

A review of the classification and taxonomic and geographic distribution of cleistogamy in Australian grasses

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ABSTRACT

Cleistogamy, self-fertilisation within a closed flower, was found in 135 Australian grass species from 46 genera within 5 subfamilies representing 14% of the species and 30% of the genera. This represents an increase from 4% of species and 12% of genera from previous records. Expressions of cleistogamy were classified into three main categories on the basis of: presence or absence of anther dimorphism, presence of amphigamy with or without spikelet peculiarities, and chasmogamous and cleistogamous spikelets on separate plants. One category of these dimorphisms involves species that have differing terminal and axillary inflorescences (amphigamy) with corresponding spikelets so different that the axillary ones appear to belong to a different genus. Dimorphisms within cleistogamous species were found in inflorescences, spikelets, florets, anthers and caryopses. The highest concentration of Australian cleistogamous grasses occurs in the subtropical climatic zone and more than three-quarters of the species are chloridoid and panicoid with nearly equal proportions. Of Australian cleistogamous grasses, 33% have C_3 photosynthetic pathway and 67% have C_4 , and the largest taxonomic groups are panicoid with 38% and chloridoid with 39%.

Keywords: amphigamy, cleistogamy, dimorphic spikelets, grasses, plant reproduction, Poaceae, reproductive dimorphism.

Introduction

Grasses occupy a diverse range of plant communities, from grasslands to rainforests, throughout the world where they have varying significance in their contribution to ecosystem dynamics, physiognomic structure, floristic diversity, biomass, conservation and economic values, and they play important roles in managing fire and grazing. Management of grassy ecosystems requires understanding of grass biology that includes their breeding systems. Grasses display a broad spectrum of breeding systems, inflorescence types and physiology (Campbell *et al.* 1983; Quiroga *et al.* 2010; Christin *et al.* 2012; Reinheimer *et al.* 2013a, 2013b). Breeding systems in grasses include asexual reproduction, both vegetative and by seeds (apomixis), and types of pollination ranging from outcrossing with self-incompatibility to self-compatible (Connor 1979; Richards 1990; Gibson 2009). Breeding systems influence both genetic structure and genetic diversity of grasses, with self-pollinating species having more genetic divergence than mixed-mating or outcrossing species (Godt and Hamrick 1998).

The predominant breeding system in grasses involves hermaphrodite florets that open briefly, mostly by the action of lodicules, to release the anthers followed by the emergence of stigmas permitting cross-pollination and thus gene flow, chasmogamy (CH; Connor 1979; Clayton 1990; Richards 1990; Chapman 1996; Groves and Whalley 2002; Gibson 2009; Kirchoff and Claßen-Bockhoff 2013; Reinheimer *et al.* 2013b). Autogamy is common in grasses where fertilisation results from pollen transfer from other spikelets on the same plant, from the same spikelet, and self-pollinating before the flower opens (preanthesis cleistogamy; bud pollination) (Stebbins 1957; Ornduff 1969; Frankel and Galun 1977; Connor 1979; Lord 1981; Cheplick and Quinn 1986; Lloyd and Schoen 1992; Whalley *et al.* 2013). A further component in the self-pollination spectrum is a system where the

flower remains closed but produces viable seeds, cleistogamy (CL) (Darwin 1877; Uphof 1938; Campbell *et al.* 1983).

Self-pollination is viewed as an evolutionary adaptation to environmental influences (Lord 1981; Lloyd and Schoen 1992; Quiroga *et al.* 2010; Sicard and Lenhard 2011; Reinheimer *et al.* 2013a, 2013b). Furthermore, the presence, abundance and, in some cases, the nature of the expression of CL, are affected by ecological, morphological and physiological factors (Lindauer and Quinn 1972; Clay 1982; Campbell *et al.* 1983; Clay and Antonovics 1985; Philipson 1986). CL has been reported as a response to various environmental influences, including herbivory, crowding, soil moisture and fertility, temperature, daylength and light intensity (Uphof 1938; Lord 1981; Campbell *et al.* 1983; De Jong and Klinkhamer 2005; Culley and Klooster 2007; Gibson 2009). Nevertheless, both facultative and obligate forms of CL are genetically controlled, although sometimes there can be incidental lodicule abortion resulting in failure of the floret to open (Frankel and Galun 1977; Campbell *et al.* 1983; Clayton 1990; Groves and Whalley 2002).

