0.1632) does not display any clear groupings or separations of *D. coenicola* and *D. divaricatissima*. Whilst specimens determined as *D. coenicola* are generally located near the upper right portion of the ordination and the *D. divaricatissima* specimens are located near the lower left portion, there is too much overlap between the species to recognise distinct entities on the basis of this analysis. PATN has predominantly based this ordination on, (in order of weight), primary branch length, maximum leaf width, anther length, the ratio of the first to second internerve width and the first internerve width.

Qualitative characters

The two traits most commonly utilised to separate *D. divaricatissima* and *D. coenicola* are the width of the first versus second lemmatal internerve space and the hairiness of the first internerve space on the lower lemma. The *D. divaricatissima* spikelet shown in Fig. 4 is a 'typical' specimen, i.e. one that exhibits *D. divaricatissima* morphology in accordance with current circumscription of the species, exhibiting a glabrous first internerve space and a wider first compared to second internerve space on the lower lemma.
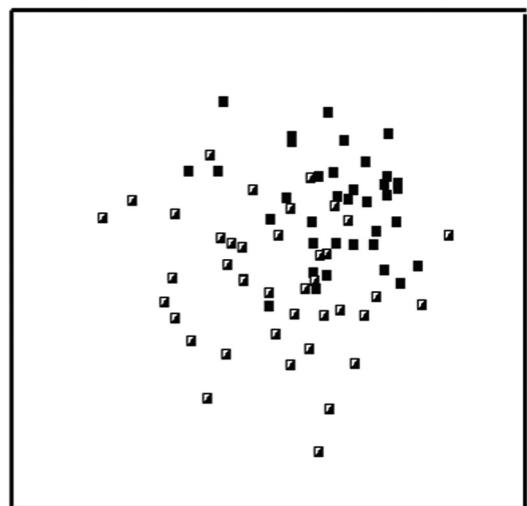
Figure 2. Dendrogram of Gower's association coefficients displaying *Digitaria divaricatissima* (diagonally divided squares) and *D. coenicola* (solid squares) specimens, based on 13 quantitative traits; groupings indicated at a similarity coefficient of 0.2798.

Figure 3. PATN ordination of *Digitaria divaricatissima* (diagonally divided squares) and *D. coenicola* (solid squares) specimens, based on 13 quantitative traits.

Figure 4. Typical spikelet of *Digitaria divaricatissima* (MEL 224184).

D. coenicola spikelets shown in Fig. 5a and 5b exhibit 'typical' *D. coenicola* morphology. These spikelets demonstrate equal lemmatal internerve spacing and a hairy first internerve space. Whilst some spikelets exhibited this morphology, many displayed contrasting morphological traits. The *D. coenicola* spikelet shown in Fig. 5c is a good example of the variation that can exist within the same spikelet. One half of the spikelet in Fig. 5c has sub-equal internerve spacing and the other possesses a distinctly wider first internerve space relative to the second. Similar to the variable internerve spacing shown in Fig. 5c, the hairiness of the first internerve can vary substantially, even within the same specimen. Many specimens were found to have hairy or glabrous first internerve spacing within the same inflorescence. Sometimes, individual spikelets had both hairy and glabrous first internerve spaces (Fig. 6).

To determine if other factors could enable species separation, simple scatter-plots were created using only the traits utilised in recent taxonomic treatments (e.g. width of lemmatal internerve space versus hairs in internerve space, the ratio of the first internerve to second internerve space, and whether either of these are correlated with leaf hairiness).

The width of the first lemmatal internerve varied greatly, from 0.08 mm to almost 0.19 mm. When *D. coenicola* and *D. divaricatissima* specimens first lemmatal internerve space width and hairiness are graphed, the specimens are not segregated nor does the graph display any clear trends (Fig.7a). When the ratio of first to second lemmatal internerve widths of *D. coenicola* and *D. divaricatissima* are graphed there is no clear distinction between species. When the hairiness of the internerve space is overlayed onto the same scatter plot there is no obvious difference between *D. coenicola* and *D. divaricatissima* specimens (Fig. 7b).

Digitaria divaricatissima and *D. coenicola* specimens also overlap with regard to leaf blade hairiness. Both have specimens with glabrous, hairy and mixed glabrous and hairy leaves. When leaf blade hairiness is combined with the ratio of the first to second internerve space width, the analysis still does not separate the species (Fig. 8).

