

## New species and variation in *Lepidobolus* (Restionaceae) from Western Australia

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### Abstract

Three new species of *Lepidobolus* are described: *L. densus* B.G.Briggs & L.A.S.Johnson, *L. eurardyensis* K.W.Dixon & B.G.Briggs, and *L. quadratus* B.G.Briggs & L.A.S.Johnson. A significant extension of range to the north-west is reported for *L. deserti* Gilg. Variation in *L. preissianus* Nees is briefly discussed.

### Introduction

Including the three described here, *Lepidobolus* Nees (1846: p. 66) comprises one species (*L. drapetocoleus* F.Muell. ex Benth.) in western Victoria and eastern South Australia and eight species in the southern half of Western Australia. It is a member of a clade of closely allied genera, along with *Desmocladus* Nees, *Catacolea* B.G.Briggs & L.A.S.Johnson, *Coleocarya* S.T.Blake, *Harperia* W.Fitzg. and *Onychosepalum* Steud., which share a 1-locular ovary, single style and indehiscent fruit. The clade is robustly supported in morphological (Linder et al. 2000) and molecular phylogenies (Briggs et al. 2000, Briggs et al. 2010). Except for *Coleocarya* in eastern New South Wales and southeast Queensland, most of these genera are plants of semiarid regions. DNA sequence data (Briggs et al. 2010) suggest that some of these genera may be para- or poly-phyletic and changes to the generic classification may be expected, but that the species of *Lepidobolus* sequenced (*L. chaetocephalus* F.Muell. ex Benth., *L. deserti* Gilg and *L. preissianus* Nees) form a well-supported monophyletic group.

Further study is needed of variation and population dynamics in *Lepidobolus* and we suspect that there may be some intergradation between the species recognised here. Nevertheless it is appropriate to provide names for the three undescribed entities that are now apparent.

### Description of new species

*Lepidobolus densus* B.G.Briggs & L.A.S.Johnson, **sp. nov.**

**Diagnosis:** distinguished among the species of *Lepidobolus* by the following combination of characters: plant caespitose; culms tall (40–70[–100] cm long), terete; cauline sheaths 5–8, oblong, (1–)1.5–2.3 cm long, caducous; male inflorescence of 1–3 spikelets, female inflorescence of 2–4 spikelets, spikelets long (1–2.5 cm long), glumes broad-ovate, mucro 1–3 mm long.

<sup>†</sup>Deceased 1997

**Type:** Western Australia: 12 km SSE of Coorow on Geraldton Highway (Midlands Road), *B. Briggs* 7758 & *L. Johnson*, 1 Oct 1984, ♀ (holo: NSW 296663; iso: PERTH, CANB, PRE).

Plant densely tufted, forming large, dense, many-stemmed tussocks to 30(–90) cm diam., the culms crowded at the base; rhizomes erect or shortly spreading, pubescent, cataphylls glabrous. Culms erect, terete, straight to sinuose, 0.4–0.7[–1] m long, 1.1–1.5 mm diam., simple, smooth to sub-rugose, glabrous, lowest internode partially pubescent; internodes 6–9. Sheaths: basal sheaths dark red-brown or black, 3–9 mm long; cauline sheaths 5–8, caducous, oblong (10–)15–23 mm long, scarious, dark toward base, light-brown in upper half, usually glabrous; margins pale and membranous; apex obtuse, rarely with a few short hairs; mucro short erect, 0.5–1.6 mm long. Inflorescence: spikelets solitary and terminal or several on the culm; subtending bracts often persistent, mucro on female bracts short or absent. Male spikelets 1–3 per inflorescence, globose to ellipsoidal, 1–2 cm long and 1–1.5 cm wide, with more than 50 fertile upper glumes and c. 14 sterile lower glumes; upper glumes oblong, attenuate, 5.0–5.8 mm long, 1.5–2.5 mm wide, with a 1.0–1.4 mm long mucro, pale- to dark-brown and often ciliate at the apex; lower glumes broader with a shorter mucro. Female spikelets 2–4 per inflorescence, ellipsoidal, 1.5–2.5 cm long and 0.5–1 cm wide; with 16–30 fertile upper glumes and 6–23 sterile lower glumes; glumes broad-ovate, c. 5 mm long, 4–4.5 mm wide, abruptly tapered to a 1.1–3.0 mm long mucro, dark-brown and ciliate toward the apex with white hairs. Male flowers: tepals 5; outer tepals keeled, oblong to obovate, attenuate, often apically ciliate, 3.5–5.3 mm long; inner tepals thin, oblong, truncate, 4.5–6 mm long; filaments 6–7 mm long; anthers 2.2–3.4 mm long. Female flowers: tepals 5, mostly membranous; outer tepals keeled, 3.2–5.5 mm long, inner tepals 2.4–4.5 mm long, rarely apically ciliate; gynoecium with a single loculus and style. Nut ovoid, dark brown to black, 1.8 mm long with a conical beak 0.8 mm long; seed ovoid, dark-brown. Killed by fire, regenerating by seed. (Fig. 1.)