A study of the history of the classification of CL for this paper elucidated a range of terminology and criteria used to define categories of CL, with some of the work on Poaceae imbedded in the broader context of studies of angiosperm CL (Table 1). The categories used by authors including Darwin (1877), Uphof (1938), Lord (1981) and Culley and Klooster (2007) to classify CL in angiosperms when applied to grass CL are informative, despite the broader scope of taxa and morphology. Also, Connor (1979) provided categories of CL in a study of the broad spectrum of breeding systems in grasses. From this background research, it was considered for the current study that most of the diversity in grass CL is captured in the categories used by Hackel (1906) and Campbell *et al.* (1983) (Table 1).

The predominant expression of CL is in the terminal inflorescences on the same plant as interspersed CL and CH spikelets that have similar overall morphology, except in some species the anthers are the same (monomorphic) and in others they are different (dimorphic) (Campbell *et al.* 1983; Freckmann and Lelong 2003; Culley and Klooster 2007; Morrone *et al.* 2008). However, CL dimorphism extends beyond anther dimorphism and Darwin (1877) referred to it as 'structural peculiarities' in what he perceived to be 'true cleistogamy' (Table 1). Connor (1998) considered that the ultimate grass CL syndrome can be expressed in the structural peculiarities of six characters relating to the CL spikelets, rarely all coinciding. The structural peculiarities include the following:

- (a) Lodicules (absence or reduced size),
- (b) Anthers and stigma-styles (reduction in size or number),
- (c) Pollen germination through the anther walls,
- (d) Floret morphology different from the CH spikelets, and the presence of cleistogenes or rhizanthogenes, i.e. highly modified obligately CL spikelets hidden in basal leaf

sheaths or subterranean respectively. Other CL structural peculiarities found in grasses include types of inflorescences (including amphigamy, different inflorescences in different places on the same plant (Chase 1918; Uphof 1938; Campbell *et al.* 1983; Thompson and Fabillo 2021; Fig. 1); CH and CL in different positions in the same terminal inflorescence; synchronicity of the CH and CL flowering; CH and CL on different plants, variations in diaspore morphology and dispersal mechanisms, caryopses (larger size, dormancy, germination) and greater seedling adaptability (Hackel 1906; Laude 1949; Clay 1982, 1983a, 1983b; Campbell *et al.* 1983; Clay and Antonovics 1985; Clay and Antonovics 1986; Bartholomew 1987; Adkins *et al.* 2002). Chase (1918) considered the differences in the morphology of the terminal spikelets and the cleistogenes in some North American chloridoid and danthonioid species (Table 2) to be so great that 'Often, if their source was unknown, they would not be placed in the same tribe' (p. 255). The CH and CL morphs can occur on separate plants of the same species (Hackel 1906; Uphof 1938; Auquier and Stace 1980).

Another category of CL involves species thought to have only CL spikelets without any CH flowers, referred to as 'CL only' and 'complete' (Table 1). Darwin (1877) believed that plants considered to be CL-only will ultimately produce seeds from CH flowers. Other authors have also expressed doubt about the existence of CL-only. For example, Campbell *et al.* (1983) in their classification of CL in grasses, did not provide a category for CL-only. Where CL-only is presumed, it has been suggested that intensive survey of the species should be conducted over its natural habitat to verify the existence of CH (Darwin 1877; Lord 1981; Campbell *et al.* 1983; Culley and Klooster 2007). For example, low frequency of the CH morph in the natural habitat of some grasses offers an explanation for apparent CL-only (Beddows 1931; Kannenberg and Allard 1967; Connor 1998).

