Two new species of *Enteropogon* Nees (*Poaceae*: *Chloridoideae*: *Cynodonteae*: *Eleusininae*) for northern Australia

E.J. Thompson

Summary

Thompson, E.J. (2023). Two new species of *Enteropogon* Nees (Poaceae: *Chloridoideae*: *Cynodonteae*: *Eleusininae*) for northern Australia. ***Austrobaileya* 13: 51−93**. Two new species, *Enteropogon pubifolius* E.J.Thomps. and *E. scabrilemma* E.J.Thomps., with morphological similarities to *E. paucispiceus* (Lazarides) B.K.Simon and *E. macrostachyus* (Hochst. ex A.Rich.) Munro ex Benth., respectively, are described and illustrated. *Enteropogon pubifolius* differs from other Australian species by a combination of characteristics including the pubescent, broader basal leaves, and *E. scabrilemma* by the scabrid broader lemmas and inflorescences with usually one or two rigid racemes. Some morphological characters used to identify Australian species of *Enteropogon* were found to be variable and consequently, a new modified key was developed to reduce potential ambiguity. Results from phenetic analyses of 43 morphological characters were used to explore hypotheses for the taxonomic relationships of the species.

Key Words: Poaceae; *Chloridoideae*; *Cynodonteae*; *Eleusininae*; *Chloris*; *Enteropogon*; *Enteropogon dolichostachyus*; *Enteropogon macrostachyus*; *Enteropogon paucispiceus*; *Enteropogon pubifolius*; *Enteropogon scabrilemma*; flora of Australia; flora of Queensland; taxonomy; new species; identification key; anatomy; micromorphology; cork cells; paraligule; stipe

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Introduction

The chloridoid genus *Enteropogon* Nees is represented by 17 species, commonly known as windmill grasses, distributed across Africa, Asia and Australia (Stapf 1934; Watson & Dallwitz 1992; Nightingale *et al.* 2005; Peterson *et al*. 2015; Simon & Alfonso 2022; Tropicos 2022). Six species have been recorded for Australia, four of which are endemic. Two of the Australian species are exclusively tropical, including *Enteropogon dolichostachyus* (Lag.) Keng ex Lazarides, a species that is also recorded across parts of Asia. Two species occur along the Australian central east coast including *Enteropogon unispiceus* (F.Muell.) Clayton that is also found in Taiwan and the Cook Islands. The other two species are widespread across the Australian arid and semi-arid zones (Lazarides 1972; Nightingale *et al.* 2005; Simon & Alfonso 2022; **Map 1**).

The taxonomic composition of *Enteropogon*, formerly included in *Chloris* Sw., has changed somewhat since its initial description. New species or combinations in *Enteropogon* (*E. coimbatorensis* K.K.Nair, S.K.Jain & M.P.Nayar, *E. paucispiceus* (Lazarides) B.K.Simon and *E. ramosus* B.K.Simon) have occurred (Nair *et al*. 1977; Simon 1984), and several species were segregated into two genera *Tetrapogon* Desf. and *Enteropogonopsis* Wipff & R.B.Shaw, (Lazarides 1972; Anderson 1974; Tothill & Hacker 1983; Jacobs & Highet 1988; Peterson *et al.* 2015). Characters used to distinguish *Enteropogon* and related taxa include leaf anatomy and micromorphology, and morphology of spikelets, inflorescences and leaf sheaths (Lazarides 1972; Carolin & Jacobs 1973; Anderson 1974; Tothill & Hacker 1983; Watson & Dallwitz 1992; Prendergast & Hattersley 1987; Wipff & Shaw 2018).

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Enteropogon, like most of the chloridoid grasses, exhibits Kranz anatomy but differs from the C_4 type known in *Chloris* (Prendergast & Hattersley 1987; Watson & Dallwitz 1992). Comparative micromorphology of chloridoid grasses that includes *E. dolichostachyus* have been presented by Anderson (1974) and Liu *et al*. (2010). Anderson (1974) provided illustrations of bicellular micro-hairs and silica bodies of several genera with morphological similarities to *Chloris*. Lemmatal micromorphology and scanning electron micrographs (SEMs) of chloridoid cork cells have been provided by several authors including Valdes-Reyna & Hatch (1991), Snow (1996) and Liu *et al*. (2010).

The breeding system of *Enteropogon* involves cleistogamy (self-fertilisation within a closed flower) (Campbell *et al*. 1983; Culley & Klooster 2007; Thompson 2021). *Enteropogonopsis chloridea* (J.Presl) Wipff & R.B.Shaw (syn. *Enteropogon chlorideus* (J.Presl.) Clayton) exhibits a very rare syndrome that involves subterranean spikelets borne on rhizomes (rhizanthogenes); these are morphologically differentiated from the spikelets in the terminal inflorescences that are chasmogamous as commonly found in the stereotypical grasses (Campbell *et al*. 1983). All Australian species of *Enteropogon* have terminal inflorescences with both cleistogamous and chasmogamous spikelets of similar morphology (Thompson 2021). The spikelets of *Enteropogon* disarticulate above the glumes and the diaspore consists of united florets (one or two fertile proximal and one sterile distal), with passive awns (Jurado *et al*. 1991; Watson & Dallwitz 1992; Cavanagh *et al*. 2019).

Recent curation of *Enteropogon* specimens held at the Queensland Herbarium (BRI) revealed two new species, *viz*. *E. scabrilemma* E.J.Thomps. and *E. pubifolius* E.J.Thomps., that are described here. The specimens of *E. scabrilemma* were stored under *E. dolichostachyus*, but the morphology of the spikelets more closely resembles *E. macrostachyus* (Hochst. ex A.Rich.) Munro ex Benth from tropical Africa. *Enteropogon scabrilemma* and *E. macrostachyus* differ from *E. dolichostachyus* by several characters including broader scabrid lemmas (**Table 1**). *Enteropogon pubifolius* was stored as an undetermined species differing most conspicuously by the hairy leaves, an unusual occurrence in the Australian species (Simon & Alfonso 2022). *Enteropogon pubifolius* is considered to have close morphological similarity to *E. paucispiceus* as they share some characters including basal leaves, a character used in the identification key to the Australian species of *Enteropogon* by Simon & Alfonso (2022) (**Table 1**).

Materials and methods

This study explores multiple hypotheses about the delimitation of species in *Enteropogon*, including some generated from phenetic analyses for the purpose of aiding accountability, repeatability and objectivity in taxonomic decision-making. The robustness of the hypotheses generated as a result of the analyses was tested using variations in data inputs. This study also reviews the morphological affinities and discriminating characters of the species and examines some distinctive characters of *Enteropogon* in the context of Poaceae.

Nomenclature, terminology and circumscription

Botanical nomenclature complies with Thompson (2022a) and Tropicos (2022).

General taxonomic concepts conform with Stuessy (2009), and *Enteropogon* species concepts follow those of Lazarides (1972) and Simon (1984).

Etymology follows Clifford & Bostock (2007).

General botanical terminology follows Harris & Harris (1994), Henslow (2009) and Beentje (2010). Terminology relating to inflorescences and spikelets follows Tothill & Hacker (1983), Jacobs *et al.* (2008), Gibson (2009) and Thompson (2021). The spikelet is a reduced inflorescence with florets subtended by bracts, *viz*. glumes, lemmas and paleas (Kellogg 2006; Endress 2010).

Most of the terminology relating to grass anatomy and micromorphology used here follows Ellis (1976, 1979) and Dengler *et al.* (1994). Bicellular micro-hairs have sometimes been referred to as salt glands as in the case of *Enteropogon macrostachyus* (Liphschitz & Waisel 1974; Jacobs 1986; Ceccoli *et al*. 2015). Diaspore stipe, lemma, rachilla and callus are depicted in **Fig. 1** for *Enteropogon* species. Diaspore stipe is defined as the portion of the diaspore from the distal tip of the callus to the junction of the rachilla and first lemma (**Fig. 1**). The chloridoid stipe has broad similarities to that found in some panicoid grasses but is distinct from a diaspore that is stipitate (Hitchcock 1950; Zuloaga 1986; Freckmann & Lelong 2003; Aliscioni *et al*. 2016; Zuloaga *et al*. 2018; Thompson & Fabillo 2021; Thompson 2022b,c). Due to a tendency for immature or aborted spikelets to have higher variability in size, shrinkage or distortion, spikelet measurements presented in the diagnoses were made from specimens with mature spikelets bearing caryopses.

Silica bodies (also referred to as phytoliths by some authors), stomata, trichomes (such as bicellular micro-hairs), prickles and hooks were classified using information provided by Ellis (1979), Amarasinghe & Watson (1990), Watson & Dallwitz (1992), Renvoize (2002), Rugolo de Agrasar & Vega (2004) and Neumann *et al*. (2017).

Cork cells, comprising a silica body and lid, on first lemmas were evaluated using four criteria *viz*., spacing, separation, size and shape (Metcalfe 1960; Ellis 1979; Valdes-Reyna & Hatch 1991; Acedo & Llamas 2001; **Fig. 2**). Metcalfe (1960) and Ellis (1979) reported cork cells on leaves and Valdes-Reyna & Hatch (1991) and Acedo & Llamas (2001) studied cork cells on lemmas, with the latter authors using characters including shape, density and length.

Classification of epicuticular wax follows Barthlott *et al.* (1998) and Ortunez & de la Fuente (2010). The paraligule is defined here as a row of hairs behind the ligule (**Fig. 3**).

Taxon sampling

Sampling included the eight Australian native species and one African species of *Enteropogon* and two species of *Chloris*. Species data was obtained from numerous accessions across the geographic distribution for each species. Forty-five specimens of *E. dolichostachyus* from Australian herbaria, collected from Australia, Sri Lanka, Papua New Guinea, Philippines and Thailand, were examined and specimens cited by other authors are listed in **Appendix 1**. The specimens of *E. macrostachyus* examined are also listed in **Appendix 1**. Two specimens of *E. scabrilemma* (*Blake 23488* and *Pullen 6829*), have been cited by other authors including Lazarides (1972), Nightingale *et al*. (2005) and Peterson *et al*. (2015) in their synopses of *E. dolichostachyus*.

Chloris divaricata R.Br. and *Chloris ventricosa* R.Br. were selected as the outgroup with the former having resemblance to *Enteropogon* at least to the naked eye, with the consequence that occasionally some specimens at BRI have been misidentified.

Cultivation of plants

All species, except *Enteropogon macrostachyus*, were cultivated in pots under the same nursery conditions in full sun at Brisbane, Australia during the period 2009–2022. Plants were propagated from five or six caryopses per species acquired from herbarium specimens, except *E. macrostachyus* for which no viable seeds were available (**Appendix 2**).

Specimens of *Enteropogon acicularis* (Lindl.) Lazarides held at BRI display some variation, particularly in inflorescence structure. To explore plasticity, plants were propagated from caryopses taken from accessions of three provenances. The three accessions were chosen because they provided viable caryopses.

Table 1. Most discriminating morphological characters from the top twenty generated from PATN cluster analysis of dataset for ***Enteropogon***, i.e. *Enteropogon dolichostachyus*, *E. macrostachyus*, *E. paucispiceus*, *E. pubifolius* and *E. scabrilemma* excluding data for outgroup, *Chloris*. Two of the top 20 most discriminating characters, Ch. 9 and 58 have been omitted from the list because the character states are the same for the five species in the table.
[1] indicates new character defined for this study.

Character code	Character	Character state				
		E. dolichostachyus	***E. macrostachyus***	***E. paucispiceus***	***E. pubifolius***	***E. scabrilemma***
1	Growth habit	tussock with stolons	tussock	tussock	tussock	tussock
2	Widest leaves (mm)	> 4	< 4	< 4	> 4	> 4
	Leaves					
4	Distribution	mostly basal	cauline	mostly basal	mostly basal	cauline
7	Ligule	fringed membrane, cilia equal length to membrane	fringed membrane, cilia equal length to membrane	ciliate membrane, cilia equal to or longer than membrane	fringed membrane, cilia equal length to membrane	fringed membrane, cilia equal length to membrane
	Inflorescence					
10	Number of racemes	digitate to subdigitate 3–9, mostly 4–6	digitate 1 or 2	digitate to subdigate 2–4	digitate to subdigate 3–5	digitate mostly 1 or 2, rarely 6
12[1]	Indumentum length at junction of racemes (mm)	> 1	> 1	> 1	< 1	> 1
	Spikelets					
17[1]	Colour of glumes when fresh	purple	green	green	green	greenish with purpose tint
	Fist lemma					
24[1]	Colour of awns when fresh	purple	purple	purple	green	purple
25[1]	Colour when dry	straw-coloured	straw-coloured	straw-coloured	dark grey	straw-coloured

Table 1. (cont.)

Character code	Character	Character state				
	First lemma micromorphology					
27[1]	Unicellular trichomes - length (µm)	to *c.* 50	to *c.* 50	glabrous	glabrous	to *c.* 160
28[1]	Density of micro-hairs	sparse to common	abundant	sparse to common	sparse to common	abundant
29[1]	Cork cell spacing on back of first lemma	regular	irregular	irregular	irregular	regular
31[1]	Cork cells - relative size	large	large	small	small	large
32[1]	Size of cork cell on lemma	large	large	small	large	large
33[1]	Relative size of silica body to total size of cork cell on lemma	> 1/2 of area	> 1/2 of area	< 1/2 of area	> 1/2 of area	> 1/2 of area
	First palea					
37	Apex shape	acute	acute to attenuate	acute	acute	obtuse
	Rachilla					
45	Presence of distal beard	absent	present	absent	present	usually present
	Second floret lemma					
48	Relative length to first lemma	< 1/3	< 1/2	< 1/3	> 1/3	< 1/2