The epithet refers to the crowded culms in a dense tussock: *densus* (Latin) = close, compact.

**Distribution:** Western Australia, in the Geraldton Sandplains, Avon Wheatbelt and Yalgoo biogeographic regions. On yellow lateritic sand and laterite gravel, often in scleromorphic heath.

**Conservation status:** Western Australian Declared Flora priority 3, i.e. poorly known taxon including some populations that are not currently endangered.

**Notes:** while still not formally named, this species was excellently illustrated and its characters outlined by Meney et al. (1999). It is characterised by its dark bases, densely crowded and moderately stout culms, caducous cauline sheaths, and long spikelets. It differs from *L. deserti* in its taller culms, much larger spikelets and upper cauline sheaths that are oblong, (1–)1.5–2 cm long, and usually caducous. *L. deserti* has culms 20–40 cm tall, spikelets 0.6–1.2 cm long and upper cauline sheaths that are ovate to broad oblong, 0.5–1.2 mm long and often persistent. The same features, and the lack of extended horizontal rhizomes, distinguish *L. densus* from *L. preissianus*.

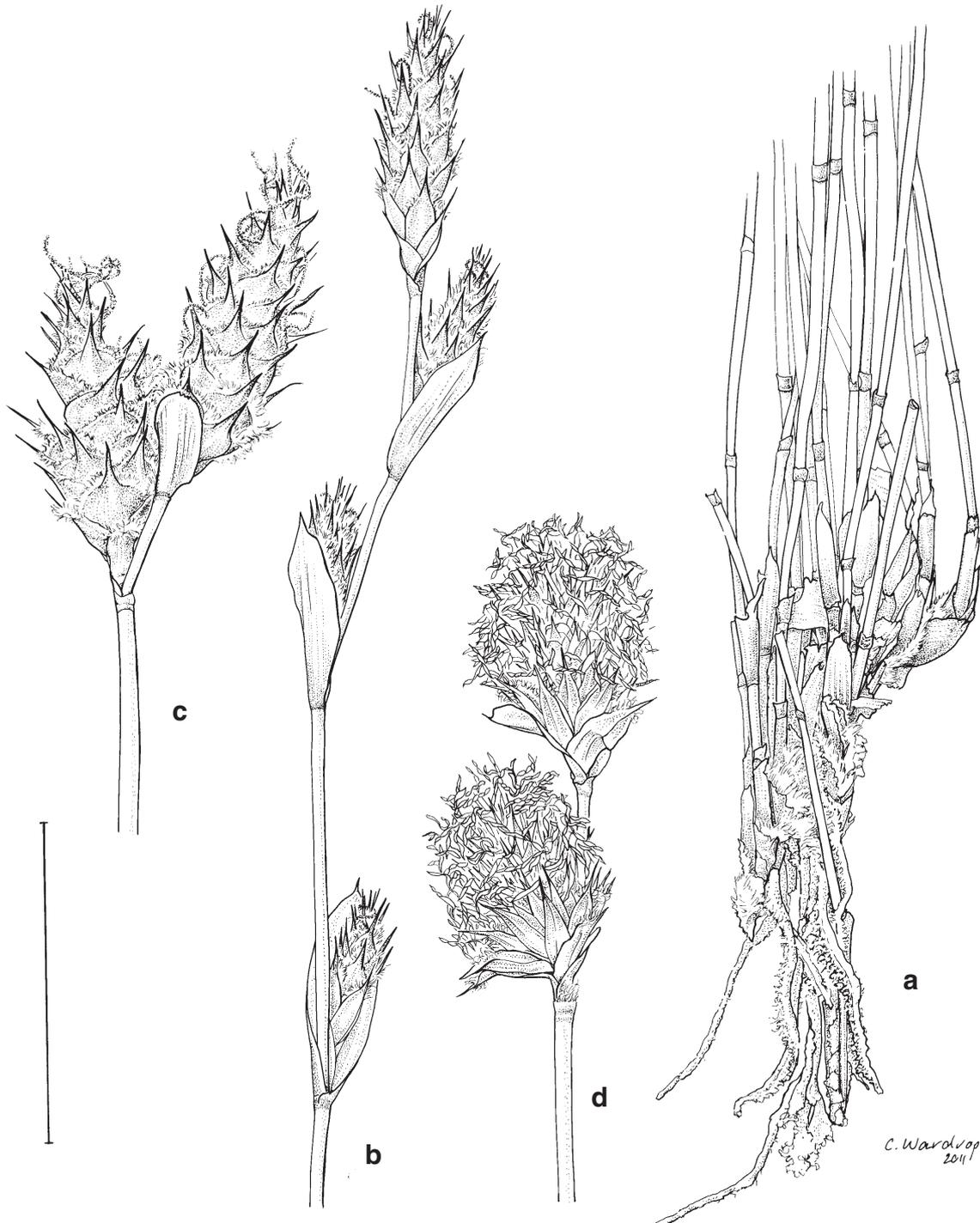
**Selected specimens examined** (north to south sequence): c. 1 km N of Withnell [as Whitnall], *C. Page* DH138, 29 Aug 2006 ♂ (PERTH); Point 11.5 km N of Sandy Point Outcamp, Dirk Hartog Island, *A. George* 11556, 5 Sep 1972 ♂ (PERTH, CANB, K); 16 miles [26 km] S of Wannoo Roadhouse, *C. Gittins* 1547a, Aug 1967 ♀ (PERTH, NSW, NBG); Kalbarri, *D. & B. Bellairs* 177.8, 1 Sep 1984 ♀ (PERTH); Kalbarri National Park, lookout north-west of the start of the Loop track, *B.G. Briggs* 8860a & *L.A.S. Johnson*, 12 Aug 1991 ♂ (NSW, PERTH); S of Oolinyarra, Murchison R., *Oldfield* s.n. ♂ (MEL, K); Ebbano, *A. Morrison*, 23 Sep 1904 ♀ (PERTH, K); 20 km NE of Yandanooka, *R. Soullier* 653, Aug 1998 (PERTH, NSW); 35.5 km NE of Brand Highway on Eneabba–Three Springs Rd, *K. Dixon*, 13 Oct 1992 ♂ (NSW, PERTH), ♀ (NSW, CANB, PERTH); 12 km SSE of Coorow on Geraldton Hwy (Midlands Rd), *B.G. Briggs* 7757 & *L.A.S. Johnson*, 1 Oct 1984 ♂ (NSW, PERTH); 18 km N of Marchagee on Midlands Rd, *B.G. Briggs* 7768 & *L.A.S. Johnson*, 1 Oct 1984 ♂ (NSW, CANB, K, MO), 7769 ♀ (NSW, AD, PERTH); 18 km N of Marchagee on Midlands road, *R.J. Cranfield* & *P.J. Spencer* 8369, 3 Nov 1992 ♀ (PERTH, K); Marchagee Nature Reserve, *N. Gibson* 4356, 3 Oct 2000 ♀ (PERTH, NSW); 6 miles [10 km] E of Ballidu, *R. Royce* 2108 ♂, 2109 ♀, 9 Sep 1947 (PERTH); Cowcowing, *M. Koch* 1210 p.p., Sep/Oct 1904 (PERTH); Trayning Reserve, *A. Chapman* 15, 5 Nov 1972 (PERTH).