It is considered that the presence of apomixis, seed production without meiosis, should be considered in all studies of CL (Connor 1979; Philipson 1986; Bicknell and Koltunow 2004). Apomixy is difficult to assess, requiring studies of progeny, cytology and embryology (Philipson 1986; Bashaw and Hanna 1990; Yu *et al.* 2000, 2003). There is little or no morphological distinction between the apomictic and sexual equivalents including some types of CL such as monomorphic CL anthers, although in the latter the anthers remain in the floret (Bashaw and Hanna 1990; Kellogg 1990; Thompson 2017). The capacity for sexual reproduction is retained for most, if not all, apomicts as exemplified by oat grasses (*Danthonia* DC.) from North America (Philipson 1986; Kellogg 1990; Carman 1997; Klingenberg and Gidaszewski 2010).

Of the twelve subfamilies of Poaceae worldwide, nine manifest some form of CL and of the nine subfamilies occurring in Australia, five have species with CL (Campbell *et al.* 1983; Culley and Klooster 2007; Soreng *et al.* 2017).

Table 1. A history of the classification of cleistogamy in Poaceae worldwide.

Author	Context of classification	Number of CL types recognised	Types of CL				
			Monomorphic anthers		Dimorphic anthers (i.e. CH and CL different)		
			CH = CL on the same plants	CL only	In the same inflorescence	On separate plants	Amphigamy
Darwin (1877)	Angiosperms	2	No 'structural peculiarities'	No category (Darwin doubted this possibility)	<div> <div>←</div> <div>'Structural peculiarities' and 'true CL'</div> <div>= anther, spikelet and inflorescence dimorphisms</div> <div>→</div> </div>		
Hackel (1906) ^A	Poaceae only	4	'Facultative' CL species (Group 1)	'CL only species' (Group 3)	No category	'Dimorphic species' (Group 2)	'Amphigamous species' (Group 4)
Uphof (1938) ^B	Angiosperms	2	'Ecological CL'	<div> <div>←</div> <div>'Genetical aspects'</div> <div>→</div> </div>			
Connor (1979)	Poaceae only	3	'CL and CH'	'CL only'	<div> <div>←</div> <div>CL and CH</div> <div>→</div> </div>		'Clandestine axillary' (<i>cleistogenes</i>)
Lord (1981) ^C	Angiosperms	4	'Preanthesis CL' 'Pseudocleistogamy'	'Complete CL'	<div> <div>←</div> <div>'True CL'</div> <div>→</div> </div>		
Campbell <i>et al.</i> (1983)	Poaceae only	4	'Type Ia. sheath fertilisation' (uppermost sheaths)	No category	'Type Ib. sheath fertilisation' (lowermost sheaths of culms)		'Type II. cleistogenes'
			'Type IVb. spikelet fertilisation' (lodicule failure)		'Type IVa. spikelet fertilisation' (spikelet bract modifications)		'Type III. rhizanthogenes'
Watson and Dallwitz (1992)	Poaceae only	2	'Exposed-cleistogamous'	No category	'Exposed-cleistogamous'		'Hidden cleistogenes' – very modified or highly modified
Culley and Klooster (2007) ^D	Angiosperms	3	'Induced CL'	'Complete CL'	<div> <div>←</div> <div>'Dimorphic CL'</div> <div>→</div> </div>		
Thompson (2017)	Poaceae only	3	Monomorphic CL anthers	No category	Dimorphic CL anthers	Polymorphism	Amphigamous CL with spikelet dimorphism

The categories and terminology used by nine authors are shown according to three main characters, relative size of chasmogamous (CH) and cleistogamous (CL) anthers, CH and CL on separate plants, and presence of amphigamy (two or more types of inflorescence in separate parts of the same plant). Arrows show the scope of the authors' categories of CL across the types of CL in the headings.

^ATranslation of categories from Uphof (1938) and by W. Stur (pers. comm.).

^B'Ecological CL', '... caused by factors of the natural environment' (i.e. facultative CL).

^C'Preanthesis' (i.e. pollination in the bud followed by anthers being released and opening to shed pollen); 'pseudocleistogamy' (i.e. where CH and CL morphology is the same); 'complete CL' (i.e. CL-only); 'true CL' (i.e. differences in CH and CL modes occur with anther, spikelet and inflorescence dimorphisms).

^D'Induced' (i.e. environmentally induced); 'complete' (i.e. CL-only); 'dimorphic' (i.e. 'prominent differences in CH and CL floral morphology').