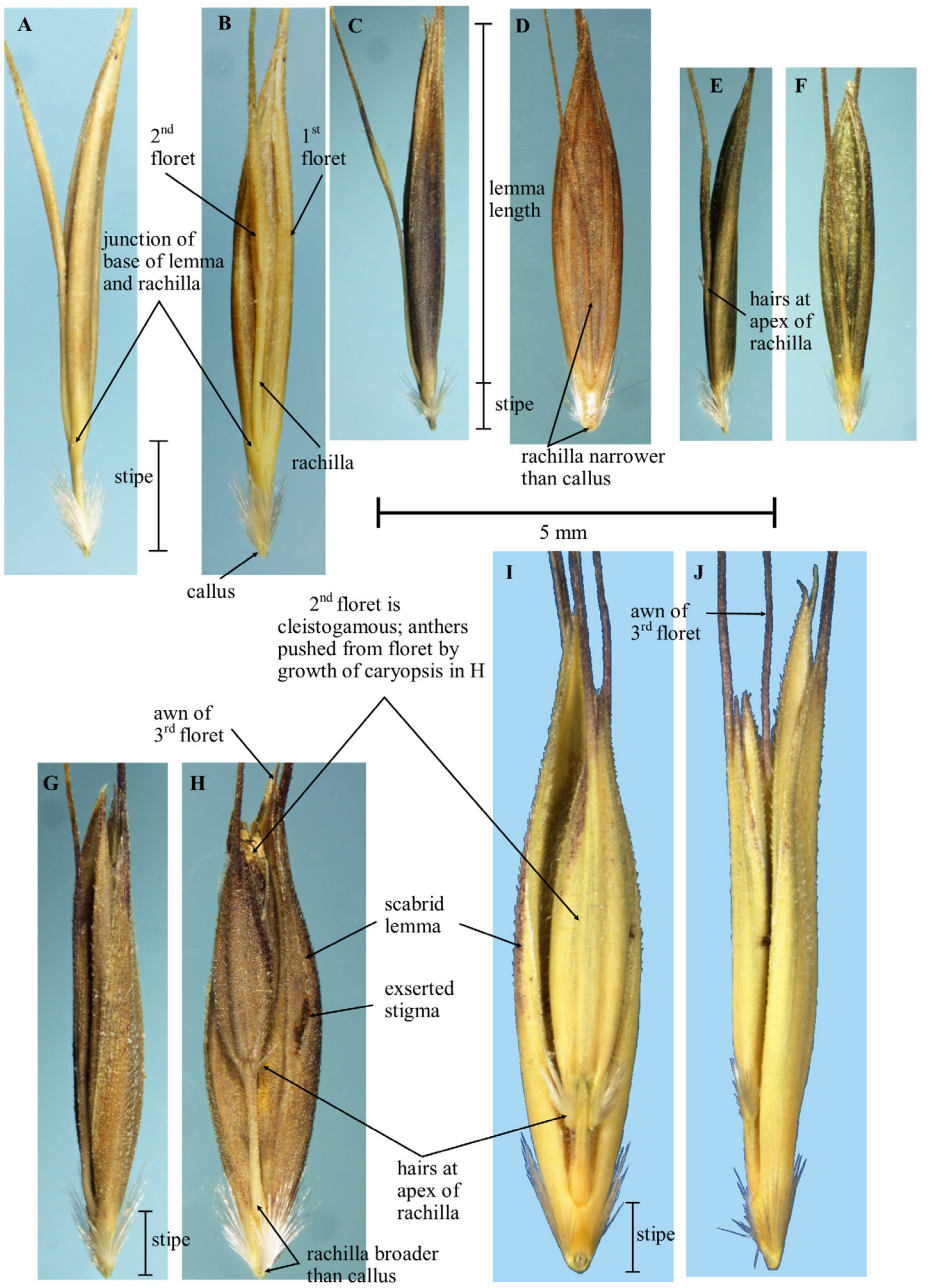

Fig. 1. Diaspores of ***Enteropogon dolichostachyus***, ***E. macrostachyus***, ***E. paucispiceus***, ***E. pubifolius*** and ***E. scabrilemma*** from ventral and lateral views. The diaspore comprises the united florets that have disarticulated leaving the glumes attached to the pedicel. A, C, E, G & J lateral views; B, D, F, H & I ventral views. A & B. ***E. paucispiceus***. C & D. ***E. dolichostachyus***. E & F. ***E. pubifolius***. G & H. ***E. scabrilemma***. I & J. ***E. macrostachyus***. A & B from *Thompson MOR842* (BRI); C & D from *Thompson MOR837* (BRI); E & F from *Thompson MOR841* (BRI); G & H from *Thompson MOR844* (BRI); I & J from *Davidse 5886* (BRI). Photos: E.J. Thompson.

The cultivated plants provided fresh material for transverse sectioning, and studies of inflorescence morphology, breeding systems, flowering and fruiting phenology, and growth habit.

Imagery

Photographs were taken using light microscopes, *viz*. Nikon SMZ25 binocular microscope with Nikon DS-Ri1 camera and images viewed using NIS-Elements BR (2020) and Leica DMLB compound binocular microscope with an industrial digital camera and images viewed using ToupView (2020). Potted plants were photographed using a Fuji FinePix SL280 digital camera.

Scanning electron micrographs (SEMs) were used to examine the surface micromorphology of lemmas, paleas, leaves, culms and caryopses. SEMs were obtained without sputter coating the specimens, using a Phenom G2 5kev scanning electron microscope with backscatter detector.

Type specimens were examined using digital images obtained from JSTOR Plants (2022).

Acquisition of data and classification of morphological characters

Three main groups of morphological characters were examined and classified for this study. These include spikelets (macro- and micromorphology of glumes, lemmas, paleas, style and caryopsis, leaves (including ligule, paraligule, anatomy of transverse sections, micromorphology of the abaxial surface) and culms (anatomy and surface micromorphology).

Characters and character states used by other authors were reviewed and further information was gathered from observation of herbarium specimens and cultivated plants (**Appendix 3**). A broad spectrum of characters was examined, and information relating to character states and plasticity was obtained from character lists, diagnostic descriptions, illustrations and keys used by other authors including Lazarides (1972), Anderson (1974) Nair *et al.* (1977), Phillips (1982), Davis (1983), Tothill & Hacker (1983), Jacobs (1986), Jacobs & Highet (1988), Lazarides *et al.* (1992), Watson & Dallwitz (1992), Van den Borre & Watson (1997), Nightingale *et al.* (2005), Liu *et al.* (2010), Giraldo-Cañas *et al*. (2012), Fahey *et al*. (2019), and Simon & Alfonso (2022).

Characters and character states were evaluated in terms of similarity, ambiguity, reliability, plasticity, practicality, repeatability and standardisation of assessment or measurement using considerations by other authors (Hillis 1987; Wagner 1989; Smith 1990; Lipscomb 1992; Hillis & Wiens 2000; Poe & Wiens 2000; Rieppel & Kearney 2002; Scotland *et al.* 2003; Wiens 2004; Smith & Turner 2005; Thompson & Fabillo 2021; Thompson 2022b, c).

Spikelet morphology

Micromorphology of first lemmas was studied using SEMs to classify silica bodies, cork cells, stomata, and macro- and micro-hairs using information provided by Hsu (1965), Anderson (1974), Ellis (1979), Valdes-Reyna & Hatch (1991), Snow (1996), Columbus (1999), Acedo & Llamas (2001), Liu *et al.* (2010), Mashau *et al.* (2015) and Olonova *et al.* (2016) (**Appendix 3**). SEMs were captured near the mid-point of mature first lemmas (bearing a caryopsis).

The morphology of caryopses included shape and size, length of scutellum, shape of hilum, embryo spermaderm, and stylopodium, as used by Reeder (1957), Jacobs & Highet (1988), Watson & Dallwitz (1992), Terrell & Peterson (1993), Soreng & Davis (1998), Snow (1998), Liu *et al*. (2005), Gandhi *et al.* (2013) and Zhang *et al*. (2014).

Leaf and inflorescence culm anatomy and surface micromorphology

Leaf and culm materials from cultivated plants and herbarium specimens were used to obtain transverse sections with the method described by Thompson (2017) as modified from Frohlich (1984). Mature leaves were selected from the upper parts of culms and sections were taken from near the middle of the leaves. Culm sections were taken from a portion just below the first inflorescence branch. Leaf and

culm transverse sections were classified by characters from the sclerenchyma, vascular bundles and parenchyma building on the information (including illustrations) provided by authors including De Wet (1960), Ellis (1976), Clifford & Watson 1977, Dengler *et al*. (1994), Columbus (1999), Renvoize (1983, 2002), Siqueiros-Delgado (2007) and Ahmad *et al*. (2012).

Leaf surface micromorphology was also studied from replicas of the abaxial surface of fresh leaves acquired using the method described by Hilu & Randall (1984). To improve ease of application, acrylic nail varnish was diluted to about 60% using acetone.

Datasets and phenetic analyses

The robustness of results from cluster analyses was explored by varying inputs, *viz*. sample composition, algorithm (ordination, classification, association measure), as well as the format of characters. This approach was adopted following findings made by other authors (Clifford & Goodall 1967; Mannetje 1967; Clifford & Williams 1973; Austin & Belbin 1982; Hilu & Wright 1982; Johnson 1982; Stevens 1991; Thiele 1993; Wills *et al.* 2000; Scotland *et al.* 2003; Wortley *et al.* 2005; Pereira *et al.* 2007; Newmaster *et al.* 2008; Zuloaga *et al.* 2014; Peichoto *et al.* 2015; Aliscioni *et al.* 2016; Thompson 2022b,c).

The baseline dataset was composed of 11 samples of *Enteropogon* species and 43 morphological characters (**Appendix 4**). The characters comprised nine vegetative characters, 41 characters relating to spikelets and inflorescences and seven relating to leaf anatomy (**Appendix 3**). The dataset consisted of 32 binary and 11 multistate characters.

Cluster analyses were conducted using PATN 4.00 (Belbin & Collins 2013). Classification analyses used the unweighted pair method with arithmetic mean (UPGMA), and dendrograms were generated using agglomerative hierarchical fusion with unweighted pair group method with a Beta value of -0.1. Two association measures were used to examine the potential impact of assumptions about the nature of the states of polymorphic characters. Of the several association measures available in the PATN package, Gower metric and Czekanowski (Bray-Curtis) (Somerfield 2008) were applied where differences between states of polymorphic characters are considered equal and unequal, respectively (L. Belbin *pers. comm*.). Three-dimensional ordination plots were generated using semi-strong hybrid multidimensional scaling (SSH). Ordination stress value (OSV) was used as the measure of closeness of fit: stress values of <0.05 = excellent, <0.1 = good, <0.1–0.15 may be OK, <0.2 = not good (Belbin https://patn.org/PATN - Finding patterns in data/, accessed 17 February 2022). Discriminating characters were generated for analysis of the baseline dataset from Kruskal-Wallis (KW) values (**Appendix 3**).

Three tests of impact, based on the methods used by Thompson (2022b, c), were conducted for comparison with results from analyses of the baseline dataset. In test 1, all multistate characters were transformed to binary format resulting in 72 characters. In test 2, four datasets in addition to the baseline were established from a list of the most discriminating characters in descending order based on KW values generated from analysis of the baseline dataset with the number of groups set at 10, corresponding to the nine putative species used in the sample. Datasets were created by successively removing batches of 5 characters with the lowest KW values starting from 40 characters, followed by 35, 30, and so on. During test 3, the effect of an outgroup was assessed by adding the two species of *Chloris* to the baseline dataset resulting in a data matrix of 13 samples and 58 characters, of which 13 were multistate (**Appendix 4**). This dataset was analysed and the test on discriminating characters (test 2) was carried out with the number of groups set at nine and datasets with batches of five characters removed. The multistate characters were transformed to binary resulting in 87 characters.

Results

Topologies generated from analyses were affected by the data format and the algorithm, but the addition of *Chloris* to the sample as an outgroup had little impact (**Figs. 4 & 5**, **Table 3**). Four clusters were consistently recovered from all topologies, *viz*. *Chloris* spp., *Enteropogon minutus* with *E. unispiceus*, *E. macrostachyus* with *E. scabriblemma*, and *E. paucispiceus* with *E. ramosus* (**Fig. 4**). In ordination topologies, *E. paucispiceus*, *E. pubifolius* and *E. ramosus* were commonly grouped. *Enteropogon dolichostachyus* was typically grouped with *E. macrostachyus* and *E. scabriblemma* in ordination topologies, but only as such in dendrogram topologies generated from analyses using Czekanowski association measure (**Figs. 4 & 5)**.

The top 20 most discriminating characters generated from cluster analysis of the baseline dataset covered a broad range of character types (**Table 1; Appendix 5**). Several of these characters are new to studies of *Enteropogon* and are useful diagnostic characters in the identification key below, while others are micromorphological characters, of which some relate to cork cells (**Fig. 2**).

Observation of the cultivated plants of *Enteropogon* revealed some character differences not always readily visible from herbarium specimens. Character differences including growth habit, number of inflorescence culms per plant and colour of spikelets, were more evident in cultivated plants of some species. For example, *E. scabrilemma* differs from *E. dolichostachyus* by having more numerous inflorescence culms per plant with leaves more obviously cauline; leaf-bearing portions of the culms elongated and occasional decumbent culms rooting at the nodes but lacking stolons; inflorescences mostly 1 or 2 racemes, and when fresh the inflorescence culms and rachis green; and racemes appearing tinted purple (**Table 1**).

Enteropogon scabrilemma and *E. macrostachyus* are morphologically similar in growth habit, inflorescence structure, and spikelet morphology (**Table 1**). The two species differ by several characters including narrower, shorter spikelets (1–1.5 mm × 5.2–6.4 mm vs 1.9–2 mm × 7–10 mm; the latter measurements for *E. macrostachyus* from Clayton *et al.* 1974) in *E. scabrilemma*.

The micromorphology of the first lemma, abaxial surface of leaves and culms of *Enteropogon dolichostachyus*, *E. paucispiceus*, *E. pubifolius* and *E. scabrilemma* differ by micro-hairs, silica bodies and cork cells (**Figs. 2, 6**–**8**). The four species can be placed in two groups based on micromorphology. Cork cells across the four species vary in spacing, distribution, size and shape (**Fig. 2**). The bicellular micro-hairs of *E. dolichostachyus* are slightly larger than the other three species (**Fig. 2**). *Enteropogon dolichostachyus* and *E. scabrilemma* share slightly larger stomata, cork cells and silica bodies. The latter pair of species also share slightly wider long cells on the surface of inflorescence culms (**Fig. 8**).

Caryopses of *Enteropogon* species vary in shape, length and width (**Fig. 9**). There was also some variation in the relative length of the scutellum, size of the stylopodium, development of the dorsal ridge and cell width on the spermaderm (**Figs. 9 & 10**).

Leaf blades, sheaths and growth habits differed between species of *Enteropogon* (**Figs. 1 & 11**, **Appendix 3)**. Indumentum of young leaves is a useful differentiating character (**Fig. 3**) but on some species the hairs are readily shed with age and mature leaves and the paraligule can be hairless.

There was a relatively small degree of variation in the anatomy of transverse sections of leaves and culms of *Enteropogon dolichostachyus*, *E. paucispiceus*, *E. pubifolius* and *E. scabrilemma* (**Figs. 12 & 13)**. All four species have clear parenchyma 8–20 cells wide by 3 or 4 cells thick above the mid-vein vascular bundle (**Fig. 12)**. The strip of cells tends to give the mid-vein a silvery appearance on fresh leaves. The other four Australian species*, viz. E. acicularis, E. minutus, E. ramosus* and *E. unispiceus,* were found to differ from the former four species by having only a few clear parenchyma cells above the mid-vein vascular bundle.