***Lepidobolus eurardyensis*** K.W.Dixon & B.G.Briggs, *sp. nov.*

**Diagnosis:** distinguished from *L. deserti* by the following characters: the hairs of the rhizomes shorter, female plants with spikelets, glumes and glume mucros larger. Differing from *L. densus* and *L. preissianus* in its slender culms, short cauline sheaths and small spikelets; also differing from *L. preissianus* in its short rhizomes.

**Type:** Western Australia: Eurardy, 27°34'6"S, 114°39'25"E, *K.W. Dixon* 1026, 4 October 2008 ♂ (holo PERTH; iso CANB, NSW)

Small tufts to larger dense tussocks. Rhizomes short, horizontal or ascending, slender (c. 3 mm diam.), pubescent with pale hairs to 4–5 mm long, partly covered by glabrous cataphylls that are dark red-brown toward the base, pale and scarious above. Culms simple, terete, straight to sinuose, 25–50 cm tall, slender, 0.5–1.0 mm diam., finely



**Fig. 1.** *Lepidobolus densus*. **a**, plant base; **b**, young female inflorescence; **c**, older female inflorescence; **d**, male inflorescence. (a & b from holotype; c from *Dixon* NSW 2611840; d from *Briggs* 7768). Scale bar: a = 3 cm; b, c, d = 2.5 cm.