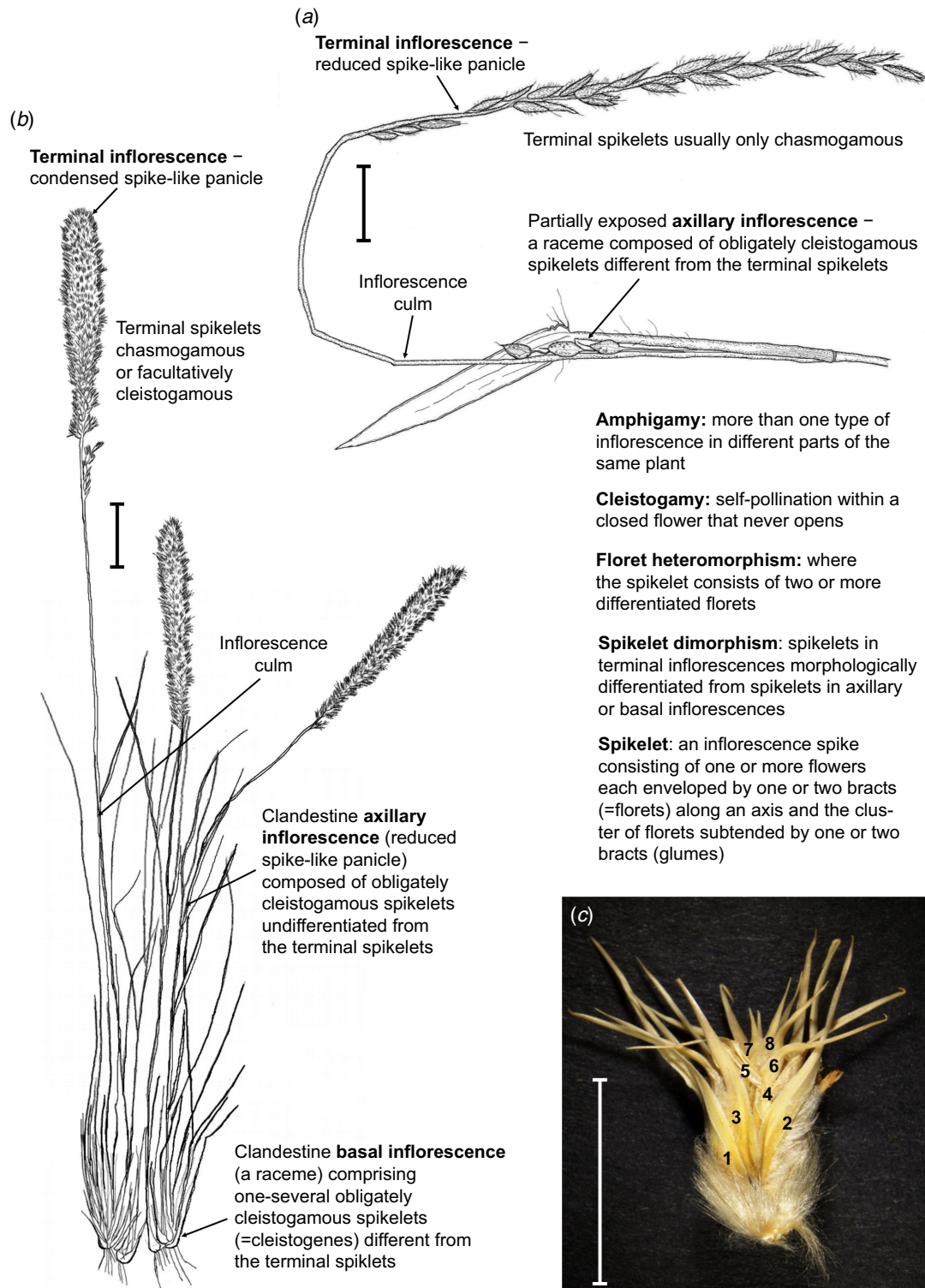


Fig. 1. Glossary of terminology relating to cleistogamy. (a) Example of amphigamy with two types of inflorescences in *Cleistochloa* sp. (Duaringa K. B. Addison 42) with corresponding dimorphic spikelets. From Thompson EJT301, B. K. Simon and M. Edginton (BRI). (b) Example of amphigamy with three types of inflorescences in *Enneapogon cylindricus*. Spikelets in terminal, axillary and basal inflorescences have multiple florets, but only the proximal floret is fertile. From Purdie 1454 (BRI). (c) Diaspore of *Astrebla squarrosa*, showing eight visible heteromorphic fertile florets (1–8), distal floret hidden. From Thompson EJT1045 (BRI). Del. E. J. Thompson. Scale bars: 10 mm.