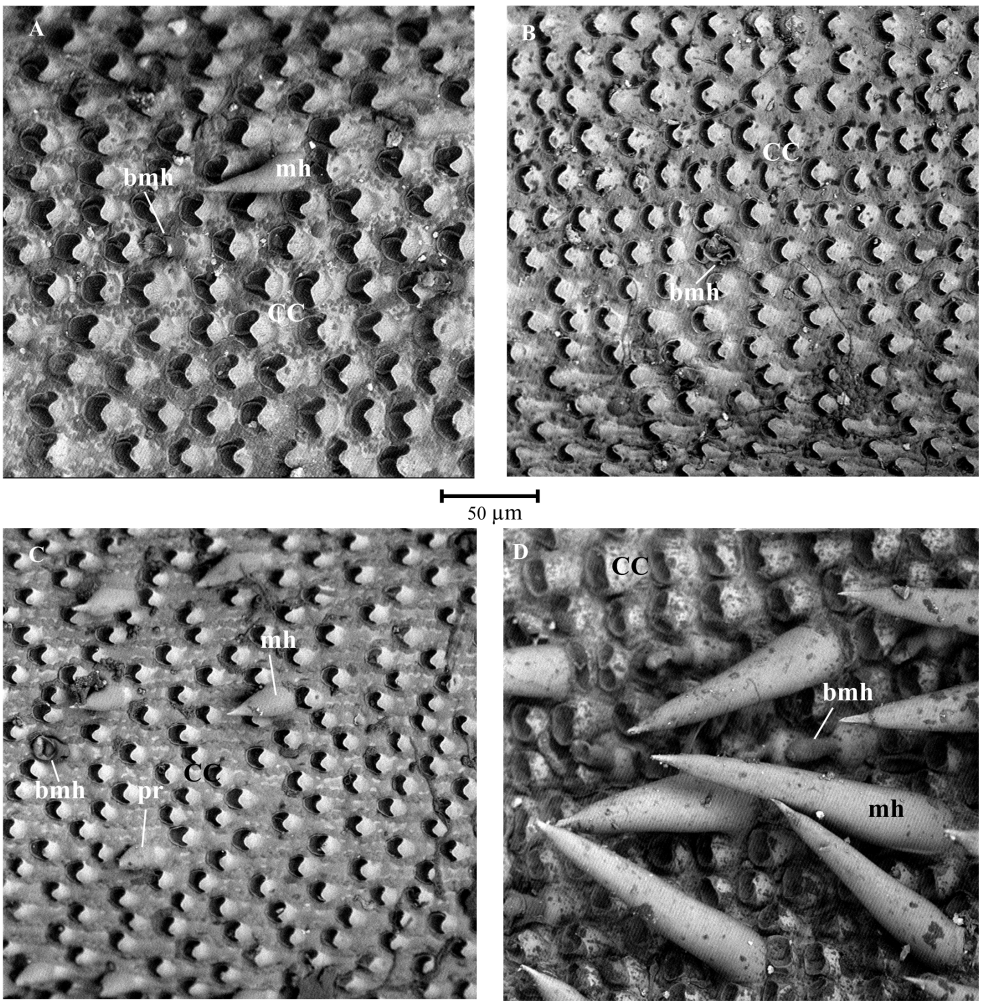

Fig. 2. Scanning electron micrographs of surface of lemmas (callus to RHS) of ***Enteropogon dolichostachyus***, ***E. paucispiceus***, ***E. pubifolius*** and ***E. scabrilemma*** with classification of cork cells. The body of cork cells comprises a silica body (dark portion) and lid. A. ***E. dolichostachyus*** (**r**, **1**, **L**, **a, c**). B. ***E. paucispiceus*** (**i**, **2**, **s**, **b, c**). C. ***E. pubifolius*** (**i**, **2**, **s**, **a, c**). D. ***E. scabrilemma*** (**r**, **1**, **L**, **a, r**). A from *Thompson MOR837* (BRI); B from *Thompson MOR842* (BRI); C from *Thompson MOR841* (BRI); D from *Thompson MOR844* (BRI). Micrographs (captured at ×1000): E.J. Thompson.

Abbreviations: **bmh** bicellular micro-hair; **CC** cork cell; **mh** macro-hair; **pr** prickle
Ratings for cork cells (for most frequent occurrences) **- Spacing**: **r** regular; **i** irregular; **separation**: **1** mostly < one diameter, **2** frequently two diameters; **size**: **s** small (< 15 µm), **L** large (> 20 µm); **size of silica body**: **a** > half of area, **b** < half of area; **shape of silica body**: **c** crescent, **r** rectangular.

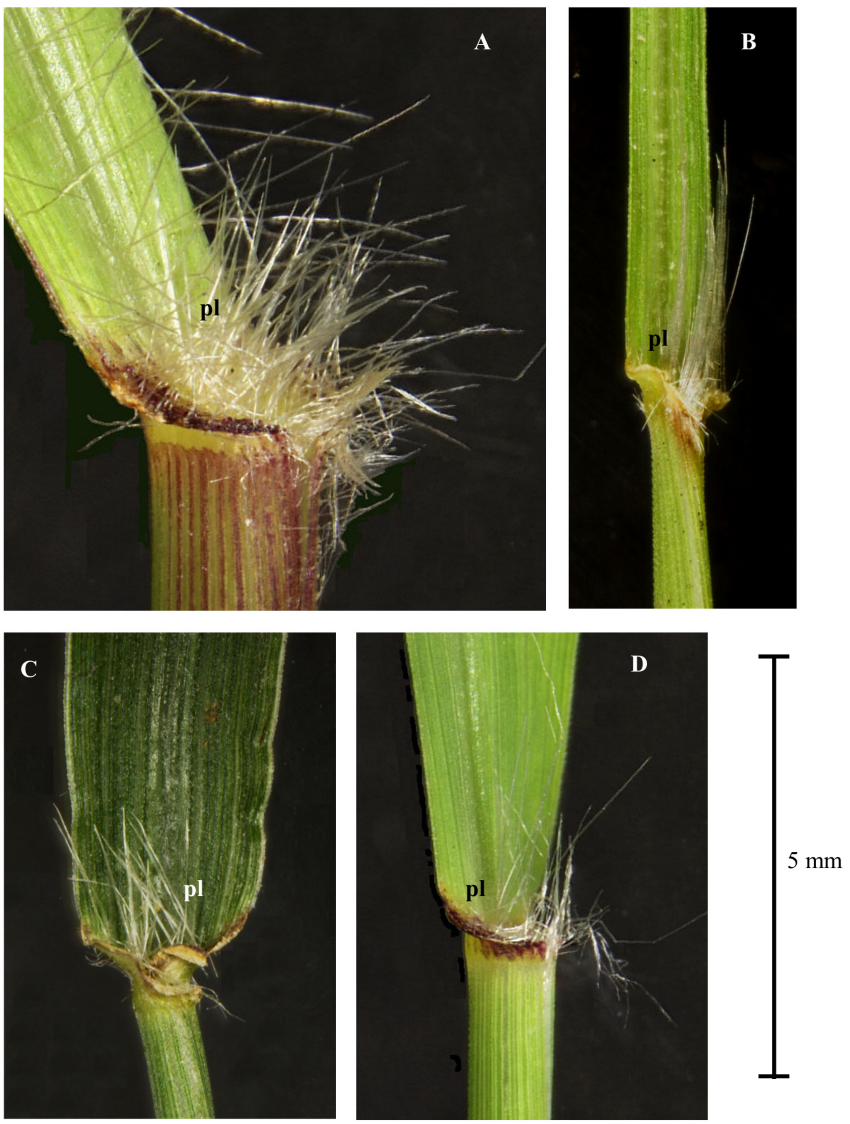

Fig. 3. Leaf, collar and sheath at the mid-point along the vegetative portion of the culm of ***Enteropogon dolichostachyus***, ***E. paucispiceus***, ***E. pubifolius*** and ***E. scabrilemma***. A. ***E. dolichostachyus***. B. ***E. paucispiceus***. C. ***E. pubifolius*** D. ***E. scabrilemma***. A from *Thompson MOR837* (BRI); B from *Thompson MOR842* (BRI); C from *Thompson MOR841* (BRI); D from *Thompson MOR844* (BRI). Photos: E.J. Thompson.
Abbreviation: **pl** – paraligule.

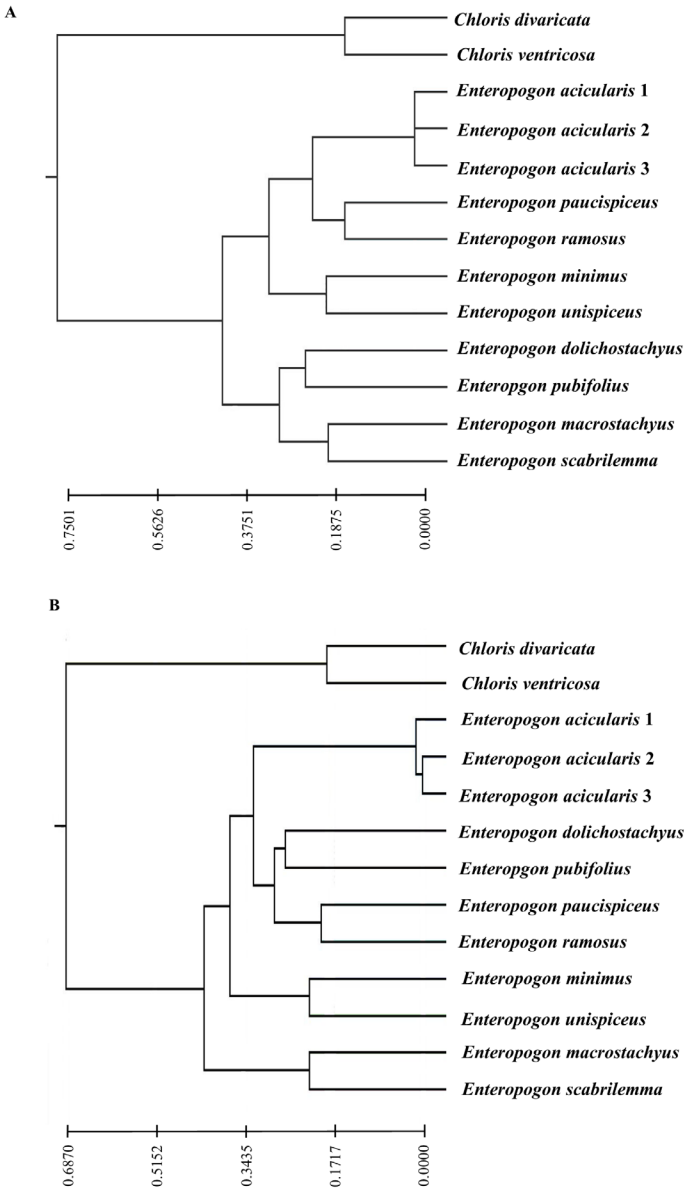

Fig. 4A & B. Variation in topologies for dendrograms generated from PATN cluster analyses for four examples of variations in analysis inputs using two datasets and two association measures (AM). Two datasets: T1, 13 samples (includes *Chloris*) and 58 characters (13 multistate); T2, all multistate characters transformed to binary format (87 characters). **A**. Dataset = T1, AM = Gower metric. **B**. Dataset = T1, AM = Czekanowski.

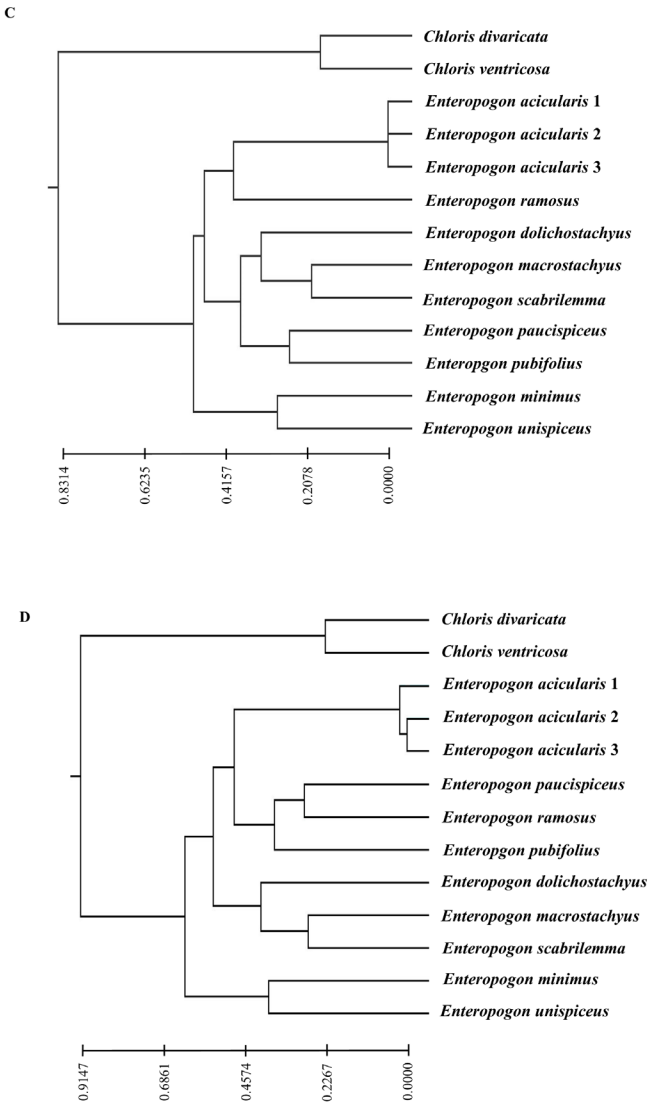

Fig. 4C & D. Variation in topologies for dendrograms generated from PATN cluster analyses for four examples of variations in analysis inputs using two datasets and two association measures (AM). Two datasets: T1, 13 samples (includes *Chloris*) and 58 characters (13 multistate); T2, all multistate characters transformed to binary format (87 characters). **C**. Dataset = T2, AM = Gower metric. **D**. Dataset = T2, AM = Czekanowski.

Other discoveries include:

- Plants of *Enteropogon acicularis* have fragile inflorescence culms that usually disarticulate at maturity, very likely as a result of the sparser peripheral layer of sclerenchyma, compared to plants of *E. ramosus* that retain the old inflorescence culms.
- *Enteropogon acicularis* and *E. ramosus* differ by the length of the diaspore stipe, *c*. 1 mm and 0.5 mm, respectively.
- The indumentum in the raceme axils differs with *Enteropogon acicularis* having hairs > 2 mm long and *E. ramosus* < 0.7 mm long. Axil indument is a reliable character on young inflorescences, but axils are sometimes glabrescent with age.
- *Enteropogon minutus* differs from all the other Australian species by having inflorescence culms with a longitudinal groove or flattened edge. The contraligule may not be evident at all leaf blade-sheath junctions on a plant.
- *Enteropogon paucispiceus* can have cleistogamous second florets.
- Besides compression, another useful character that can be used to distinguish spikelets of *Chloris* and *Enteropogon* is the reltive width of the first and second florets with Chloris having the second florets about half the width of the first, but occasionally *Chloris divaricata* R.Br. was observed in herbarium specimens to be like *Enteropogon* with narrow second florets.

Discussion

This study used results from phenetic analyses of a comprehensive set of morphological characters to provide an objective and repeatable process to aid decision making for alpha and beta taxonomy (Stuessy 2009; Thompson 2022b, c). The additional new morphological characters observed for *Enteropogon* were useful in discriminating the Australian species and helped provide information on the plasticity of some of the characters used in identification keys. The study affirmed the significance of the role of cultivation of plants over several years as part of the process of gathering information on flowering, fruiting and growth habit (Thompson 2017, 2019, 2022b, c). Also, the results from cluster analyses supported the initial intuitive sense of similarities and differences in the putative species and provided potentially useful discriminating morphological characters for phylogenetic reconstructions that include molecular sequence data for correlated genes.