tuberculate, finely striate with ridges over the outer vascular bundles, glabrous, internodes 5–6. Cauline sheaths usually caducous, oblong, 6–10 mm long, scarious, dark- to light-brown, glabrous; margins pale, membranous; apex obtuse; mucro short, 0.5–1 mm long. Inflorescence of 1–4 spikelets which are sessile or on slender branches to 22 mm long; bracts subtending spikelets ovate to oblong, usually persistent, 3–10 mm long, the apex blunt with a short mucro. Male spikelets globular, c. 1 cm long; glumes narrow oblong, c. 3 cm long, blunt, pale brown, ciliate at the apex, with a mucro c. 1 mm long; 5–8 lower glumes larger and persistent when upper glumes have fallen. Female spikelets ellipsoidal or narrow ellipsoidal, 0.8–1.3 cm long and 0.5 cm wide; with c. 15 fertile upper glumes and several sterile lower glumes; glumes ovate, attenuate, 4–5 mm long, c. 2 mm wide, light- to darkish-brown, apically ciliate with short white hairs, with a slender black mucro 2–3 mm long; spikelets shattering and glumes and flowers readily falling from the axis on drying. Male flowers: tepals 5, membranous; outer tepals oblong, keeled, shortly aristate, 4–4.5 mm long, 1.5 mm wide; inner tepals longer, oblong to narrow spatulate, truncate, c. 5 mm long. Female flowers: tepals 5, membranous; outer tepals lanceolate, keeled, acuminate, 3–3.5 mm long, apically ciliate; inner tepals spatulate to ovate, c. 2 mm long; gynoeceum with a single loculus and style. Nut mostly shed with tepals attached, ovoid, dark brown to black, 1.5 mm long with a rounded or conical beak 0.5–1.2 mm long; seed globular, brown, 1 mm long. Suspected to be fire sensitive and regenerating by seed. (Fig. 2.)

The epithet refers to the Type locality, Eurardy Station, in the central west of Western Australia.

**Distribution:** Western Australia, on the Geraldton Sandplains. Known from about 70 km ENE of Geraldton and inland from Kalbarri, which is about 140 km further north. Grows in yellow sand to yellow sandy loam, in shrubland or with *Ecdeiocolea*.

**Conservation status:** poorly known, and in an area insufficiently visited by botanists. As the species is potentially fire sensitive and appears to be restricted in distribution, we recommend that it receive priority conservation status.

**Notes:** distinguished from *L. deserti* Gilg in its lack of very long (1–2 cm), white hairs on the rhizomes; less conspicuously ciliate male glumes; female spikelets, glumes and glume mucros all larger. Differing from *L. densus* in its slender culms, short cauline sheaths and smaller spikelets, and from *L. preissianus* in these features and in its short rhizomes.

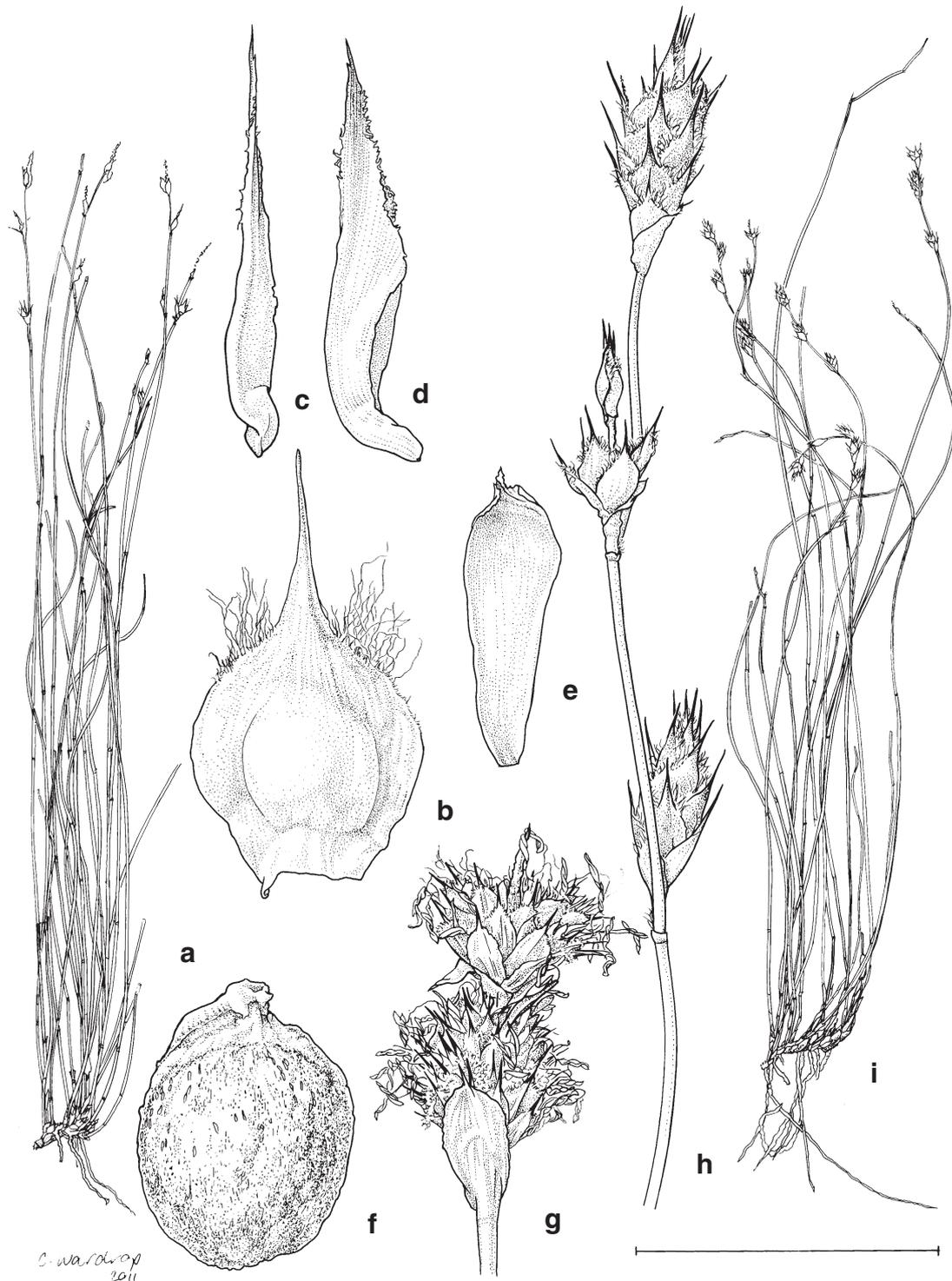
**Specimens examined:** Geraldton–Mt Magnet Road between Erangy Spring Rd and Moore Rd, B.G. Briggs 9911, 20 Oct 2008 ♀ (NSW, PERTH); Moore Road, 6.9 km S of Geraldton–Mt Magnet Road, B.G. Briggs 9916 ♂, 9917 ♀, 20 Oct 2008 (NSW, PERTH).