Discussion

The current treatments of *D. coenicola* and *D. divaricatissima* present a number of inconsistencies that do not allow ready recognition of the two taxa. In this study we measured 13 different quantitative traits on 76 specimens. PATN did not separate the specimens into two groups, corresponding with *D. coenicola* and *D. divaricatissima*, but rather, into three groupings that did not accord well with the specimen's determinations or other patterns of morphology or distribution. Rather the results suggest these species are probably better recognised as a single, although variable species. To date, there have been no accounts formally suggesting the two species should be merged, although some (Walsh & Entwisle 1994; Webster 1987) have suggested that that the characters currently separating the species are highly inconsistent.

Species separation has traditionally been supported by qualitative traits. The four characteristics frequently used are (a) leaf blade hairiness, (b) first versus second lemmatal internerve width (a derived qualitative trait), (c) hairiness of the first lemmatal internerve and (d)

Figure 5. Typical spikelets of *Digitaria coenicola* a). (MEL 590127) and b). (MEL 590175). Non-typical spikelet of *Digitaria coenicola* c). (MEL 590158).

number of nerves on the lower lemma (often hard to determine accurately).

Hairy leaf blades have been typically associated with *D. coenicola*, whereas *D. divaricatissima* has glabrous leaf blades (Simon *et al. ined*.). Our observations indicate that this division is not always accurate. Many *D. divaricatissima* and *D. coenicola* specimens showed both glabrous and hairy leaf blades, whereas some possessed solely glabrous or hairy leaf blades. With such overlap between the degree of hairiness, this character does not support the retention of two species. We suspect that leaf blade hairiness is, at least in some cases, ontogenetic and perhaps also an ecotypic trait. Younger plants observed in the field (up to one year old) had long, dense hairs on leaf blades, whereas older plants (2

years plus) in the same population had either glabrous leaf blades or ones with much shorter, sparser hairs.

Digitaria coenicola is generally regarded as having a hairy first lemmatal internerve space while *D. divaricatissima* has glabrous first internerve spaces (e.g. Simon *et al. ined.)*. Our results were not so distinct. *D. coenicola* specimens had both hairy and glabrous internerve spaces, specimens of *Digitaria divaricatissima* with 'authoritative' determinations exhibiting similar variation. There were also individual spikelets on some specimens that displayed both hairy and glabrous first internerve spaces.

It has been commonly accepted that *D. coenicola* has equal lemmatal internerve spacing whereas *D. divaricatissima* has a larger first versus second internerve

Figure 6. Non-typical spikelets of *Digitaria divaricatissima* (MEL.590174, both spikelets from the same specimen).

space (e.g. Sharp & Simon 2002). When we measured all internerve spaces (to within 0.01 mm accuracy) we obtained different results to previous studies. For both species, all but two specimens had a larger first versus second internerve space. The majority of specimens had first lemmatal internerve spaces up to 1.75 times the width of the second internerve. This contrasts previous findings that record *D. coenicola* as having subequal inter-nerve spacing.

Specimens exhibit significant geographical variation. Key characters which are geographically variable are

lemmatal internerve spacing and the hairiness of the lower lemma. Whilst our results from the southern part of the species' range are highly variable, specimens from the Northern Territory (hitherto all identified as *D. coenicola*) are generally consistent with respect to the internerve spacing and hairiness of the lower lemma.