Examination of herbarium specimens and observation of cultivated plants for this study revealed that some characters such as growth habit and number of racemes per inflorescence, used in keys to identify some Australian species of *Enteropogon*, can lead to ambiguous identifications. For example, Nightingale *et al*. (2005) and Simon & Alfonso (2022) used "leaves mostly basal" and "leaves cauline" as distinguishing characters. The distribution of leaves on live plants is usually evident as either basal or cauline in *Enteropogon*. However, some herbarium specimens comprise only one or two culms, thus presenting potentially ambiguous character evaluation, especially when both the specimen and the label notes (including sometimes misleading terminology) are inadequate. Growth habit characters can be more evident when observed on living plants. This was exemplified by the stoloniferous habit of cultivated plants of Australian provenances of *E. dolichostachyus*. Further ambiguity in the identity of *E. dolichostachyus* was encountered due to variations in descriptions and illustrations in floras over its geographic range across northern Australia, New Guinea, Timor, China, India, and the Philippines, the latter location where the type specimen was collected (Bor 1960; Lazarides 1972; Hsu 1978; Lazarides *et al.* 1992; Noltie 2000; Barkworth 2003; Nightingale *et al.* 2005; Bixing & Phillips 2006). It is possible that more than one taxon currently identified as *E. dolichostachyus* is present across Asia.

The inflorescences of *Enteropogon acicularis* also exhibit degrees of plasticity in number and orientation of racemes, indumentum of the axils and culm diameter. Inflorescences of the cultivated plants of *E. acicularis* occasionally consisted of only five

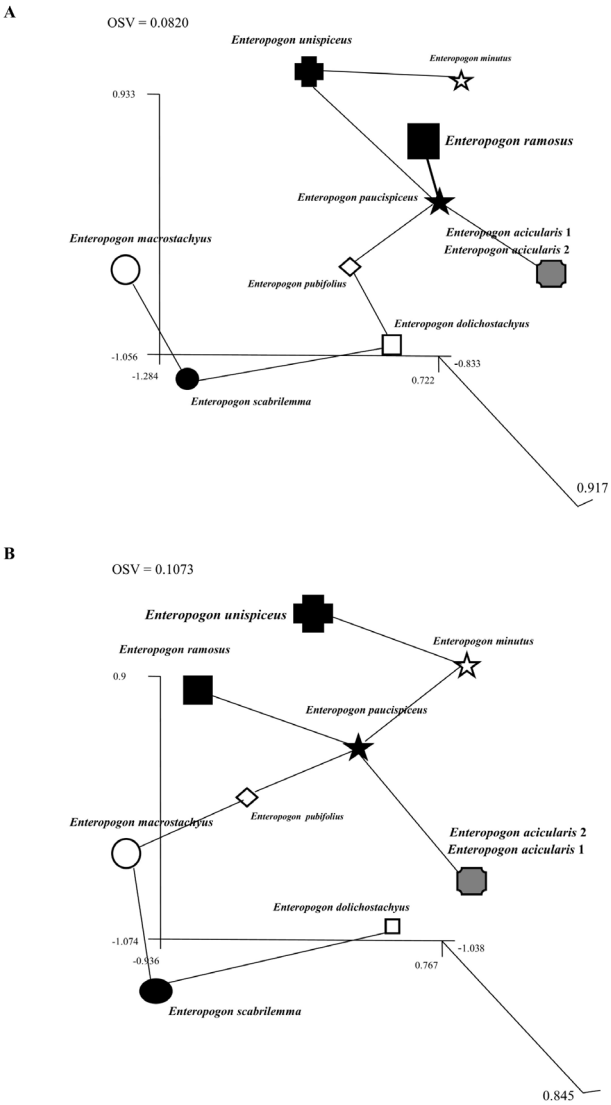

Fig. 5A & B. Variation in topologies for 3-D ordinations generated from PATN principal component analyses using semi-strong, hybrid multidimensional scaling for four examples of variations in analysis inputs using four datasets and two association measures (AM). Four datasets: B1, baseline dataset with 11 samples and 43 characters (11 multistate); B2, as for B1 but with multistate characters transformed to binary (72 characters); T1, 13 samples (includes *Chloris*) and 58 characters (13 multistate); T2, all multistate characters transformed to binary format (87 characters). **A**. Dataset = B1, AM = Gower metric. **B**. Dataset = B2, AM = Czekanowski.

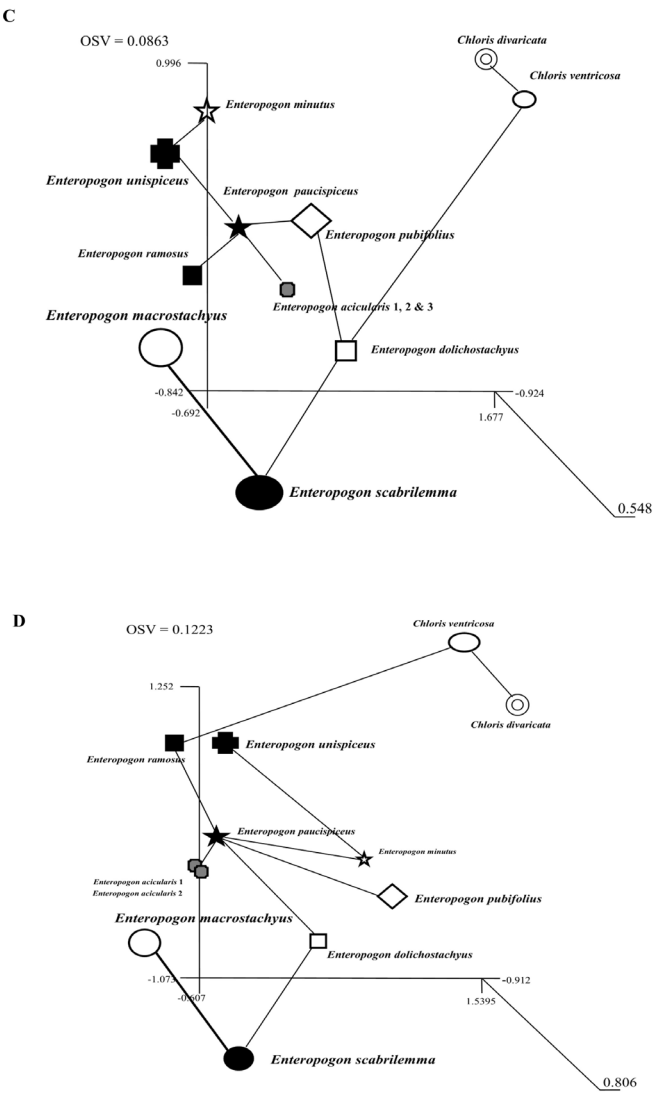

Fig. 5C & D. Variation in topologies for 3-D ordinations generated from PATN principal component analyses using semi-strong, hybrid multidimensional scaling for four examples of variations in analysis inputs using four datasets and two association measures (AM). Four datasets: B1, baseline dataset with 11 samples and 43 characters (11 multistate); B2, as for B1 but with multistate characters transformed to binary (72 characters); T1, 13 samples (includes *Chloris*) and 58 characters (13 multistate); T2, all multistate characters transformed to binary format (87 characters). **C**. Dataset = T1, AM = Gower metric. **D**. Dataset = T2, AM = Gower metric.

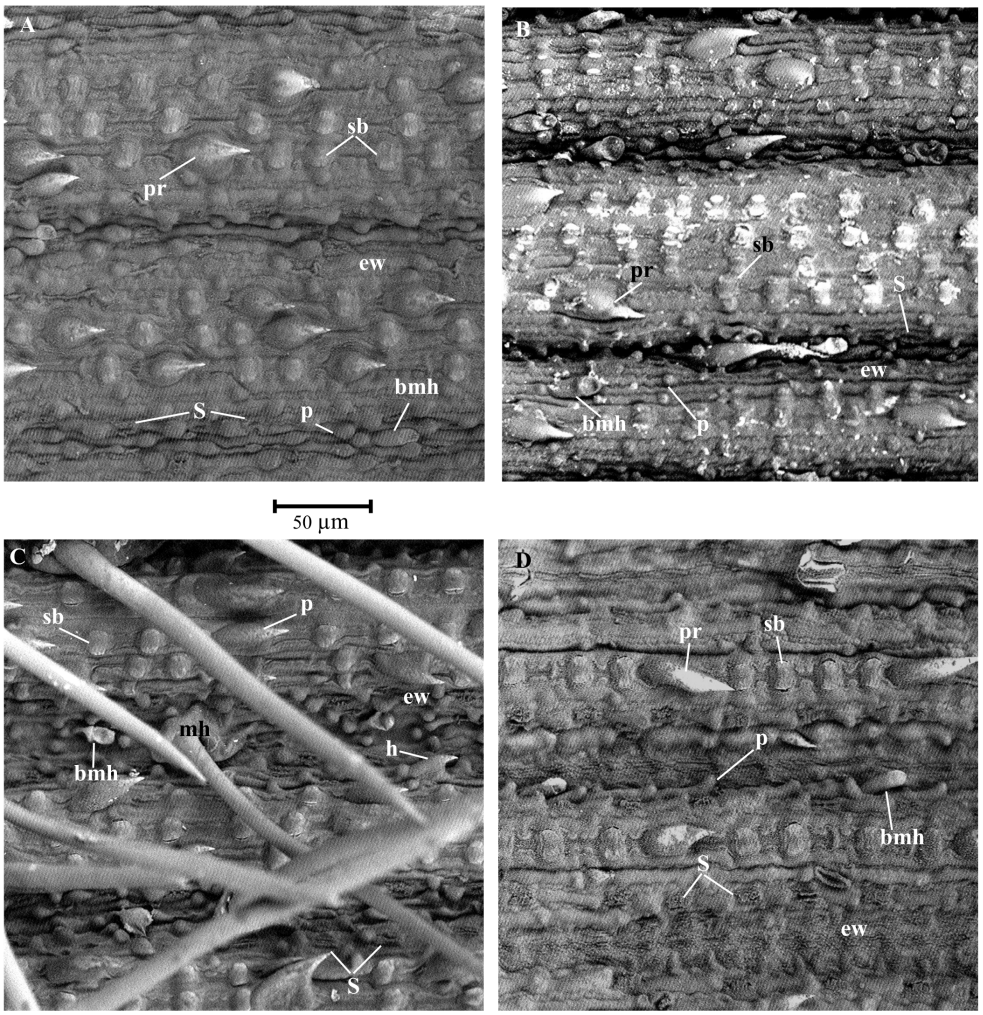

Fig. 6. SEM micrographs of abaxial leaf surface of ***Enteropogon dolichostachyus***, ***E. paucispiceus***, ***E. pubifolius*** and ***E. scabrilemma*** (apex to RHS). A. ***E. dolichostachyus***. B. ***E. paucispiceus***. C. ***E. pubifolius***. D. ***E. scabrilemma***. A from *Thompson MOR837* (BRI); B *Thompson MOR842* (BRI); C from *Thompson MOR841* (BRI); D from *Thompson MOR844* (BRI). Micrographs (captured at ×1000): E.J. Thompson.

Abbreviations: **bmh** bicellular micro-hair; **ew** epicuticular wax (variable thickness layer); **h** hook; **mh** macro-hair; **p** papillae; **pr** prickle; **sb** silica body; **S** stoma.

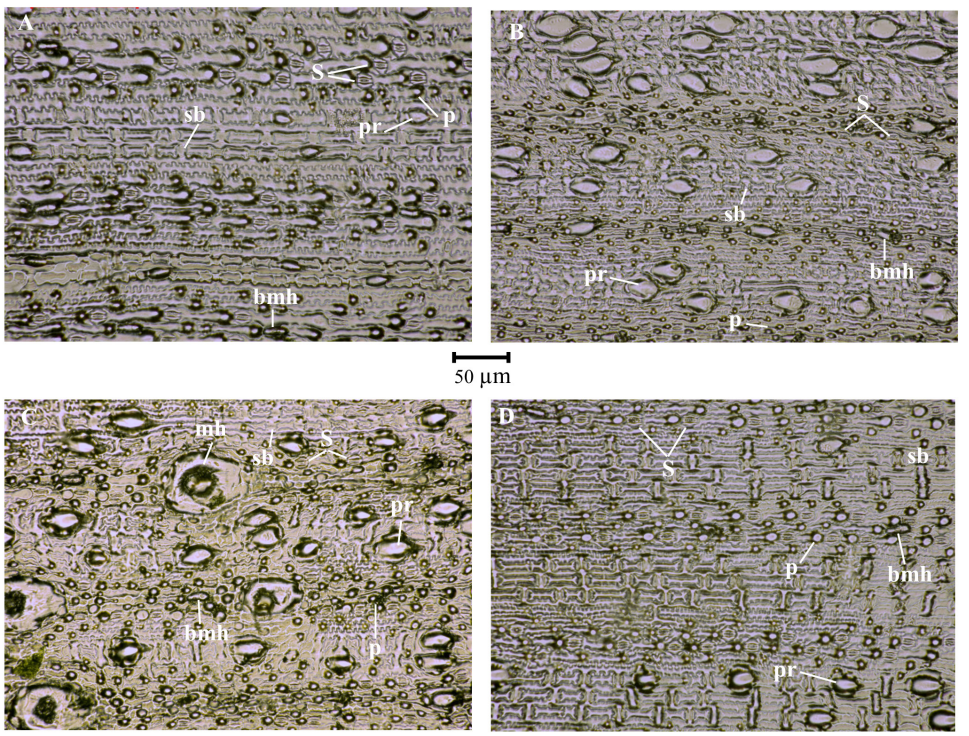

Fig. 7. Replica of abaxial leaf surface of ***Enteropogon dolichostachyus***, ***E. paucispiceus***, ***E. pubifolius*** and ***E. scabrilemma*** (apex to RHS). A. ***E. dolichostachyus***. B. ***E. paucispiceus***. C. ***E. pubifolius***. D. ***E. scabrilemma***. A from *Thompson MOR837* (BRI); B *Thompson MOR842* (BRI); C from *Thompson MOR841* (BRI); D from *Thompson MOR844* (BRI). Photos: E.J. Thompson.

Abbreviations: **bmh** bicellular micro-hair; **mh** macro-hair; **p** papillae; **pr** prickle; **sb** silica body; **S** stoma.

racemes overlapping with the number found in the closely related *E. ramosus* (Simon 1984; Nightingale *et al*. 2005). Culm width just below the raceme junction, a character not used in other studies of *Enteropogon*, was found to be positively correlated with number of racemes for *E. acicularis* ranging from 0.6 to 2.1 mm for 5 to 14 racemes, rarely 24, while for *E. ramosus* the corresponding ranges were 0.4 to 0.8 mm, occasionally 0.9, and 1 to 5, rarely 6.