***Lepidobolus quadratus*** B.G. Briggs & L.A.S. Johnson, *sp. nov.*

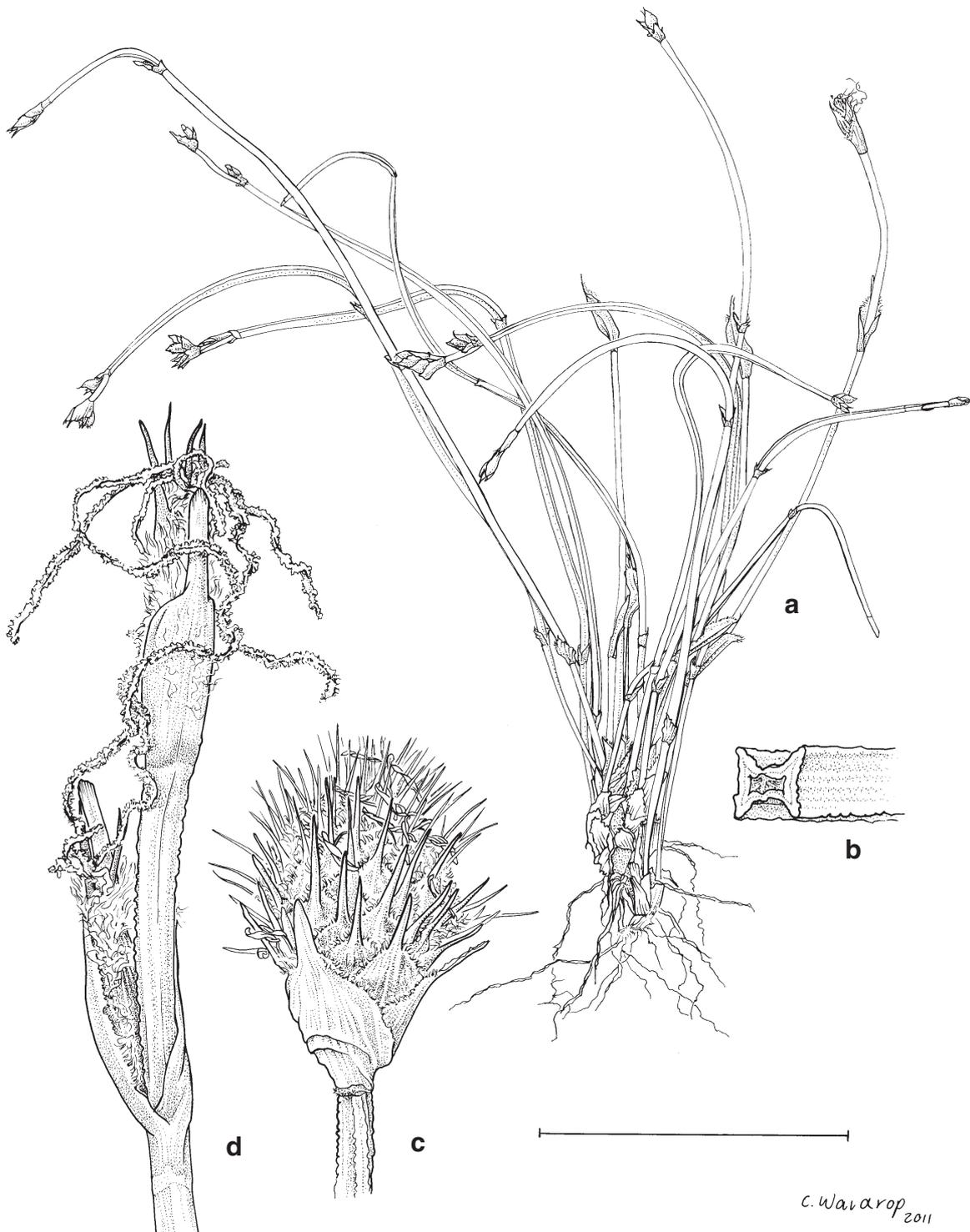
**Diagnosis:** Distinguished among the species of *Lepidobolus* by the following combination of characters: plant caespitose; culms 9–30 cm long, sharply angled, square in cross-section, with 1–3 culm sheaths; cauline sheaths mostly persistent, 0.6–1.9 cm long; male spikelets solitary, females 1–2 per culm.