While scoring *D. divaricatissima* for the analysis, a number of specimens were observed with characteristics that distinguished them from all other specimens. Instead of the fine, spreading, sometimes tangled hairs on the intramarginal keels of the lemmas,
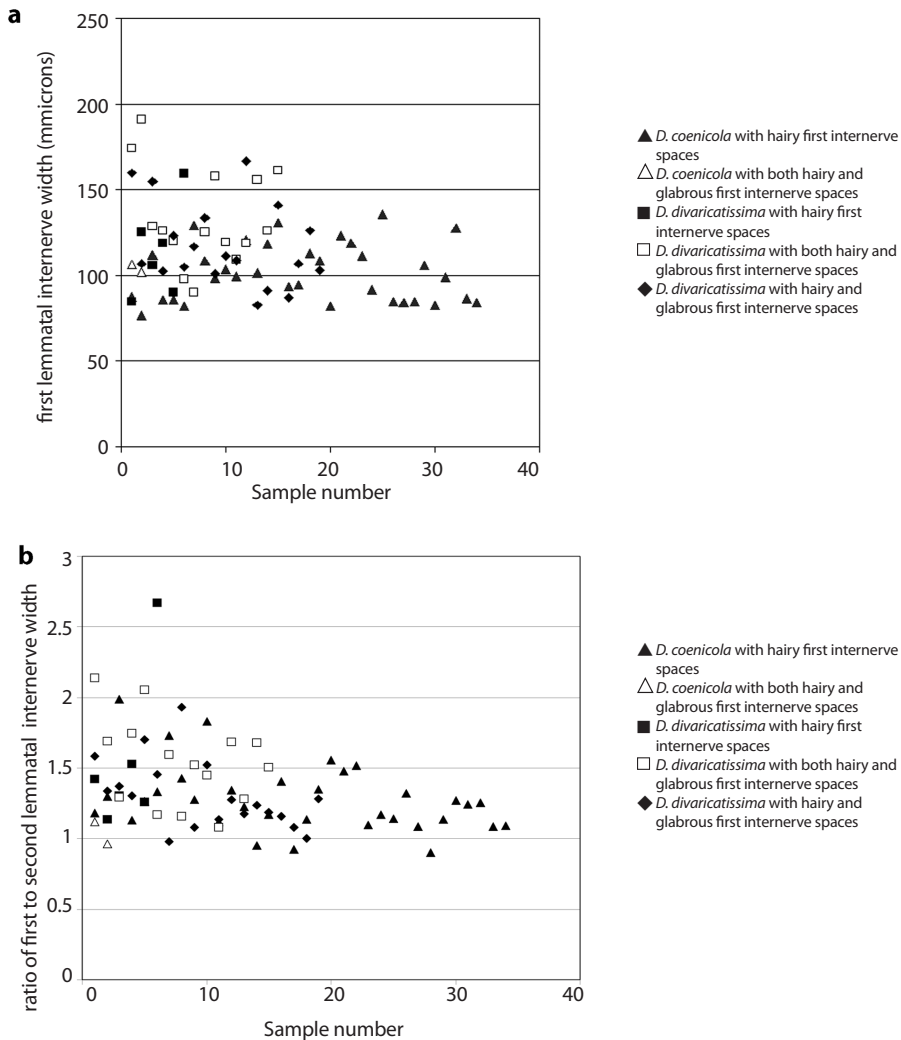

Figure 7. a). The width of the first lemmatal internerve space of *Digitaria coenicola* compared to *D. divaricatissima* specimens; b). The ratio of first to second lemmatal internerve space width of *Digitaria coenicola* compared to *D. divaricatissima* specimens. Specimens with the first internerve space hairy, glabrous or both are indicated. The X-axis does not indicate dimension, but the number (randomly) assigned to each specimen in this plot.

they possessed distinctive coarse, hollow, tubercle-based bristles (Fig. 9). This group of specimens also had less hairy leaves and primary branch axils than other specimens. All had glabrous internerves on the lower lemma. These match the type of *Digitaria macractinia* (Benth.) Hughes, a taxon synonymised with *D. divaricatissima* in contemporary treatments (e.g. Webster 1987; Sharp & Simon 2002; Simon *et al. ined*). Henrard (1950) and Webster (1984) discussed the significance of these bristles ('setaceous hairs' *sensu* Webster 1984) as taxonomic characters and indicated that they were produced in a number of not necessarily closely related species. Henrard (1950) used this character to recognise distinct taxa at specific or intraspecific rank, whereas Webster generally acknowledged it as occasional variation within species (although generally present in *D. ctenantha* (F. Muell.) Hughes) and not warranting further taxonomic recognition. Our observations found this highly distinctive character to be consistent within collections (unlike those characters previously employed to distinguish *D. coenicola* and *D. divaricatissima*) and we advocate taxonomic recognition of such plants. To date, we have only found material of this entity amongst specimens from Queensland.

The results of the numerical analysis, our examination of herbarium material and field populations suggest that *D. coenicola* should be regarded as synonymous with *D. divaricatissima* as outlined below. We propose that plants with hollow, tubercle-based bristles on the lower lemmas, previously referable to *D. macractinia* but subsequently included in *D. divaricatissima* be recognised again. We provide a new varietal combination for these, *Digitaria divaricatissima* var. *macractinia*. (Benth.) H.L.Stewart & N.G.Walsh.