The diaspore stipe found in species of *Enteropogon* and in some other chloridoid grasses has not been reported as a discriminating morphological character in other studies (Lazarides 1972; Watson & Dallwitz 1992; Van Der Borre & Watson 1997). In Australian *Enteropogon*, the stipe is most pronounced, about 1 mm long, in *E. paucispiceus* and *E. ramosus* whereas in all the other Australian species it is < 0.6 mm long (**Fig. 1**). The stipe is uncommon in other Australian chloridoid genera with the diaspore composed of united florets such as in *Astrebla* F.Muell., *Chloris*, *Oxychloris* (F.Muell.) Lazarides, and also in subtribe *Eleusininae*. The stipe reaches its most conspicuous development in Australian chloridoid grasses in *Oxychloris* where it is *c.* 2 mm long. Furthermore, the stipe is absent in *Eragrostis* N.M.Wolf where the composition of the diaspore is highly variable with some African species having united florets and in

the Australian species the diaspore ranging from the caryopsis alone to an individual floret with or without the rachilla or palea (Palmer *et al*. 2005). Another form of diaspore stipe occurs in andropogonoid grasses including *Elionurus* Willd., reported by Thompson (2017: 156) as a "proximal beak". Although the stipe can have similarities in function for dispersal and burial, differences in the structure of the diaspore across grass taxa suggest ontogenetic differences, for example as found in many chloridoid grasses that have disarticulation above the glumes compared to andropogonoid grasses where disarticulation occurs below a spikelet pair (Peart 1979; Cheplick 1998; Cavanagh *et al*. 2019).

The paraligule found in some chloridoid grasses is also an uncommon occurrence in panicoid taxa but is rarely used as a discriminating character. Paraligules were recorded for species of *Paspalum* L. as "hairs behind the ligule" by Rua & Aliscioni (2002) and have been found useful by the author (unpubl.) in aiding identification of the Australian species.

The frequency distribution of species of *Enteropogon* by climatic zones follows a broadly similar trend to that of Poaceae collectively in Australia (**Map 1**; Thompson 2021). The highest frequencies of species occur in tropical and subtropical zones across the Northern Territory and Queensland.

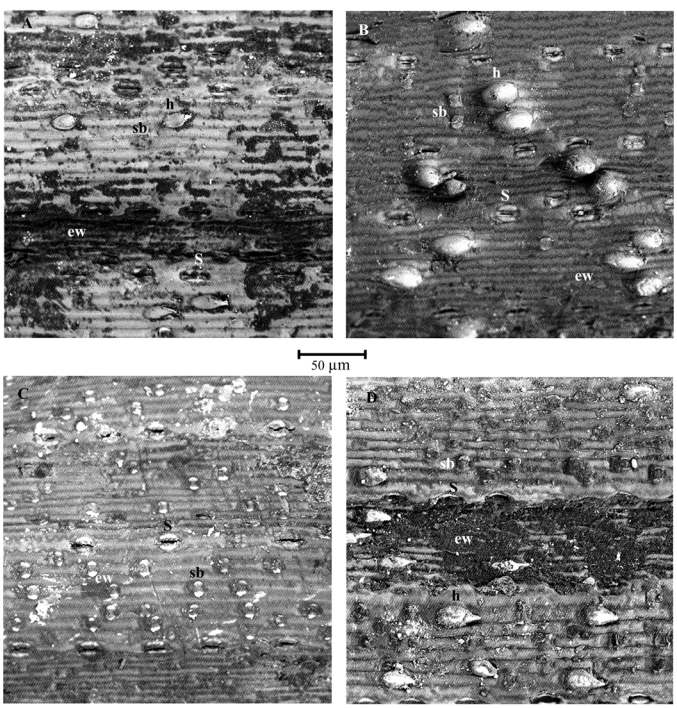

Fig. 8. SEM micrographs of surface of terminal inflorescence culm of ***Enteropogon dolichostachyus***, ***E. paucispiceus***, ***E. pubifolius*** and ***E. scabrilemma*** (apex to RHS). A. ***E. dolichostachyus***. B. ***E. paucispiceus***. C. ***E. pubifolius***. D. ***E. scabrilemma***. A from *Thompson MOR837* (BRI); B from *Thompson MOR842* (BRI); C from *Thompson MOR841* (BRI); D from *Thompson MOR844* (BRI). Micrographs (captured at ×1000): E.J. Thompson.

Abbreviations: **ew** epicuticular wax (variable thickness layer); **h** hook; **sb** silica body; **S** stoma.

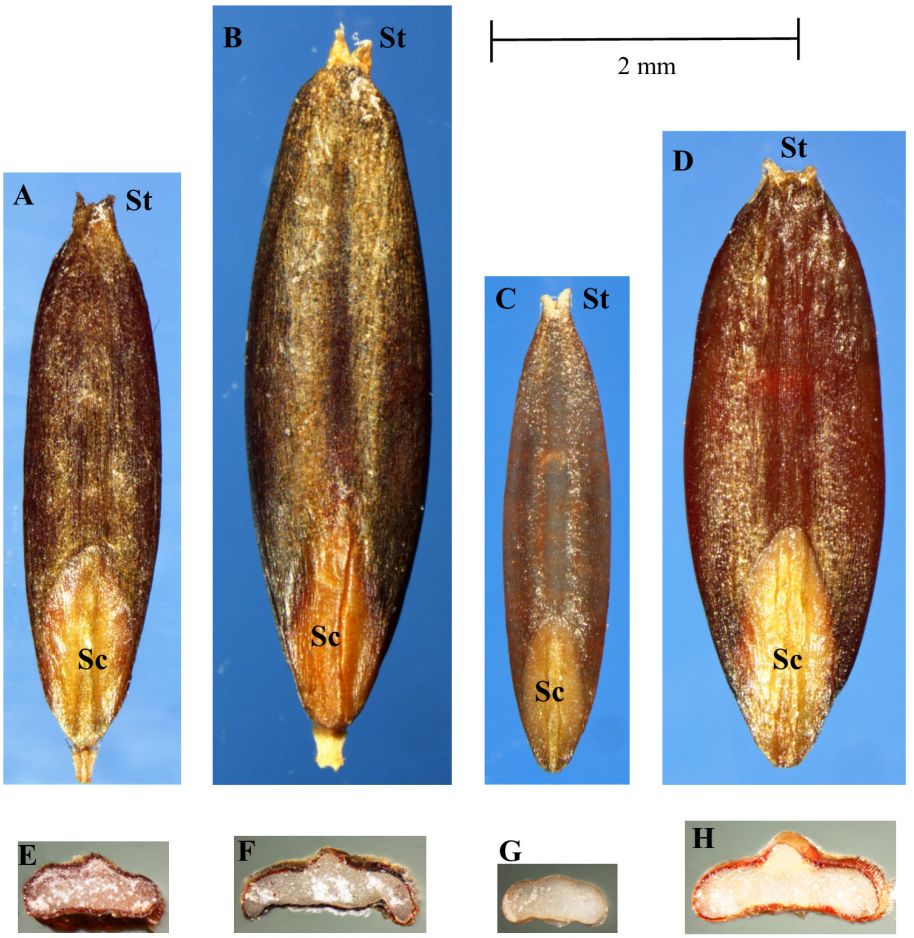

Fig. 9. Caryopses of ***Enteropogon dolichostachyus***, ***E. macrostachyus***, ***E. paucispiceus***, **E. *pubifolius*** and ***E. scabrilemma*** from dorsal view and cross-section just above scutellum. A & E. ***E. dolichostachyus***. B & F. ***E. macrostachyus***. C & G. ***E. pubifolius***. D & H. ***E. scabrilemma***. A from *Thompson MOR837* (BRI); B from *Davidse 5886* (BRI); C from *Thompson MOR844* (BRI); D from *Thompson MOR841* (BRI). Scale bar = 4 mm. Photos: E.J. Thompson.

Abbreviations: **Sc** scutellum; **St** stylopodium.

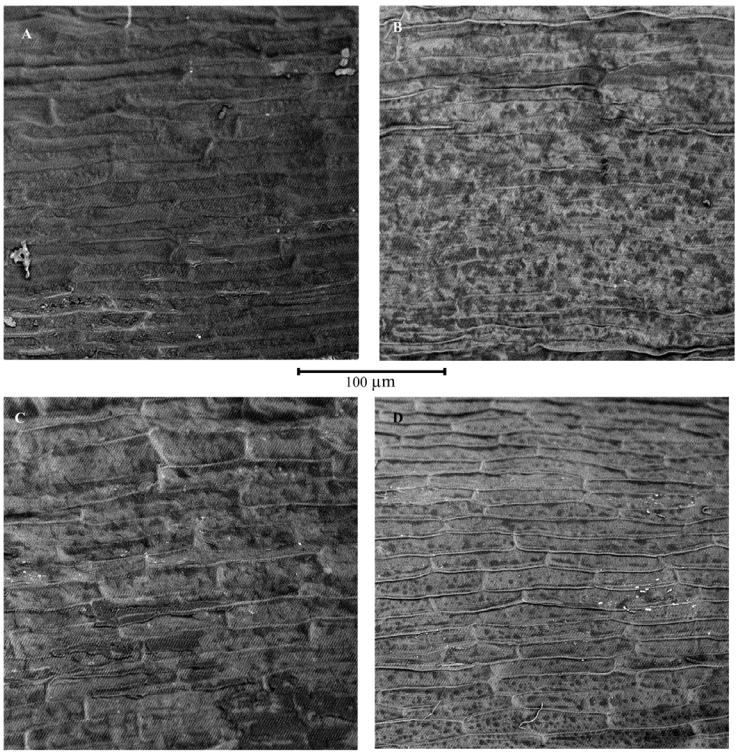

Fig. 10. SEM micrographs of caryopsis endosperm of ***Enteropogon dolichostachyus***, ***E. macrostachyus***, ***E. paucispiceus***, ***E. pubifolius*** and ***E. scabrilemma*** from dorsal view. A. ***E. dolichostachyus***. B. ***E. macrostachyus***. C. ***E. scabrilemma***. D. ***E. pubifolius***. A from *Thompson MOR837* (BRI); B from *Davidse 5886* (BRI); C from *Thompson MOR844* (BRI); D from *Thompson MOR841* (BRI). Micrographs (captured at ×1000): E.J. Thompson.

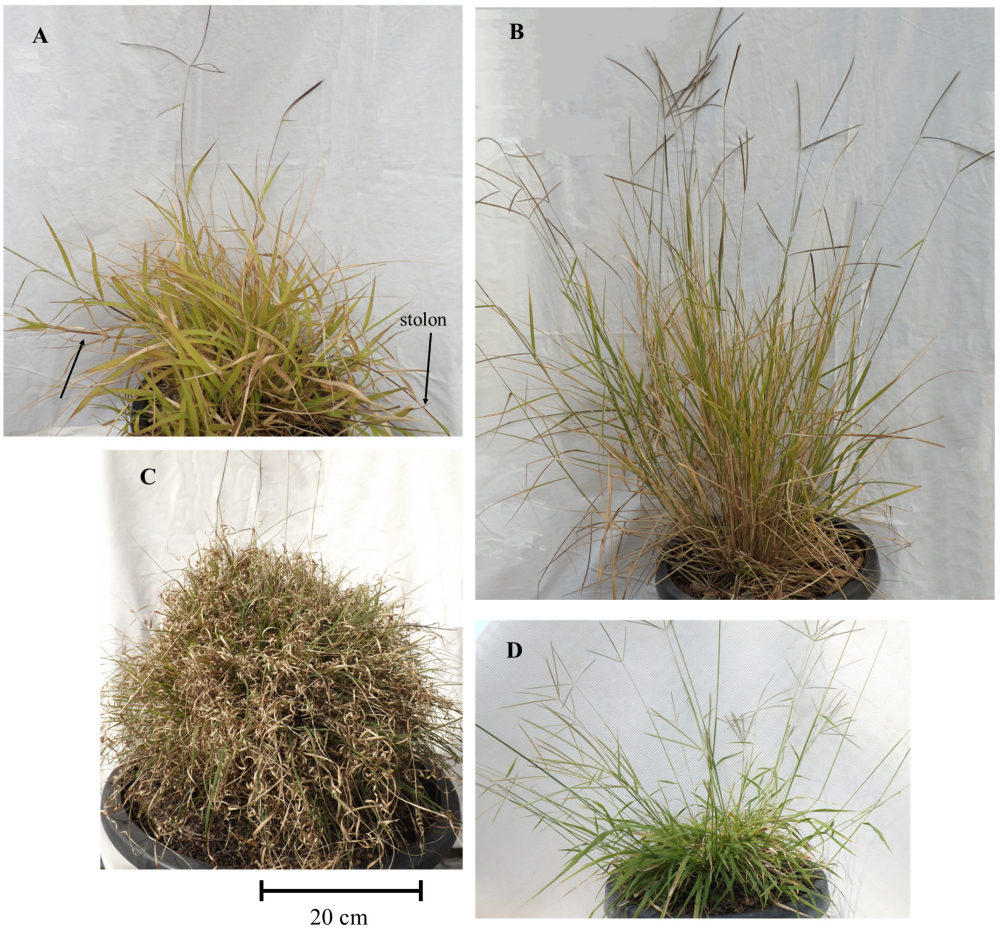

Fig. 11. Growth habit of cultivated plants of ***Enteropogon dolichostachyus***, ***E. paucispiceus***, ***E. pubifolius*** and ***E. scabrilemma.*** A. E. ***dolichostachyus***. B. ***E. scabrilemma***. C. ***E. paucispiceus***. D. ***E. pubifolius.*** A. from *Thompson MOR837* (BRI); B. from *Thompson MOR844* (BRI); C. from *Thompson MOR842* (BRI); D. from *Thompson MOR841* (BRI). Photos: E.J. Thompson.

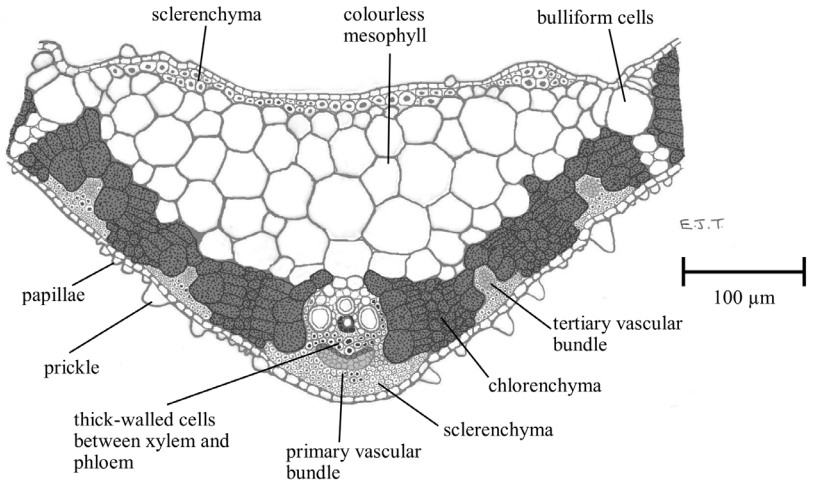

Fig. 12. Transverse section of fresh leaf at mid-vein of ***Enteropogon scabrilemma***. Broad-leaved species of *Enteropogon* exhibit variation in thickness (up to 6 cells) and width (up to c. 16 cells) of parenchyma above the mid-vein and some narrow-leaved species have none or few of these cells. From *Thompson MOR844* (BRI). Del. E.J. Thompson.