**Type:** Western Australia: 2 miles [3.2 km] N of Badgingarra, C. Gittins 1723a, Sep 1967 ♀ (holo: NSW 102485; iso: CANB, MEL, PERTH)

Plant densely tufted; rhizome pubescent; cataphylls glabrous. Culms erect or spreading, quadrangular, the angles prominent and often scabrous, the sides concave when dry or ribbed, straight or flexuose, 9–30 cm long, 0.7–1.5 mm diam., glabrous or sparsely pubescent, yellowish-green, brittle when fresh; internodes few. Sheaths: basal sheaths oblong to broad-ovate, dark red-brown, glossy 0.7–2.8 cm long, often shortly pubescent, apex acute with a short lamina, c. 2.5 mm long; cauline sheaths 1–3, usually persistent, broadly spatulate, lax and open, 0.6–1.9 cm long, greenish to light- to dark-brown; apex obtuse to truncate to emarginate; margin narrowly membranous with white hairs; lamina 2–7 mm long. Inflorescence: male spikelets mostly solitary and terminal on the culm; female 1–2 on the culm; subtending bracts rigid, ovate or broad ovate, ciliate, 2–3 mm long, with a stout blunt green mucro 2–2.5 mm long. Male spikelets ovoid, 7–14 mm long, 3.5–8.0 mm wide; upper glumes 20–60 (–c. 100), ovate, aristate, 3–4.5 mm long, ribbed, light- to dark-brown, glossy; margin with white hairs; mucro 1.5–2.5 mm long; lower 5–8 glumes with shorter mucros and subtending abortive flowers. Female spikelets narrow-cylindrical when young, becoming ellipsoidal and broader with age, 7–8 mm long, initially 1.5–2.0 mm wide but becoming more than twice as broad; the lower 4–6 glumes sterile and the upper 7 or 8 fertile, similar to males, abaxial surface partially pubescent; mucro erect, to 1.5 mm long. Male flowers: tepals 5, ± equal in length, 2.5–4.0 mm long, oblong to oblanceolate, obtuse to acute and very shortly ciliate; filaments 3.8–4.2 mm long; anthers 0.9–1.4 mm long. Female flowers: tepals 1 or 2, folded, truncate, 1.5 mm long; gynoeceum with a single loculus and style. Nut ovoid, 2.0–2.5 mm long. Seed ovoid, brown, c. 1.1–1.7 mm long. Killed by fire, an obligate seeder species. (Fig. 3.)



**Fig. 2.** *Lepidobolus eurardyensis*. **a**, habit; **b**, glume (female); **c**, **d**, outer tepal, dorsal and lateral views; **e**, inner tepal; **f**, fruit; **g**, male inflorescence; **h**, female inflorescence; **i**, habit. (a–e from holotype; f from *Briggs 9916*; g from *Briggs 9911*; h from *Briggs 9916*). In (a) the glumes and flowers have fallen, leaving only the spikelet axes and bracts. Scale bar: a, i = 12 cm; b = 6 mm; c–e = 3 mm; f = 2 mm; g, h = 1.5 cm.