Table 2. List of cleistogamous grass genera worldwide with amphigamous inflorescences and dimorphic CL spikelets.

Subfamily	Tribe or subtribe	Genus	N	D	T	CL type	Position of CL spikelets on plant				Notes
							1	2	3	4	
Bambusoideae	Olyrineae										
	Parianinae	<i>Pariana</i>	4	CA	R	3c	CH only			xxx	
Chloridoideae	Cynodonteae										
	Eleusininae	<i>Enteropogonopsis</i>	1	NA	D	3c	CH only?			xxx	Information obtained from drawings in Hitchcock (1950) and herbarium specimens viewed on JSTOR
	Muhlenbergiinae	<i>Muhlenbergia</i>	2	NA, SA	P	3b	Mixed CH and CL	xxx	xxx		
	Gouininae	<i>Triplasis</i>	2	NA	P	3b	Mixed CH and CL	x	xxx		
	Eragrostideae	<i>Cottea</i>	1	NA, SA	P	3b	CH-only	xxx	xxx		
	Cotteinae	<i>Enneapogon</i>	3	A, Af	P	3b	CH-only or CL-only and mixed CH and CL	x	xxx		Axillaries rarely with apical spikelets CH
	Uniolinae	<i>Uniola</i>	1	A	P	3a		xxx			
Danthonioideae	Danthonieae	<i>Danthonia</i>	21	NA, SA	P	3b	CH-only or C-only and mixed CH and CL	xxx	xxx		
Oryzoideae	Ehrharteae	<i>Microlaena</i>	2	A, NZ	P	3a	Mixed CH and CL	xx			
Panicoideae	Paniceae										
	Boivinellinae	<i>Amphicarpum</i>	2	NA, SA	R	3c	CH-only			xx to xxx	Rhizanthogene morphology grades from similar to terminals to distinctly different
	'The cleistogamy group' ^A	<i>Calypochloa</i>	3	A	RP	3a	CH-only; mixed CH and CL	xxx			
		<i>Cleistochloa</i>	3	A	RP	3a	CH-only	xxx			
		<i>Dimorphochloa rigida</i>	1	A	RP	3a	CH-only	xx			CL spikelets on apical subordinate branches
		<i>Dimorphochloa</i> spp.	5	A	R	3a	CH-only	xxx			
		<i>Simonachne</i>	1	A	R	3a	CH-only	xx			
	Paspaleae	<i>Paspalum</i>	1	NA	P	3c	CH-only			xx	
	Paspalinae										
Pooideae	Stipeae	<i>Amelichloa</i>	5	SA	P	3b	Mixed CH and CL	x	xxx		
		<i>Amphibromus</i>	1	SA	P	3b	CH-only	xx	xxx		
		<i>Nasella</i>	3	SA	P	3b	Mixed CH and CL	xx	xxx		
	Poeae										
	Poinae	<i>Libyella</i>	1	Af	R	3c	CH-only			x	Herbarium specimens viewed on JSTOR

^AThompson and Fabillo (2021).

N, number of species; D, distribution: A Australia; Af Africa; CA Central America; NA North America; SA South America; NZ New Zealand; T, terminal inflorescence type: D digitate; P panicle; R raceme; RP spike-like panicle to raceme; CL type: 3a, plants with dimorphic axillary spikelets; 3b, cleistogenes present; 3c, rhizanthogenes present; Position of CL spikelets on plant: 1, fertilisation mode of spikelets in terminal inflorescences, 2, axillary inflorescence, 3, cleistogenes present, 4, rhizanthogenes present. Degree of difference between terminal and CL axillary spikelets, cleistogenes or rhizanthogenes: x, very similar; xx, different, recognisable as the same genus but different enough to be considered another species; xxx, distinctly different, fitting the Chase (1918) syndrome. xx and xxx fit Darwin's (1877) 'true CL'.