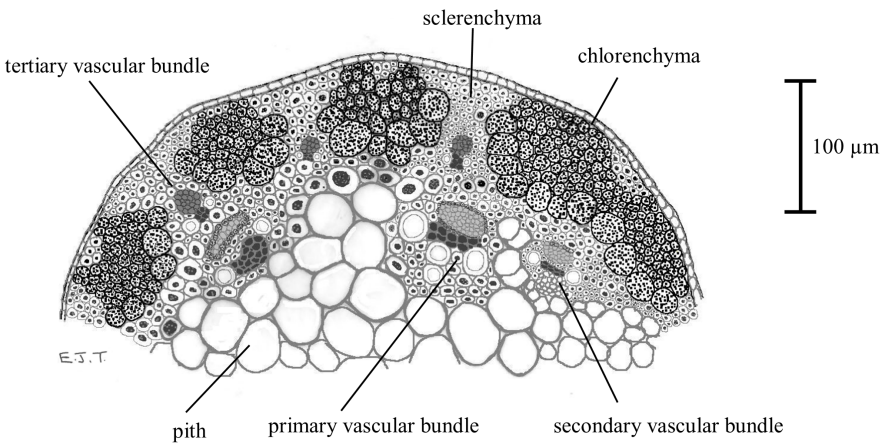

Fig. 13. Transverse section of portion of inflorescence culm of ***Enteropogon scabrilemma***. Morphology and anatomy of the Australian species shows little variation except for *E. minutus* that has semi-circular cross-section and *E. acicularis* with lower density of primary vascular bundles. From *Thompson MOR844* (BRI). Del. E.J. Thompson.

Taxonomy

Key to the Australian species of *Enteropogon* (modified from Simon & Alfonso (2011))

1 Diaspore with an elongated stipe, > 1 mm long **2**
1. Diaspore with a stipe < 0.7 mm long **3**

2 Culms robust; leaves cauline, drying flat, often coiled; hairs at raceme junction *c*. 0.5 mm long . . . . . **E. ramosus**
2. Culms slender; leaves basal, drying flat and straight; hairs at raceme junction > 2 mm long . . . . . **E. paucispiceus**

3 Number of racemes > 7; culms > 0.9 mm wide just below junction of racemes . . . . . **E. acicularis**
3. Number of racemes < 7; culms < 0.9 mm wide **4**

4 Leaves with pilose abaxial surface, > 2 mm wide . . . . . **E. pubifolius**
4. Leaves glabrous abaxially, width varies **5**

5 Leaves < 1.5 mm wide; racemes usually 1 (–3); awn of basal lemma < 9 mm long . . . . . **E. unispiceus**
5. Leaves > 1.5 mm wide; racemes 1 or more; awn of basal lemma > 9 mm long **6**

6 Lemma of proximal floret < 3.8 mm long; contraligule present; inflorescence culm furrowed or flattened on one side . . . . . **E. minutus**
6. Lemma of proximal floret > 3.5 mm long; contraligule usually absent; inflorescence culm circular in cross-section **7**

7 First floret > 1 mm wide; racemes usually 1–2 (–4) . . . . . **E. scabrilemma**
7. First lemma smooth or sparsely scabrid; racemes usually 6 . . . . . **8**

8 First lemma conspicuously scabrid; widest leaves < 3 mm. . . . . **E. acicularis**
8. First lemma smooth or sparsely scabrid; widest leaves *c*. 6 mm . . . . . **E. dolichostachyus**

1. Enteropogon pubifolius E.J.Thomps., **sp. nov.**

Similar to *Enteropogon paucispiceus* (Lazarides) B.K.Simon differing by having pilose broader leaves, spikelets drying dark grey, short diaspore stipe and rachilla with a distal beard. **Type:** Queensland. Ex-situ CULTIVATED: Ashgrove (ex Cape Melville National Park, Mookai Creek), 1 May 2019, *E.J. Thompson MOR841* (holo: BRI [AQ1023144, comprising two sheets]).

Perennial grass, 30–90 cm high, tussock-forming, occasionally with decumbent culms rooting at the nodes. Fertile culms erect, rigid, 3–7 noded, < 0.9 mm wide, internodes short giving the appearance of basal leaves. Leaf blades 3–15 cm long, 3–4.5 mm wide, drying flat; abaxial leaf blade epidermis: pilose with tuberculate-based simple hairs to 0.3 mm long and scabridulous with prickles; densely papillate in the intercostal zone; epicuticular wax present. Ligule a fringed membrane, 0.1–0.2 mm long; paraligule hairs to 3.2 mm long. Leaf sheaths usually shorter than the internodes, glabrous, bearded at the orifice with stiff hairs *c*. 2.7 mm long, round on the back; collar glabrous. Inflorescence a digitate to subdigitate panicle with 3–5 racemes, 40–80 mm long, *c*. 1.6 mm wide and 1.4 mm thick, divaricate, with or without a pseudo-node with a subtending reduced leaf and sheath to 9.8 mm long, or with a bract-like scale to 0.3 mm long; rachis *c*. 0.3 mm wide. Spikelets with 2 or 3 florets. Glumes narrow lanceolate, membranous, glabrous; lower glume 1.6–2 mm, entire, apex acute to awned, awn *c*. 0.5 mm long; upper glume

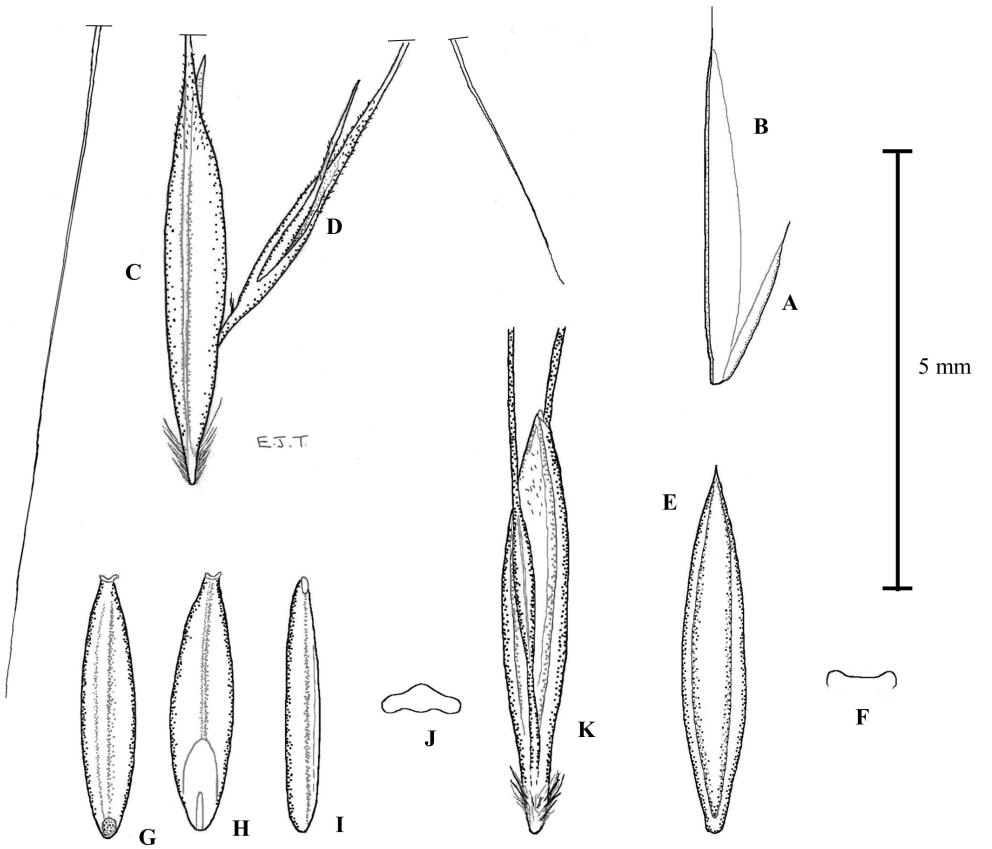

Fig. 14. Spikelet of ***Enteropogon pubifolius***. A. lower glume. B. upper glume. C. dorsal view of first floret. D. ventral view of second floret and dorsal view of third floret (second floret manipulated outward). E. dorsal view of first palea. F. transverse view of first palea. G. ventral view of caryopsis. H. dorsal view of caryopsis. I. Lateral view of caryopsis. J. transverse view of caryopsis. K. ventral view of first floret with dorsal view of second floret. All from *Thompson MOR841* (BRI). Del. E.J. Thompson.

4–4.3 mm long, apex attenuate to awned, awn to 0.9 mm long. Florets 2 or 3, 1 fertile, stipe *c*. 0.4 mm long. Lowest lemma elliptical, 4.1–5.1 mm long, 0.6–0.8 mm wide, membranous, smooth; apex acute, bilobed, lobes to 0.3 mm long; awn 7.5–8.5 mm long, straight, filiform. Palea subequal to lemma, membranous, minutely scabrid between the keels, apex acute. Anthers 3, chasmogamous 0.9–1 mm long; cleistogamous 0.7–0.9 mm long. Caryopsis of first floret 2.5–2.9 mm long, *c*. 0.7 mm wide. First rachilla *c*. 1.2 mm long, sometimes bearded towards the apex with hairs *c*. 0.3 mm long. Second lemma 1.4–1.9 mm long, 0.2–0.3 mm wide; awn 3.7–6.5 mm long. Palea present or absent, subequal to lemma. Second rachilla 0.2 mm long. Third lemma to 1.8 mm long, *c*. 0.1 mm wide; awn 1.4–1.9 mm long. Micromorphology of the lemmas: surface densely covered in relatively large cork cells and sparsely scabridulous with prickles and simple micro-hairs to *c*. 50 µm long; bicellular micro-hairs to 26 µm long (**Figs. 1, 6, 7, 14, 15**).

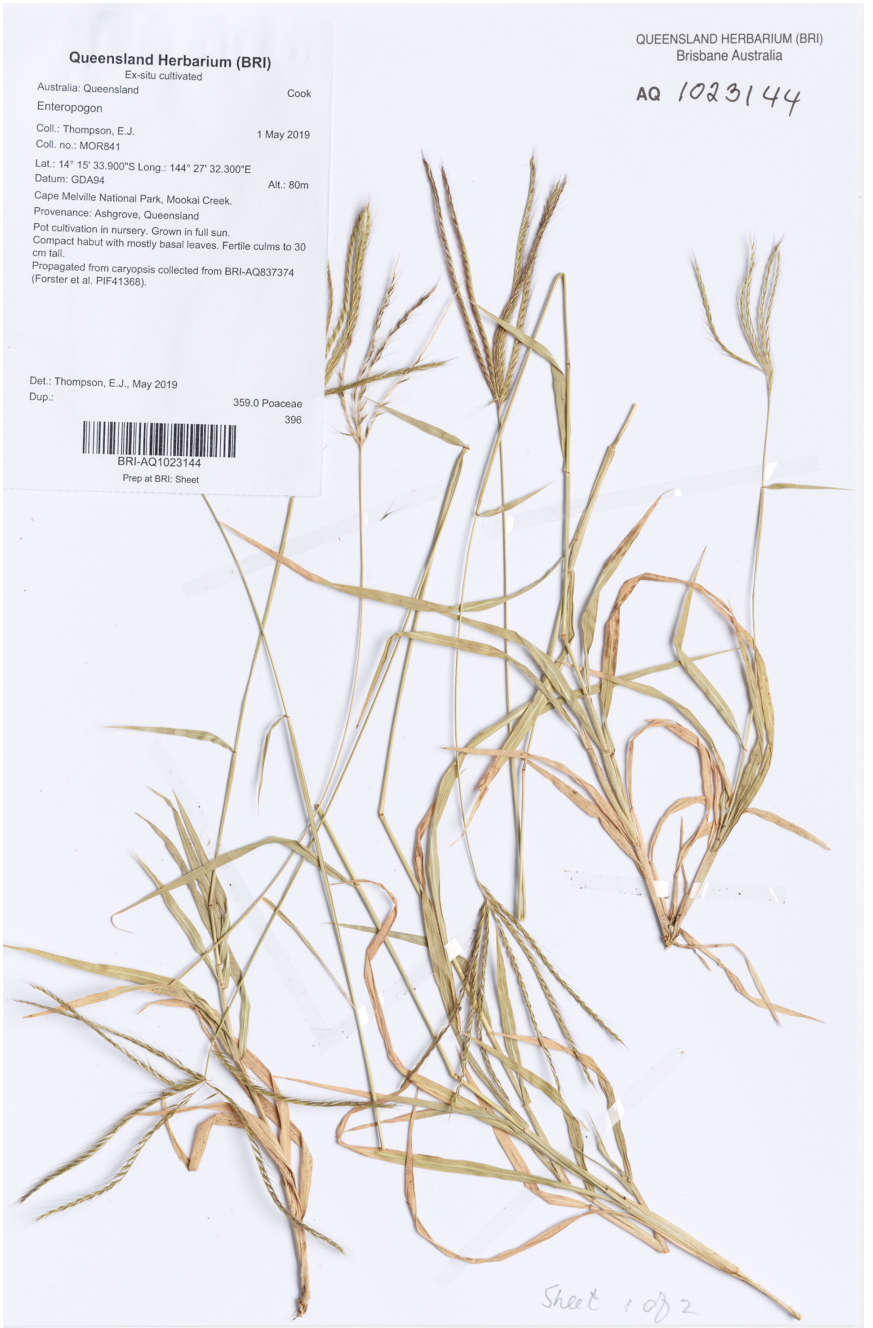

Fig. 15. Holotype specimen of ***Enteropogon pubifolius***. Sheet 1 of 2. Photo: Queensland Herbarium.

***Additional specimens examined*: Queensland.** Cook District: Cape Melville National Park, Mookai Creek, May 2014, *Forster PIF41368, S.L. Thompson & Cape Melville Traditional Owners* (BRI); Kings Plains Station, near Kings Plains Lake, Apr 2015, *McDonald KRM16891 & E.J. Thompson* (BRI); Alkoomie Station, Melody Rocks, Apr 2016, *McDonald KRM18361 & Forster* (BRI).

***Distribution and habitat*:** *Enteropogon pubifolius* is endemic to the tropical east coast of Queensland, Australia from northwest of Cooktown up to Cape Melville (**Map 2**). Plants have been collected from tussock grassland dominated by *Triodia microstachya* R.Br. intermingled with small copses of vinethicket on exposed granite bluffs and clifflines at Cape Melville; from small vinethicket patches on limestone karst on Alkoomie Station northwest of Cooktown and from a lake edge in woodland dominated by eucalypts and melaleucas at Kings Plains Station.

***Phenology*:** Plants produce flowers and fruits mostly in April–May.

***Notes*:** *Enteropogon pubifolius* has similarities to *E. paucispiceus* in growth habit and inflorescence typology. The spikelets dry dark grey (**Fig. 1**).

***Etymology*:** The specific epithet is derived from Latin and refers to the pubescent leaves.

***Conservation status*:** *Enteropogon pubifolius* is known from three herbarium specimens collected from three locations about 120 km apart. Populations at these sites are not accurately known so further field assessment is required. However, it is suggested that this species should be considered **Vulnerable** based on Criterion B2a (IUCN 2019) and a formal conservation status nomination should be made.