**Fig. 3.** *Lepidobolus quadratus*. **a**, habit; **b**, culm cross section; **c**, male inflorescence; **d**, female inflorescence. (a & b; from holotype; c from Gittins 1723b; d from Briggs 8604). Scale bar: a = 6 cm; b = 0.5 mm; c = 1.2 cm; d = 6 mm.

The epithet refers to the sharply angled culms that are square in cross-section; *quadratus* (Latin) = four-cornered, square.

**Distribution:** Western Australia, on the Geraldton Sandplains, from near Eneabba south to the Moore River. On laterite or on sand with lateritic gravel, in scleromorphic heath.

**Conservation status:** Western Australian Declared Flora priority 3.

**Notes:** while still not formally named, this species was illustrated and its characters described in Meney et al. (1999). The culm angles are marked by thickening of the subepidermal sclerenchyma as well as a group of sclerides in the chlorenchyma and a vascular bundle in the angle, rather than being due to enlargement of epidermal cells as occurs in some other Restionaceae (*Cytogonidium*, *Dielsia*) with angled stems. Ribbing of the faces of the stem is over outer vascular bundles. *L. quadratus* resembles *L. chaetocephalus* in the tufted base, dark cataphylls and spikelets with short mucros; differing in the four-angled culms. *L. chaetocephalus* has terete culms and is generally a larger plant.

**Selected specimens examined:** Western Australia: c. 8 km S of Eneabba, A. Hopkins, 20 Oct 1978 (PERTH); c. 3 km W of Brand Highway on Green Head Road, B.G. Briggs 8604, L.A.S. Johnson, K. Meney, J.Pate & P. Linder, 7 Sep 1990 ♀ (NSW, PERTH); c. 3 km SE of Mt Lesueur, 3.9 km N of Jurien–Coomaloo road on track E of Mt Lesueur, B.G. Briggs 7478 & L.A.S. Johnson, 29 Sep 1984 ♀ (NSW, AD, PERTH); Hi Vallee, Warradarge, M. Hislop 1788B, 24 Oct 1999 ♂ (PERTH, NSW); SW of Coomaloo Creek, near junction of Brand Hwy, R. Hnatiuk 770568, 9 Aug 1977 ♂ (PERTH); 6 km W of Brand Hwy on Cervantes Rd, Badgingarra Natl Park, K. Wilson 2706a ♂, 2706b ♀, 2 Oct 1979 (NSW); 2 miles north of Badgingarra, C.H. Gittins 1723b, Sep 1967 ♂ (NSW, CANB, PERTH); 2 miles north of Badgingarra, A.S. George 6714, 13 Aug 1965 ♂ (PERTH, NSW); c. 6 km E of Badgingarra, B.G. Briggs 7457 & L.A.S. Johnson, 28 Sep 1984 ♀ (NSW, CANB, NBG, PERTH, PRE, RSA); 5 km SE of Badgingarra, G. Keighery 2559, 10 Sep 1979 ♀ (PERTH); 1.5 km W of Mount Lesueur, E.A. Griffin 2093, 1 Sep 1979 ♂ (PERTH); 5 km S of junction of Mimegarra Road and Brand Highway, B.J. Keighery 126B, 9 Jul 1988 ♂ (PERTH, NSW); 15 miles [24 km] N of Regans Ford, A.S. George 11334, 13 Aug 1972 ♂, ♀, (PERTH, K).

### Extension of range of *Lepidobolus deserti* Gilg

Previous collections of this species have been from the Victoria Desert and Kalgoorlie region of southern inland Western Australia, with two specimens from about 300 km further west: i.e. 19 km W of Sharman Well, Perrinvale Station (29°02'S, 120°15'E), R.J. Cranfield 7148, 7 Sep 1988 ♂ (PERTH); 22 km E of Janies Well, Riverina Station (29°11'S, 120°49'E), R.J. Cranfield 7537, 19 Sep 1988 (PERTH).

We now report extensions of range to the north-west by a further 350 km with the following two collections: NE Lochada Station, E of Morawa (29°04'06"S, 116°46'19"E), D.J. Edinger 6018, 17 Sep 2006 ♂ (PERTH); Kirkalocka, Lat: 28°33'61"S Long: 117°54'09"E, K.W. Dixon 1044, 29 July 2006 ♂, ♀ (PERTH, NSW). The Kirkalocka location is more heavily wooded with a variety of taller shrubs, small trees and mallees than locations in the Great Victoria Desert.