Taxonomy

Digitaria divaricatissima (R.Br.) Hughes var. *divaricatissima Bull. Misc. Inform. Kew* 1923: 314 (1923)

Panicum divaricatissimum R.Br., *Prodr.* 192 (1810); *Leptoloma divaricatissima* (R.Br.) Chase, *Proc. Biol. Soc. Wash.* 29: 192 (1906). T: Port Jackson, *R.Brown Iter Australiense 6118*; holo: BM; iso: BRI, E, K (photo BRI).

Panicum divaricatissimum var. *glaberrimum* Benth. *in part*, *Fl. Austral.* 7: 468 (1878). T: Rockhampton and neighbourhood, *A. Thozet s.n.*; lecto (here chosen): MEL!; isolecto: BRI. Remaining syntype: Peak Downs, *Burkitt s.n.*; syn: K(photo BRI). Rejected type: Gracemere, *P.A.O'Shanesy* 1441 (MEL590177!, BRI).

Panicum divaricatissimum var. *normale* Benth., *Fl. Austral.* 7: 468 (1878). T: Keppel Bay, Qld, *R.Brown*; syn: BM; Port Jackson, N.S.W., *R.Brown*; syn: BM.
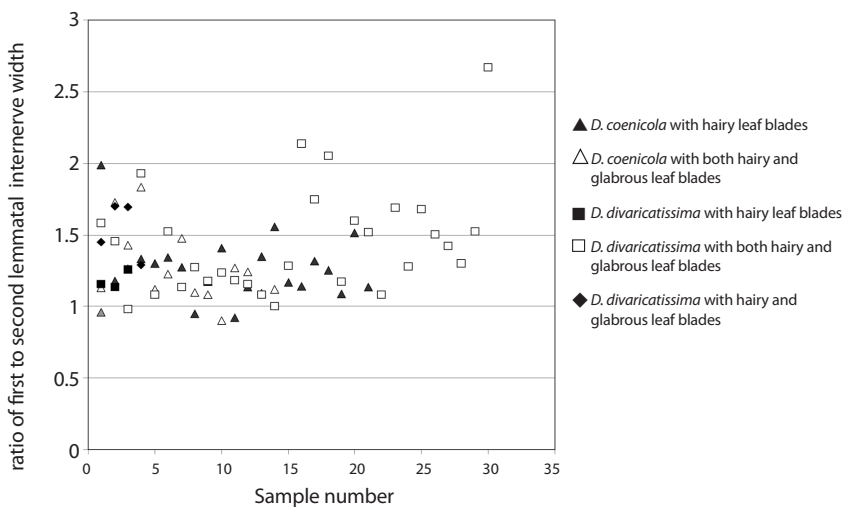

Figure 8. The ratio of first to second lemmatal internerve space width for *Digitaria coenicola* compared to *D. divaricatissima* specimens. Specimens with leaf blades hairy, glabrous or both are indicated. The X-axis does not indicate dimension, but the number (randomly) assigned to each specimen in this plot.

Figure 9. Typical spikelet of *Digitaria divaricatissima* var. *macractinia* (590214) with the upper glume removed.

D. divaricatissima (R.Br.) Hughes var. *dasyantha* Henrard, *Monogr. Digitaria* 199 (1950). T: Austr: haud rara, *Hugel s.n.*; syn: ?W; in Australia tropica, *Bauer s.n.*; syn: ?W.

Panicum tenuissimum var. *polychaeton* Domin*, Bibl. Bot.* 85: 296 (1915). T: Süd-Queensland: Tambourine Mountains, in den Regenwäldern, *K.Domin s.n., Mar*. 1910; holo: PR..

Panicum coenicola F.Muell., *Trans. & Proc. Roy. Soc. Victoria* 1: 45 (1855) as *coenicolum*; *Leptoloma coenicola* (F.Muell.) Chase, *Proc. Biol. Soc. Wash.* 19: 192 (1906). T: towards Morunde, and near Cudnaka, S.A., *F.Mueller s.n.*; holo; MEL!; iso: BRI, K.

D. macractinia (Benth.) Hughes subsp. *leichhardtiana* Henrard, *Monogr. Digitaria* 830 (1950). T: in railway enclosure, Blair Athol, Leichhardt District, Qld, 16 Mar. 1935, *S.T.Blake 8091 p.p.*; holo: L , iso: BRI, K.

D. macractinia (Benth.) Hughes var. *nudiflora* Henrard, *Monogr. Digitaria* 831 (1950). T: near Rockhampton on mid slopes of Mt Berserker, Qld, 6 Mar. 1937, *S.T.Blake 12721 p.p.*; holo: L; iso: BRI, K.