2. Enteropogon scabrilemma E.J.Thomps., **sp. nov.**

Similar to *E. macrostachyus* (Hochst. ex A.Rich.) Munro ex Benth., differing by having smaller spikelets with longer and more slender rachillas. **Type:** Queensland. Ex-situ CULTIVATED: Ashgrove (ex Riversleigh Station, on a remote mining exploration track), 1 May 2019, *E.J. Thompson MOR835* (holo: BRI [AQ1023137]).

***Illustrations*:** Lazarides (1972: 26; although the specimen source was not cited, morphology including collar and ligule (Figs. 48E&F) and spikelet with bearded rachilla apex (Fig. 49K) match *E. scabrilemma*).

Perennial grass, 70–90 cm high, tussock-forming, occasional decumbent culms rooting at the nodes. Culms erect, wiry, 5–8 noded, < 0.9 mm wide. Leaf blades 4–45 cm long, 2–9 mm wide, drying flat. Ligule 0.3–0.4 mm long; paraligule to 4.5 mm long. Leaf sheaths usually longer than the internodes, bearded at the orifice with stiff hairs 2–4 mm long, rounded on the back; collar glabrous. Inflorescence a digitate panicle with 1–5 racemes, 90–120 mm long, *c*. 1.5 mm wide and 2.5 mm thick, divaricate; rachis 0.5–0.6 mm wide, relatively stiff. Spikelets with 2 or 3 florets. Glumes narrow lanceolate, membranous, acute to awned, glabrous; lower glume 1.7–2.7 mm, entire, awn to 0.9 mm long; upper glume 4.2–5.6 mm long, awn to 1.9 mm long. Florets 2(or 3), 1 or 2 fertile; stipe *c*. 0.6 mm long. Lowest lemma chartaceous, elliptical, 4.1–6.5 mm long, 1–1.5 mm wide, scabrous; apex acute, bilobed, lobes to 0.3 mm long; awn filiform, straight, 10.7–16.4 mm long. Palea subequal to lemma, chartaceous, scabrid, apex acute, bilobed. Anthers 3, chasmogamous 1.5–1.7 mm long; cleistogamous *c*. 1.4 mm long. Caryopsis of first floret 3.5–4.9 mm long, 0.9–1.3 mm wide, keeled dorsally, ventrally concave. First rachilla 1.4–2.4 mm long, glabrous or bearded towards apex with hairs to 0.4 mm long. Second lemma, sterile or fertile, scabrid; fertile: cleistogamous, to 3.1 mm long and 0.7 mm wide; infertile: *c*. 1.1 mm long; awn 3.9–7.3 mm long. Palea present or absent, equal to lemma. Anthers 3, 1.2–1.8 mm long. Caryopsis of second floret *c*. 2.2 mm long, to 0.7 mm wide. Second rachilla 1–1.3 mm long. Third lemma sterile, vestigial to 1 mm long, awn *c*. 1.3 mm long. **Figs. 16 & 17**.

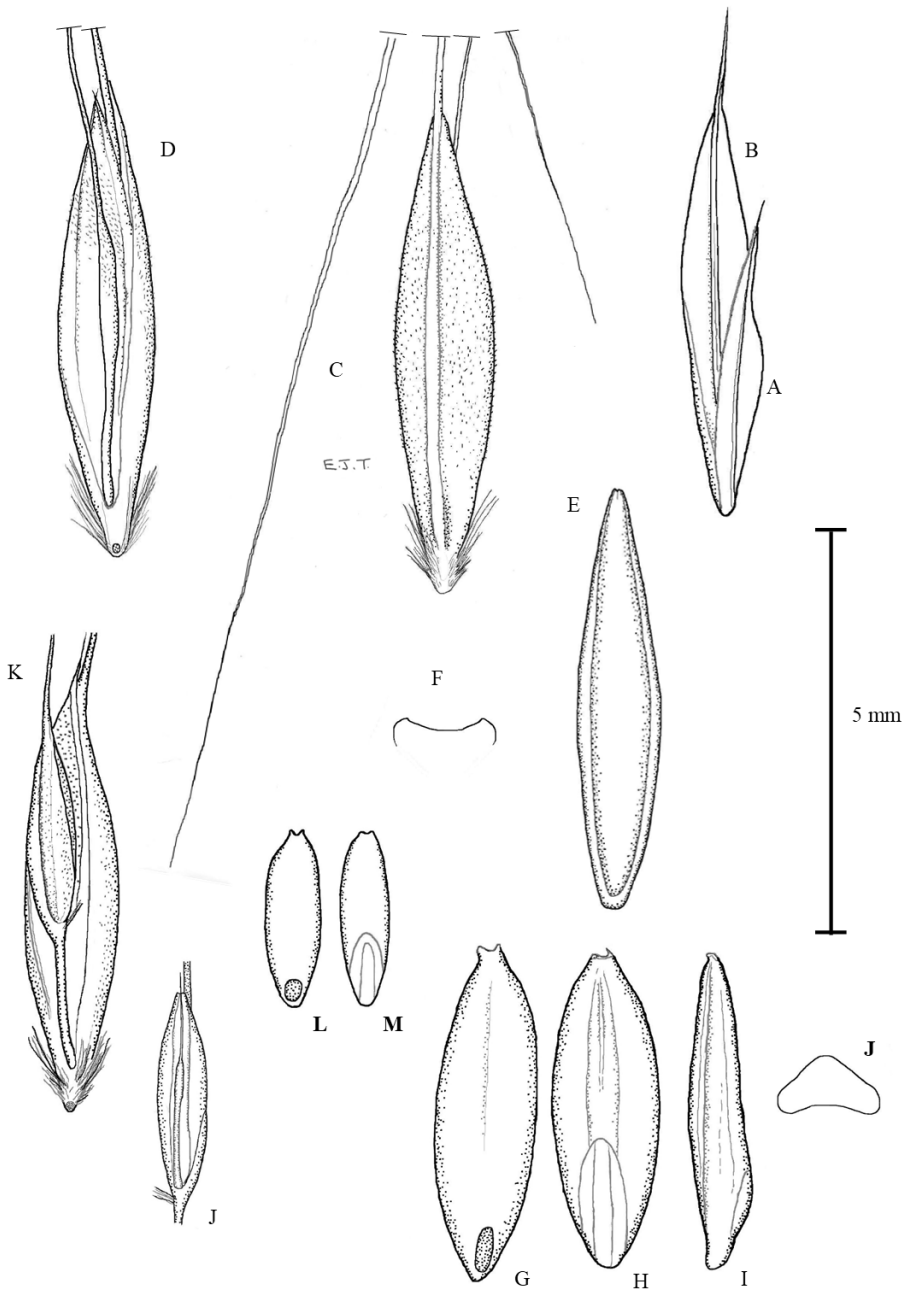

Fig. 16. Spikelet of ***Enteropogon scabrilemma***. A. lower glume. B. upper glume. C. dorsal view of first floret. D. ventral view of first floret and dorsal view of second floret. E. dorsal view of first palea. F. transverse view of first palea. G. ventral view of caryopsis. H. dorsal view of caryopsis. I. transverse view of caryopsis. J. dorsal view of fertile second floret showing third floret. K. ventral view of spikelet showing dorsal view of fertile second floret. L. ventral view of caryopsis from second floret. L. dorsal view of caryopsis from second floret. All from *Thompson MOR844* (BRI). Del. E.J. Thompson.

Fig. 17. Holotype specimen of ***Enteropogon scabrilemma***. Photo: Queensland Herbarium.

***Additional specimens examined*: Papua New Guinea.** Central Province: *c*. 1 mile [1.6 km] N of Kapa Kapa, Rigo Sub-district, July 1972, *Pullen 3278* (CANB); Tavai Creek area, *c*. 46 miles [74 km] SE of Port Moresby, Apr 1967, *Pullen 6829* (BRI). **Australia. Western Australia.** 3 km E of Cape Leveque, N Dampier Peninsula, *Carter 397* (PERTH); Gibb River – Kalumburu Mission Road; *c*. 2 km NE of Carson River crossing, 115 km (by road) NE of Mitchell River turnoff, *c*. 175 km NW of. Wyndham, Jun 1976, *Beauglehole 51960* (CANB); Long Island, Buccaneer Archipelago, NE of Derby, Apr 1997, *Martin CB101* (CANB); 13.5 km NE of Crystal Head on SW Osbourne Island, Mar 1989, *Keighery 10639* (PERTH); *Martin CB101* (PERTH); 3 km E of Cape Leveque, N Dampier Peninsula, May 1989, *Carter 397* (PERTH); Long Island, Buccaneer Archipelago, NE of Derby, Apr 1997, *Martin CB101* (PERTH); Wyndham, East Kimberley, Apr 1992, *Mitchell 2320 & Willing* (PERTH); Behind sand dune cemetery at One Arm Point, about 200 m N of Broome, Jul 1997, *Mitchell 4809* (BRI). **Northern Territory.** S of Wollogorang Station. Plot 1421, Oct 1998, *Harwood 535* (DNA). **Queensland.** Burke District: Riversleigh Station, on a remote mining exploration track, Jun 2006, *Booth CAM28-1 & Kelman* (BRI). Cook District: Princess Charlotte Bay, Aug 1980, *Buckley 6203* (BRI); *ibid*, Aug 1980, *Buckley 6330* (BRI); 2 km S of Bathurst Heads Camping Area, Kalpowar, Aug 2016, *Thompson SLT16513.1, Ross, Ross & Wallace* (BRI); Kings Plains Station, Kings Creek track, Apr 2017, *McDonald KRM19351, Forster & Paradise* (BRI); Cooktown, Quarantine Bay, May 1970, *Blake 23488* (BRI). **CULTIVATED.** Ashgrove, Mar 2017, *Thompson MOR836* (BRI); Ashgrove, Jun 2020, *Thompson MOR844* (BRI).

***Distribution and habitat*:** *Enteropogon scabrilemma* is widespread in coastal tropical Australia (Kimberley of Western Australia, top end of the Northern Territory, Cape York Peninsula, Queensland) and southern Papua New Guinea (**Map 2**). Plants occur in eucalypt dominated woodlands on sandy substrates such as dunes or alluvium along watercourses.

***Phenology*:** Dates of herbarium collections reveal flowering and fruiting throughout the year. Cultivated plants bore flowers mostly in summer.

***Affinities*:** Although specimens of *Enteropogon scabrilemma* were originally identified as *E. dolichostachyus*, *E. scrabilemma* has more morphological similarities to the African species, *E. macrostachyus*. *Enteropogon scabrilemma* and *E. macrostachyus* are very similar in growth habit, leaf size and distribution, and inflorescence characteristics including the number of racemes and spikelet imbrication. Both species have relatively broad scabrid spikelets and rachillas with a distal beard but *E. macrostachyus* has much larger lemmas (**Fig. 1**).

***Notes*:** *Enteropogon scabrilemma* has "monomorphic cleistogamous anthers" as defined by Thompson (2021) where the chasmogamous and cleistogamous anthers are of the same size. The second florets can be reduced to a lemma or sometimes present fertile with cleistogamous caryopses (**Fig. 16**). Spikelets dry straw-coloured (**Fig. 1**).

The additional specimens *of Enteropogon scabrilemma* cited above have mostly been stored in Australian herbaria as *E. dolichostachyus.*

Two specimens, *Keighery 10125* (CANB) from North Kimberley and *Lazarides 5635* (CANB), have morphological similarities to *Enteropogon scabrilemma* and *E. minutus*, respectively. The former specimen differs from *E. scabrilemma* by the smaller spikelets, slender growth habit and narrower leaves and the latter specimen differs from *E. minutus* by the larger spikelets and absence of contraligule.

***Etymology*:** The specific epithet is derived from Latin and refers to the scabrid lemmas.

***Conservation status*:** *Enteropogon scabrilemma* has a wide distribution; however, its abundance at any of its known locations is unclear. Further field investigation is required before its conservation status can be assessed.

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Appendix 1. List of vouchers of ***Enteropogon dolichostachyus*** and ***E. macrostachyus*** examined for the study.

Specimens cited by [1]Lazarides (1972); [2]Nightingale *et al*. (2005); [3]Peterson *et al*. (2015)

Specimen with dubious identification; more material required from the collection location on Middle Percy Island, Queensland

#Specimen with dubious identification; more material required from the collection location on Middle Percy Island, Queensland

syntype *Chloris dolichostachya*; viewed on JSTOR Plants (2022)

Collection location: **Au** Australia, **Af** Africa, **C** China, **E** East Timor, **P** Philippines, **S** Sri Lanka, **T** Thailand

E. dolichostachyus		
Anderson BES PEA 096 (PERTH) **Au**	*Gould 13702 & Cooray* (CANB) **S**	*Mitchell 4418* (PERTH) **Au**
Clayton 5118 (CANB) **S**	*Handasyde TH 4383* (PERTH) **Au**	*Menz BES MyM 041* (PERTH) **Au**
Clayton 5267 (CANB) **S**	*Handasyde THOO 245* (CANB) **Au**	*Mitchell 7960* (BRI; PERTH) **Au**
Clayton 5559 (CANB) **S**	*Harwood 535* (DNA) **Au**	*Muller s.n.* (CANB) **Au**
Clayton 5568 (CANB) **S**	*Hopkins BAO201* (PERTH) **Au**	*Nee s.n.* (MA30) **P**[##]
*Clayton 5809 (*CANB) **S**	*Kenneally KFK 10214 & Hyland* (PERTH) **Au**	*Russell-Smith 3970 & Lucas* (DNA) **Au**
Clayton 5863 (CANB) **S**	*Latz 10497* (BRI) **Au**[2]	*Ryves 22* (BRI) **T**
Clayton 5941 (CANB) **S**	*Lazarides 5635* (CANB) **Au**[1#]	*Ryves SL98/152 & Clement* (BRI) **T**
Cowie 191 (DNA) **Au**	*Lazarides 7416* (CANB) **Au**[3]	*Shin-Ming Ku 1697* (CANB) **C**
Cowie 493 (BRI) **Au**	*Low Choy 3209 & Mahney* (DNA) **Au**	*Tagawa 326, Iwatsuki & Fukuoaka* (CANB) **T**
Cowie 7988 & Mangion (DNA) **Au**	*Merrill 9275* (BRI) **P**	*Thompson MOR837* (BRI) **Au**
Cowie 13277 (BRI) **Au**	*Merrill 1308* (BRI) **P**	*Thompson MOR843* (BRI) **Au**
Dunlop 10227 & Cowie (DNA) **Au**	*Mitchell 4418* (BRI) **Au**	*Van Beusekom 2564* (CANB) **T**
Gould 13046 (CANB) **S**	*Mitchell 4809* (BRI) **Au**	
Gould 13690 (CANB) **S**[2]	*Mitchell 6491* (CANB) **E**	
E. macrostachyus		
Smook 917 (BRI) **Af**	*Davidse 5886* (BRI) **Af**	*Ryves K110 & Clement* (BRI) **Af**
Smook 7369 (BRI) **Af**	*Strickland 92* (BRI) cult. ex. **Af**	*Ryves 91K/247 & Clement* (BRI) **Af**
Gonde 48 (BRI) **Af**	*Rattray 1252* (BRI) **Af**	*Ryves 91K/110 & Clement* (BRI) **Af**

Appendix 2. Source of caryopses for propagation of cultivated plants of ***Chloris*** and ***Enteropogon***

Species	Voucher	Location
C. divaricata	*Forster PIF46376 & Leiper* (BRI)	south-eastern Queensland
C. ventricosa	*Thompson MOR806* (BRI)	south-eastern Queensland
E. acicularis 1	*Thompson EJT361 & Wang* (BRI)	south-eastern Queensland
E. acicularis 2	*Richter DR714 & Smith* (BRI)	western Queensland
E. acicularis 3	*Pennay CP309 & Richter* (BRI)	western Queensland
E. dolichostachyus	*Cowie 13277* (BRI)	Northern Territory
E. minutus	*Mostert MM395* (BRI)	central Queensland
E. paucispiceus	*Columbus 5103 et al.* (BRI)	central Queensland
E. pubifolius	*Forster PIF41368 et al*. (BRI)	north-eastern Queensland
E. ramosus	*Thompson MOR839* (BRI)	south-eastern Queensland
E. ramosus	*Thompson MUT98 & Speed* (BRI)	central Queensland
E. scabrilemma	*Booth CAM28-1 & Kelman* (BRI))	north-western Queensland
E. unispiceus	*Thompson EJT846 & Simon* (BRI)	south-eastern Queensland

Appendix 3. List of morphological characters.