Since the work on classification of grass CL by Campbell *et al.* (1983) and Culley and Klooster (2007), more information has been gathered about CL in Australian grasses. Until now ~46 native grasses within 18 genera (~12%) have

been recorded with CL representing ~4% of the native species in Australia compared to ~3% of species and 10% of genera worldwide (Campbell *et al.* 1983; Watson and Dallwitz 1992; Culley and Klooster 2007).

The aim of this study is to review the classification of CL expressed in grasses by examining the morphological and physiological variation, and geographic and taxonomic distributions of Australian species. The study also investigates possible morphological relationships of the expressions of the CL types.

Materials and methods

Information gathered for this study and presented in Table 3 came from five main sources *viz.*, herbarium specimens, images of herbarium specimens on JSTOR Global Plants (<http://plants.jstor.org/>, accessed March 2020), field observations, plants cultivated by the author, and the literature. Most of the information provided in Table 3 was obtained from examination of numerous herbarium specimens. Multiple spikelets of several specimens for each species were examined to determine frequency, abundance, distribution on the plant, and characteristics of the expression of CL. Targeting of taxa for detailed inspection was based on the records of CL in grass genera by Campbell *et al.* (1983) and Culley and Klooster (2007). For example, few specimens of species of *Aristida* L. were examined because of the absence of records of CL in Australian species. However, extensive searches of specimens were made in subtribes such as Andropogoninae (subfamily Panicoideae, tribe Andropogoneae) where several taxa have been recorded with CL and the expression of CL is potentially facultative or has sporadic occurrence.

Taxonomic classification and nomenclature are based on Brown and Bostock (see <http://data.qld.gov.au/dataset/censusof-the-queensland-flora-2020/>, accessed 16 June 2021) and IPNI (<https://anbg.gov.au/apni/>, accessed 14 May 2021) for genera and species and Soreng *et al.* (2017) for higher-order taxa including tribes and subtribes (Table 3). Characters used in the identification of tribes and subtribes as defined by McClusker (2002) have been noted.

Terminology follows Tothill and Hacker (1983), Jacobs *et al.* (2008), Gibson (2009) and Beentje (2010). The term spikelet defines the basic inflorescence of a grass. Spikelets consist of one or more florets which can be sterile, male-only, female-only or composed of a pistil and usually three stamens enveloped by one or two bracts (lemma with or without palea) subtended by one or two additional bracts (glumes). The spikelet equates to a spike in the broader context of inflorescences (Kellogg 2006; Endress 2010). Terminology used for general types of inflorescences follows Tothill and Hacker (1983). Some of the less commonly used terminology that has been used in relation to grass CL is presented in Fig. 1. Heteromorphism is used in this study to refer to variation in the elements of a compound character (Fig. 1) (Schoen and Lloyd 1984; Maxwell *et al.* 1994; Culley and Klooster 2007; Lerner *et al.* 2008). Other authors referred to this variation as somatic

polymorphism (Harper *et al.* 1970; Sorensen 1978; Dore and McNeill 1980; Silvertown 1984; Maxwell *et al.* 1994).

CL was confirmed by the presence of both anthers and stigmas enclosed within the spikelet accompanied by a partially to fully developed caryopsis. Chasmogamy was determined by either of four conditions, *viz.* the presence of exerted anthers alone, exerted anthers and stigmas, stigmas alone in the absence of anthers (filaments present), or caryopsis present with absence of anthers and stigmas. Length of CH and CL anthers was measured and recorded for all CL species so as to fill gaps in the literature (Table 3). Anther lengths were measured for each fertile floret in the case of some multi-floreted chloridoid species (Fig. 1) and some panicoid species with staminate lower floret or pedicellate spikelet. Stigma size was also observed. Field collections were conducted so as to order to provide sufficient flowering and fruiting material for some species, as mentioned below.

Ex situ plants were cultivated and plants were also propagated from caryopses for some species. The caryopses were acquired from herbarium specimens and field collections. For most species, caryopses were manually de-husked and scarified by scraping off a small area of pericarp just above the apex of the scutellum. Plants were cultivated in pots under nursery conditions with daily watering. Some C₃ and C₄ species were cultivated in both full sun and partial shade to examine potential impact of light conditions on the presence and abundance of CL.