Shortly rhizomatous, more or less caespitose, perennial. *Culms* erect to decumbent, 20–70 cm tall, 2–7 noded. *Leaves*: sheaths hairy or glabrous; ligule 0.8-3.7 mm long; blades flat, 2–22 cm long, 2–7 mm wide, hairy or glabrous, scabrous. Primary branch axil with fine to dense hairs. *Racemes* 4–10, usually devoid of spikelets at base, long and rigid, simple, 5–36 cm long. Central axis 2–9 cm long. Pedicels 0.3–8.3 mm long, apices cupuliform. *Spikelets* 8–30 on a typical lowermost primary branch, hairy, paired, lanceolate or elliptical, 3.4–5.1 mm long, 0.9-1.4 mm wide; lower glume 0.4-1.6 mm long, ovate oblong, elliptical or triangular, 0-1 nerved, membranous, smooth, glabrous, acute to obtuse or rounded to cleft rounded; upper glume 1.7–5 mm long, as long as spikelet, triangular or lanceolate, 3-7 nerved, with ciliate or non-ciliate margins and sub-margins, hairy, villous, rounded, acuminate, or acute. *Lower floret*; lemma 3–5 mm long, hairy, with indumentum shorter than the spikelet, without hair tufts, with a hairy or glabrous first internerve space, with the first internerve space wider than the second or equal to the second, with margins or submargins glabrous, 5-7 nerved; palea vestigial, or absent. *Upper floret* shorter or subequal to the lower floret; lemma 2.9–5 mm long, brown, cartilaginous to indurate, muricate, lanceolate, acute to acuminate, mucronate, lanceolate, apiculate. *Umbrella Grass or Finger Panic Grass*.

Habitat and Distribution: Arid, semi-arid and drier temperate areas of all mainland States, but apparently rare in Western Australia.

Note on type: Bentham included O'Shanesy 1441 as a type of *P. divaricatissimum* var *glaberrimum*. We include this specimen in *P. divaricatissima* var *macractinia*.

Digitaria divaricatissima var. *macractinia* (Benth.) Heather L.Stewart & N.G.Walsh, comb. nov.

Panicum macractinium Benth., *Fl. Austral.* 7: 468 (1878); *Leptoloma macractinia* (Benth.) Chase, *Proc. Roy. Soc. Wash.* 19: 192 (1906); *Panicum divaricatissimum* R.Br. var. *macractinium* (Benth.) Domin, *Biblioth. Bot.* 85: 293

(1915); *Digitaria macractinia* (Benth.) Hughes, *Bull. Misc. Inform. Kew* 1923: 314 (1923). T: Herbert's Ck, *Bowman s.n.*; lecto: K; isolecto: BRI, MEL!, *fide* D.K.Hughes, *loc. cit.*

D. macractinia subsp. *muelleriana* Henrard, *Monogr. Digitaria* 865 (1950) *nom. inval* ,(this is the type variety as stated by Henrard *loc cit*).

Differing significantly from the typical variety only in the presence of a line of stiff, hollow bristles arising from a tuberculate ridge on the intramarginal keels of the lower lemma (Fig. 9). Furthermore, all specimens examined to date have glabrous internerves on the lower lemma, and spikelet length is in the upper range of measurements for the species (4.0–5.1 mm long).

Representative specimens: **QUEENSLAND**: Warwick, *H.Beckler s.n., s.d.* (MEL); Rockhampton, *P.A.O'Shanesy, s.n., s.d.* (MEL); New Holland, *Banks & Solander*, 1770 (MEL595109); Gracemere, 4.i.1874, *P.A.O'Shanesy 1441* (MEL); Between Lanefield and Rosewood, 12.iv.1930, *C.E.Hubbard 2134* (K, MEL); Between Laidley and Forest Hill, 28.ix.1930, *C.E.Hubbard 5350* (K, MEL594826); Wington Island, NE of Mackay, *A.R.Bean 16690 & I.G.Champion* 26.vi.2000 (BRI, MEL305885).

Habitat and Distribution: Known to us only from Queensland, from scattered localities between Mackay and Ipswich areas, up to about 100 km inland, but undoubtedly commoner than our records suggest as we have not had the opportunity to examine material from other Australian herbaria. Collectors' notes indicate that it grows on 'heavy black soil' and 'sand or coral rubble' in open country and in 'littoral rainforest and strand communities'.