This range extension highlights the potential importance of yellow sand ridges as major refugia or dispersal conduits for taxa found in the Great Victoria Desert. We suggest that further botanical work is required on yellow sand ridge communities on the margins of the south west, as these may represent an important ecological community that has been previously overlooked for its biodiversity values.

### Intraspecific variation and intergradation between *Lepidobolus* species

Interspecific hybrids or notable variation within species has not been reported in many genera of Australian Restionaceae, but are a feature of some species of *Lepidobolus* in Western Australia. *L. preissianus* and *L. chaetocephalus* have widely overlapping distributions and commonly occur intermixed with no sign of hybridisation. Similarly, *L. quadratus* is distinct where it occurs within the ranges of both of these species, and intergradation involving the rare and restricted *L. basiflorus* has not been reported. Collections within the ranges of *L. deserti* Gilg and *L. spiralis* K.A. Meney and K.W. Dixon are too few to give information on whether these co-occur with other *Lepidobolus* species, although some specimens may give evidence of intergradation between *L. preissianus* and *L. spiralis*. Also, some specimens suggest intergradation between *L. preissianus*, *L. densus* and *L. eurardyensis* where these occur together or in nearby locations.

**Variation within *Lepidobolus preissianus*:** this widespread species, extending from Dirk Hartog Island and Kalbarri throughout the southwest to Cape Arid (Meney et al. 1999), includes plants of very diverse appearance. A lectotype, *Preiss 1755(p.p.)*, was designated by Briggs & Johnson (1998: p. 28). When he described the species, Nees (1846: p. 66) recognised two varieties within it and these were later elevated to subspecies rank

(Briggs and Johnson 1998), i.e. *L. preissianus* Nees subsp. *preissianus* and subsp. *volubilis* (Nees) B.G. Briggs & L.A.S. Johnson. Those authors have also used an unpublished name '*L. preissianus* subsp. *arcuatus*' in herbarium annotations and this was also mentioned as an unpublished name by Meney et al. (1999).

These names indicate the three most distinctive variants within the species, and there is some geographic pattern to the variation.

*L. preissianus* subsp. *preissianus* occurs in sand-plain heath vegetation primarily from Kalbarri National Park in the north to the Perth region, in a belt predominantly west of longitude 116°E. It is characterised by smooth, glabrous, straight culms 0.8–1.5 mm diam. and predominantly straight rhizomes, the cataphylls with pale margins. In the extreme north of its range (e.g. Kalbarri) plants mostly have stout and tortuous to sinuose culms.

*L. preissianus* subsp. *volubilis* occurs on white to yellow sandy soils, mainly E of longitude 116°E, and extending inland to the Coolgardie/Kalgoorlie area, and SE to the Lake King region. It is distinguished by its stout (1–1.8 mm diam.), rough, pubescent, grey to green sinuous culms and predominantly straight rhizomes. Cataphylls are brown but usually pale toward the margin or apex. In the Goldfields region, around Merredin and east to Coolgardie, the characters of stout, densely pubescent, sinuose culms are especially pronounced.

The unpublished name '*L. preissianus* subsp. *arcuatus*' was applied to plants at the south and south-west of the range of the species, occurring mostly on brownish or grey clayey sand, in moist sites. The plants have slender (0.7–1.0 mm diam.), slightly rough, usually glabrous, green culms and mostly arcuate (downward looping) rhizomes with dark cataphylls. The culms are often more widely spaced (c. 5 mm apart) than in the two named subspecies.

In some localities, plants with the features of *L. preissianus* subsp. *preissianus* and subsp. *volubilis* co-occur without apparent intermediates. Over much of the distribution, however, most plants show a spectrum of features that suggest intergradation between *preissianus* and *volubilis*, or between either of these and '*arcuatus*'. To the south-east of Perth, some plants show features suggesting intergradation of all three. Since a large proportion of plants cannot be placed in any of the 'subspecies', we are not formalising '*arcuatus*' as a third subspecies, and we suggest that the two named subspecies names be applied only where it seems useful to do so, at least until further studies are made. More detailed investigation may give reason to recognise these or other taxa to record the variation which we now treat as infraspecific.

### Acknowledgments

Thanks are owed to Bush Heritage Australia and their former Chief Executive Officer Doug Humann whose encouragement to visit the Eurardy Station has resulted in the resolution of a new taxon.

Carolyn Connelly (née Porter) and Siegfried Krauss gave expert technical assistance; Adam Marchant made available DNA data in advance of publication; Catherine Wardrop was responsible for the illustrations, and Peter Wilson assisted with Latin diagnoses although, following change in the ICBN, we have not included these. Russell Barrett, John Pate and Kathy Meney helped through fieldwork opportunities and discussions that provided valuable insights.

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