Discriminating characters in terms of highest to lowest Kruskal-Wallis values, shown in brackets [ ] after each character, were generated from PATN analysis of the dataset composed of 10 samples of *Enteropogon* and 42 morphological characters using Gower association measure at the nine-group level.

[1] indicates new characters defined here and not used for the taxa in this study by other authors.

Vegetative

1. Growth habit: caespitose (0), rhizomatous (1), tufted with stolons (2)[09]

2. Widest leaves: < 4 mm (0), > 4 mm (1)[20]

3. Cross-sectional shape of back of leaf sheath just below collar especially when fresh and green: curved (0), keeled (1)[18]

4. Distribution of leaves: mostly basal (0), along culms (1)[14]

5. Leaf indumentum on abaxial surface: glabrous to very sparse (0), pilose (1)[38]

6.[1] Leaves with adaxial clear parenchyma at mid-vein (evident as pale strip on dry leaves or greyish on fresh leaves): no (0), yes (1)[33]

7. Ligule: fringed membrane, cilia equal length to membrane (0), ciliate membrane, cilia equal to or longer than membrane (1)[06]

8. Contraligule: absent or rarely present (0), present (1)[42]

9.[1] Paraligule: absent (0), with short hairs, < 3 mm long (1), long hairs, > 3 mm long (2)[04]

Inflorescences

10. Number of racemes: mostly 1–2 (0), usually 4–5 (1), mostly >7 (2)[02]

11. Rachis width relative to spikelet: c. equal (0), narrower (1)[36]

12.[1] Length of indumentum at junction of racemes: glabrous or hairs 0.1 mm long (0), short (c. 0.5 mm) (1), medium (< 1 mm) (2), long (1–3 mm) (3)[16]

13.[1] Culm (just below raceme junction) cross-sectional shape (dry specimens): circular (0), flattened or concave on one side (1)[43]

14.[1] Modal culm width: < 0.8 mm wide (0), > 0.8 mm wide (1)[25]

Spikelets

15.[1] Stipe: absent or short (0), conspicuous (1)[24]

16. Number of fertile florets per spikelet: one (0), up to two (1)[21]

Glumes

17. Colour of glumes when fresh: green or purple (0), pink (1), purple (2)[05]

18. Relative length of lower glume to upper glume (excluding awn if present): < 1:2 (0), c. 1:2 (1)[37]

1st lemma

19. Compression: dorsi-ventral (0), lateral (1)

20. Texture: membranous to chartaceous (0), cartilaginous (1)[29]

21. Lemma apex: lobes inconspicuous or absent (0), present (1), conspicuous (2)[22]

22. Lemma width: < 1.0 mm, > 1.0 mm (1)[28]

23. First lemma awn length relative to body: *c*. 1.5 times as long (0), 1.5–2 times as long (1), three times as long or more (2)[27]

24.[1] Colour of awns when fresh: purple (0), green (1), pink (2)[10]

25. Colour of mature lemma when dry: straw coloured (0), purple (1), dark grey to black (2)[01]

26.[1] Length of anthers: *c*. 0.4 mm (0), 0.5–1 mm (1), 1.1–1.9 mm (2)[35]

27.[1] Length of micro-hairs on lemma: absent (0), < 60 µm (1), 60–120 µm (2)[03]

28.[1] Density of micro-hairs at middle of lemma: absent or rarely present (0), sparse to common (1), abundant (2)[07]

29.[1] Cork cell spacing: regular (0), irregular (1)[17]

30.[1] Cork cell separation: < one diameter (0), frequently two diameters (1)[31]

31.[1] Size of cork cells (µm): small (< 15 µm) (0), large (> 20 µm) (1)[19]

32.[1] Relative size of silica body to total size of cork cell: < half of area (0), > half of area (1)[12]

33.[1] Cork cell silica body shape: crescent (0), rectangular (1)[30]

34. Relative length of proximal cell to distal cell of bicellular micro-hairs: *c*. equal (0), shorter (1)

1st palea

35. Keels of first palea: minutely scabrid (0), minutely ciliate (1)

36. Shape of apex of first palea: acute (0), obtuse (1)

37. Apex of first palea: entire (0), bifid (1)[11]

Stigmas

38. Stigma colour: purple (0), pink (1)

39.[1] Length of longest stigma branches: < 200 µm (0), *c*. 300 µm (1)

40.[1] Spacing of stigma branches: close (0), wide (1)[40]

41.[1] Shape of apex of stigma lobes: pointed (0), rounded (1)

Caryopsis

42.[1] Shape in transverse section: flattened with a ridge on the dorsal surface (0), triangular (1)

43.[1] Caryopsis width to length ratio: < 1: 3 (0), *c*. 1:3 (1)[41]

44. Scutellum length relative to caryopsis: c. 1/3 (0), *c*. ½ (1)

1st rachilla

45. Rachilla with distal beard: no (0), yes (1)[13]

46.[1] Width of rachilla relative to callus: narrower (0), as broad (1)[23]

47. Relative length of rachilla to 1st lemma (including lateral lobes): 20–29% (0), 30–40% (1), *c*. 50% (2) [32]

2nd lemma

48. Relative length of second lemma to first lemma: 1/3 or less (0), *c*. ½ (1), > ½ (2)[08]

49. Second lemma awn length relative to 1st lemma awn: less than half (0), *c*. half (1), *c*. equal (2)[34]

50. Width of 2nd lemma relative to 1st: much narrower (0), *c*. half as wide (1)

51. Second lemma lobes: inconspicuous or absent (0), conspicuous (1)[39]

Leaf and culm anatomy

52.[1] Relative size of lateral bulliform cells to median in triads in leaf transverse section: *c*. ½ half (0), *c*. 1/3 (1)

53.[1] Relative size of thick-walled cells in abaxial arc vs. adaxial arc of inner ring of vascular bundle of leaf mid-vein: smaller (0), larger (1)

54. Shape of outline of abaxial sclerenchyma below vascular bundle of leaf mid-vein: even (0), irregular (1)

55.[1] Width of layer of thick-walled cells between xylem and phloem of vascular bundle of leaf mid-vein: 1 cell (0), 2 or 3 cells (1)

56.[1] Transverse strip of sclerenchyma between chlorenchyma and cuticle of culm: absent (0), present (1)

57.[1] Spacing of culm vascular bundles associated with chlorenchyma: close (0), wide (1)[26]

58.[1] Inner primary vascular bundles of culms encircled by clear cells: no (0), yes (1)[15]

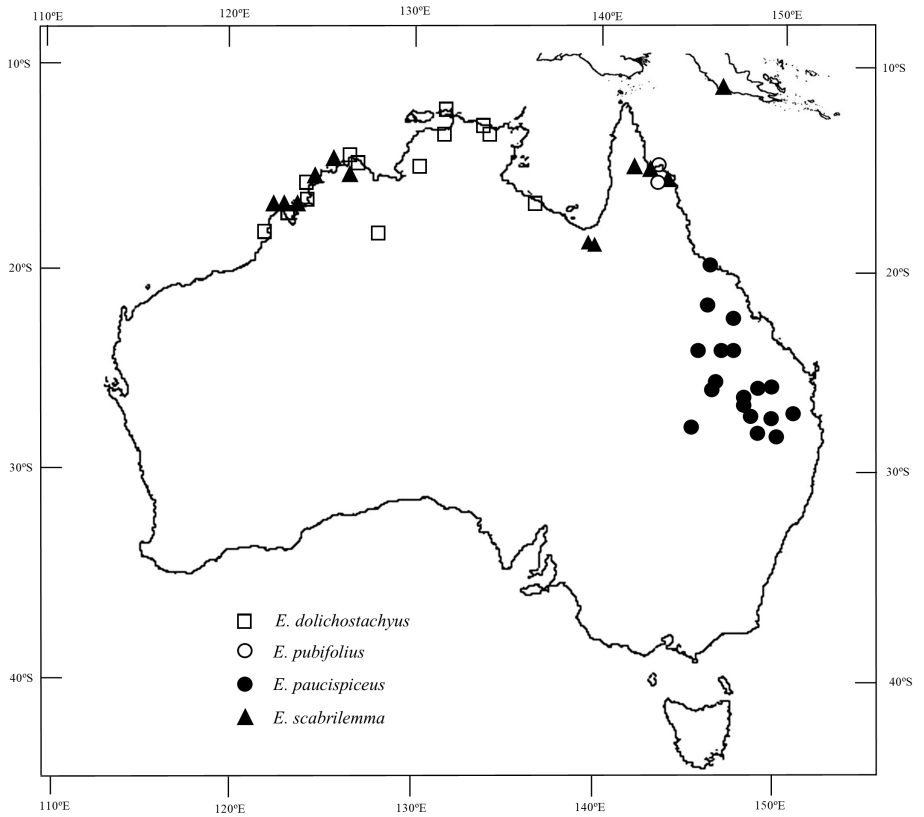
Appendix 4. Data matrix used for the morphometric anlaysis of species of *Enteropogon*, with *Chloris* as outgroup taxa.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58
Chloris divaricata	2	0	1	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	2	0	2	0	2	0	1	1	1	1	0	1	0	0	1	1	0	1	1	1	1	1	0	1	0	0	2	1	1	1	1	1	1	0	0	0	0	0
Chloris ventricosa	2	1	1	0	1	1	0	0	0	1	1	1	0	0	0	0	2	0	0	0	2	1	0	0	2	1	0	0	1	1	0	1	0	0	1	1	0	1	1	1	1	1	0	1	0	0	2	1	0	1	0	1	1	1	0	0	0	0
Enteropogon acicularis 1	1	0	1	0	0	1	1	0	0	2	1	3	0	1	0	0	2	1	1	0	0	0	0	0	1	2	2	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	1	1
Enteropogon acicularis 2	1	0	1	0	0	1	1	0	0	2	1	3	0	1	0	0	2	1	1	0	0	0	0	0	1	2	2	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	1	1
Enteropogon acicularis 3	1	0	1	0	0	1	1	0	0	2	1	3	0	1	0	0	2	1	1	0	0	0	0	0	1	2	2	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	1	1
Enteropogon dolichostachyus	2	1	1	0	0	1	0	0	2	1	1	3	0	0	0	0	2	0	1	0	0	0	0	0	1	2	1	2	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0
Enteropogon macrostachyus	0	0	1	1	0	1	0	0	2	0	1	3	0	0	0	1	0	1	1	1	1	1	0	0	0	2	1	1	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	1	1	0	2	1	0	1	0	0	0	1	1	0	0
Enteropogon minimus	0	0	0	1	0	0	0	1	1	1	0	3	1	0	0	0	2	1	1	0	0	0	2	2	2	2	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0
Enteropogon paucispiceus	0	0	0	0	0	1	1	0	2	1	1	3	0	0	1	0	0	1	1	0	0	0	0	0	2	0	2	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0
Enteropogon pubifolius	0	1	0	0	1	1	0	0	2	1	1	2	0	0	0	1	0	1	1	0	1	0	0	1	2	2	1	1	1	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	1	1	0	0	0
Enteropogon ramosus	0	0	1	1	0	1	1	0	0	1	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1	1	0	1	1
Enteropogon scabrilemma	0	1	1	0	0	1	0	0	2	0	1	3	0	0	0	1	2	1	1	1	1	1	1	0	1	2	2	2	0	0	1	1	1	1	0	0	1	0	0	0	0	0	1	0	1	1	1	2	0	0	0	0	0	1	1	0	0	0
Enteropogon unispiceus	0	0	1	1	0	0	0	0	1	0	1	2	0	0	1	0	1	1	1	0	0	0	0	0	2	2	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	1	1	0	0

Appendix 5. Results from cluster analyses using PATN

Variable	Description of variation	Remarks
Algorithm	Classification and ordination analyses using two association measures, Czekanowski (Bray & Curtis) and Gower metric	Topologies for dendrograms differ most notably by the variable position of *E. dolichostachyus*. The latter is clustered with *E. scabrilemma* and *E. macrostachyus* in dendrograms generated from analyses using Czekanowski, and with *E. pubifolius* from Gower. *E. minimus* and *E. unispiceus* consistently form a cluster. Topologies for ordinations consistently show three major groups 1. *E. dolichostachyus*, *E. scabrilemma* and *E. macrostachyus*, 2. *E. minimus* and *E. unispiceus*, and 3. *E. acicularis*, *E. pubifolius*, *E. ramosus* and *E. paucispiceus*.
Sample set composition	Two sets of samples: 1. baseline without *Chloris* comprising 11 samples and 2. with *Chloris* comprising 13 samples	Corresponding topologies from analysis of datasets with and without *Chloris* were concordant for dendrograms and for ordinations.
Character format	All characters transformed to binary format. Two character sets: 1. 72 binary characters from baseline with 43 characters with 11 multistate 2. 87 binary characters for sample that includes *Chloris* from 58 after characters with 13 multistate	Both sets of topologies for dendrograms and ordinations were affected by the format of the characters. The position of *E. ramosus* was affected in dendrograms but the composition of the three major groups (see above) were maintained in ordinations.
Character set composition	Five datasets were developed from a list of the most discriminating characters based on Kruskal-Wallis (KW) values generated from analysis of the baseline dataset using both association measures. The five datasets were established by successively removing groups of five characters with the lowest KW values, i.e. 40, 35, 30 and so on.	Topologies for dendrograms and ordinations were affected for datasets of 30 characters or less.

Map 1. Frequency (number of species) distribution of ***Enteropogon*** in Australia within climatic zones modified from BoM (2020) following Thompson (2021). Data from AVH (2021) and Nightingale *et al*. (2005).



Map 2. Australian distribution of ***Enteropogon dolichostachyus***, ***E. paucispiceus***, ***E. pubifolius*** and ***E. scabrilemma***.