The 54 species listed in Table 3 were cultivated to observe a possible influence of environmental conditions on the presence and type of CL, and spikelet and inflorescence morphology. Plants of most species were maintained over a period of 5 years but some annual species of *Schizachyrium* Nees were re-propagated from caryopses for only two successive years. Several trials were conducted with CL-only plants by varying conditions, including full sun *v.* shaded and strongly pruned *v.* unpruned.

Field surveys of *Astreba* F.Muell. and *Spathia* Ewart and Davies were conducted near Camooweal and Winton, north-western Queensland in April and November 2016.

CL classification for this study was based on categories defined by other authors (Table 1) and CL morphology observed from herbarium specimens and cultivated plants. The morphological characters used to define the CL types include the following:

- CL and CH anthers equal size in the case of monomorphic CL anthers or unequal size in the case of dimorphic CL anthers.
- CH and CL spikelets in the same inflorescence.
- Presence of amphigamy, *i.e.* different inflorescences in different places on the same plant.
- CH and CL spikelet differences such as reported by Hubbard (1933a, 1933b), Blake (1941), Campbell *et al.* (1983) and Connor (1998).
- CH and CL spikelets on different plants.

Table 3. List of Australian native cleistogamous grasses.

Subfamily or tribe	Subtribe	Species	R	Florets	L	P	T	C	Ia	Ib	Ic	2a	2b	2c	2d	3a	3b
Chloridoideae																	
Cynodonteae	Dactylocteninae	<i>Acrachne racemosa</i>	y	I	a	C ₄	P	S, Ds		0.2 ^A							
				Ax						0.2							
		<i>Dactyloctenium radulans</i>	n		a	C ₄	D	S, D, Ds, M	0.3–0.4								
Eleusininae		<i>Astrebale elymoides</i> [cv.]	n	I ^B /CH ^C	P	C ₄	R	D, Ds							2.8–2.9		
				I ^B /CL ^C		C ₄	R								0.3–1.0		
		<i>Astrebale lappacea</i> [cv.]	y	I ^B /CH ^C	P	C ₄	R	D, Ds							1.7–1.8		
				I ^B /CL ^C		C ₄	R								0.3–0.6		
		<i>Astrebale pectinata</i> [cv.]	y	I ^B /CH ^C	P	C ₄	R	D, Ds							1.2–1.9		
				I ^B /CL ^C		C ₄	R								0.1–0.9		
		<i>Astrebale squarrosa</i> [cv.]	n	I ^B /CH ^C	P	C ₄	R	D, Ds							1.9–2.5		
				I ^B /CL ^C											0.8–1.2		
		<i>Brachyachne ambigua</i>	n		a	C ₄	D	T	0.2								
		<i>Brachyachne ciliaris</i>	y		a	C ₄	D	S, D, Ds	0.4								
		<i>Brachyachne convergens</i>	n		a	C ₄	D	S, D, Ds	0.4								
		<i>Chloris pectinata</i>	n		a	C ₄	D	S, D, Ds	0.2								
		<i>Chloris ventricosa</i> [cv.]	n		P	C ₄	D	S, M	0.6–0.7								
		<i>Dinebra decipiens</i> [cv.]	n		P	C ₄	P	S, M	0.2–0.4								
		<i>Diplachne fusca</i> var. <i>muelleri</i>	n		P	C ₄	P	S, D, Ds	0.2–0.4								
		<i>Enteropogon acicularis</i> [cv.]	n		P	C ₄	D	S, D, Ds	0.8–1.2								
		<i>Enteropogon dolichostachyus</i> [cv.]	n		P	C ₄	D	T	1.0–1.2								
		<i>Enteropogon minutus</i> [cv.]	n		P	C ₄	D	S, Ds	0.4–0.5								
		<i>Enteropogon paucispiceus</i> [cv.]	n		P	C ₄	D	S	1.4								
		<i>Enteropogon ramosus</i> [cv.]	n		P	C ₄	D	S, D, Ds	1.0–1.6								
		<i>Enteropogon unispiceus</i> [cv.]	n		P	C ₄	D	S	0.7–1.1								
Eragrostideae	Cotteinae	<i>Tripogon loliiformis</i> [cv.]	n		P	C ₄	R	S, D, Ds, M	0.2–0.4								
		<i>Enneapogon asperatus</i>	y		P	C ₄	P	Ds	0.6–0.8								
		<i>Enneapogon avenaceus</i>	n	I/CH	P	C ₄	P	D, Ds				0.5–0.7					
				I/CL								0.2–0.5					
				2/CH								0.3–0.4					
				2/CL								0.3–0.6					