Notes: Henrard (1950, pp. 864, 865) indicates that his *D. macractinia* subsp. *muelleriana*, is the 'typical form'. The other 2 infraspecific entities (subsp. *leichhardtiana* and var. *nudiflora*) lack bristles on the lemmas and are regarded as the typical variety of *D. divaricatissima*.

Further collections of this possibly rare taxon are required for an accurate assessment of its conservation status. We encourage field workers to note consistency of the characters outlined above, so that its rank may more confidently be reviewed if required.

References

Belbin, L. (2004). *PATN. Pattern analysis package* (version 3.02), CSIRO: Canberra.

Clayton, W. and Renvoize, S. (1986). *Genera Graminum: grasses of the world*. Royal Botanic Gardens Kew **13**, 1–389.

Conn, B.J. (1992). 'Vegetation and natural regions of Victoria' in D.B. Foreman & N.G. Walsh (eds), *Flora of Victoria* vol. 1. pp 79–158. Inkata Press: Melbourne.

Gower, J.C. (1971). A general coefficient of similarity and some of its properties. *Biometrics* **27**, 857–871.

Harden, G.J. (1993). *Flora of New South Wales*, vol. 4. NSW University Press: Sydney, Australia.

Henrard, J.T. (1950). *Monograph of the genus* Digitaria, Universitaire Pers. Leiden: Netherlands.

Hughes, D. (1923). The Genus *Panicum* of the *Flora Australiensis*. *Bulletin of Miscellaneous Information* **9**, 305–14.

Sharp, D. and Simon, B. (2002). *AusGrass: Grasses of Australia*. CSIRO Publishing: Collingwood, Victoria, Australia.

Simon, B.K., Weiller, C.M. and Webster, R.D. *ined*., *Flora of Australia* Volume 44B, Poaceae 3. CSIRO Publishing/ Australian Biological Resources Study (ABRS): Canberra, Australia.

Vega, A., Rua, G., Fabbri, L. and Rugolo de Agrasar, Z. (2009). A morphology-based cladistic analysis of *Digitaria* (Poaceae, Panicoideae, Paniceae), *Systematic Botany*. **34**, 312–323.

Walsh, N.G. (1994). '*Digitaria* (Poaceae)' in Walsh, N.G. and Entwisle. T.J. (eds), *Flora of Victoria* vol. 1, pp. 606–610. Inkata Press: Melbourne, Australia.

Walsh, N.G. and Stajsic, V. (2007). *A census of the vascular plants in Victoria*, edn 8. Royal Botanic Gardens Melbourne: Victoria.

Webster, R.D. (1984). A revision of the genus *Digitaria* Haller (Paniceae: Poaceae) in Australia. *Brunonia* **6**, 131–216.

Webster, R.D. (1987) *The Australian Paniceae (Poaceae)*. J. Cramer: Berlin.

Wheeler, D.J., Jacobs, S.W. and Norton, B.E. (1982). *Grasses of New South Wales*. University of New England: Armidale, Australia.

Appendix 1

Table of all characters measured. The 13 characters in bold were used in the final quantitative analysis, the 5 italicised characters were utilised in qualitative analysis. The remaining 11 were excluded when PATN analysis demonstrated they did not contribute at all to the species separation or amalgamation.

Characters	Measurements/states
Blade	
Maximum width	mm
Hairiness	glabrous, sparse or dense
Cataphyll length	mm
Ligule	
Maximum length	mm
Sheath	
Hairiness	glabrous, sparse or dense
Primary branches	
Maximum length	mm
Hairiness of axil	glabrous, very fine, fine or hairy
Scabrosity	glabrous or scabrous
Inflorescence	
Maximum length	mm
Pedicel	
Maximum length	mm
Spikelet	
Maximum length	mm
Minimum length	mm
Maximum width	mm
Shape	lanceolate or elliptical
Hairiness	glabrous, appressed, semi-appressed or wooly
Lower/outer/first glume	
Length	mm
Shape	ovate, lanceolate, triangular, truncate top
Number of nerves	0 or 1
Upper/inner/second glume	
Maximum length	mm
Minimum length	mm
Number of nerves	
Hairiness of margins	appressed, semi-appressed, woolly
Lemma	
Maximum length	mm
Minimum length	mm
Number of nerves	
Hairiness of internerve space adjacent to mid-nerve	glabrous, hairy
Width of internerve space adjacent to mid-nerve	mm
First vs second internerve width	equal, bigger or smaller
Anther length	mm