(Continued on next page)

Table 3. (Continued).

Subfamily or tribe	Subtribe	Species	R	Florets	L	P	T	C	Ia	Ib	Ic	2a	2b	2c	2d	3a	3b
				2/CL								0.3–0.4					
				3/CH, CL								0.3–0.4					
		<i>Enneapogon caeruleus</i>	y	I/CH	P	C ₄	P	D, Ds									0.3–0.6
				I/CL ^C													0.3–0.6
				Ax/cl ^C													0.4–0.6
				Cleis													0.2–0.3
		<i>Enneapogon cylindricus</i>	y	I/CH	P	C ₄	P	D									0.2–1.2
				I/CL													0.2–0.9
				Ax/ch													1.0–1.1
				Ax/cl													0.2–0.4
				Cleis													0.2–0.4
		<i>Enneapogon eremophilus</i>	y	CH	P	C ₄	P	D, Ds	0.4–0.9								
				CL					0.7								
	Eragrostidinae	<i>Ectrosia anomala</i>	y		a	C ₄	P	T	0.4–0.5								
		<i>Ectrosia blakei</i> [cv.]	y		a	C ₄	P	T	0.2–0.7								
		<i>Ectrosia confusa</i>	n		a	C ₄	P	T, Ds	0.3–0.4								
		<i>Ectrosia danesii</i>	y		a	C ₄	P	T, Ds			0.2–0.4						
		<i>Ectrosia gulliveri</i>	n		a	C ₄	P	T, S, Ds	0.2–0.3								
		<i>Ectrosia nervilemma</i>	n		a	C ₄	P	T	0.2–0.5								
		<i>Ectrosia scabrida</i>	y		a	C ₄	P	T, Ds	0.2–0.4								
		<i>Eragrostis alveiformis</i>	n		P	C ₄	P	S, M	0.4–0.5								
		<i>Eragrostis basedowii</i>	n		a	C ₄	P	S, D, Ds			0.2						
		<i>Eragrostis concinna</i>	n		P	C ₄	P	T, S, Ds			0.1–0.3						
		<i>Eragrostis confertifolia</i>	n		a	C ₄	P	D, Ds	0.2–0.4								
		<i>Eragrostis cumingii</i>	n		a	C ₄	P	T, S, D, Ds	0.2–0.3								
		<i>Eragrostis elongata</i>	n		P	C ₄	P	T, S, D, Ds, M	0.2–0.3								
		<i>Eragrostis fallax</i> [cv.]	n		P	C ₄	P	T, S, D, Ds, M			0.2–0.3						
		<i>Eragrostis hirticaulis</i>	n		P	C ₄	P	T	0.5–0.6								
		<i>Eragrostis lacunaria</i>	n		P	C ₄	P	S, D, Ds	0.1–0.2								
		<i>Eragrostis longipedicellata</i>	n		P	C ₄	P	S	0.2–0.3								

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Table 3. (Continued).

Subfamily or tribe	Subtribe	Species	R	Florets	L	P	T	C	1a	1b	1c	2a	2b	2c	2d	3a	3b
		<i>Eragrostis megalosperma</i>	n		P	C ₄	P	S	0.4–0.5								
		<i>Eragrostis microcarpa</i>	n		P	C ₄	P	D, Ds	0.1								
		<i>Eragrostis parviflora</i>	n		a	C ₄	P	S, D, Ds, M	0.2–0.3								
		<i>Eragrostis pubescens</i>	n		P	C ₄	P	T, S	0.2–0.3								
		<i>Eragrostis sororia</i>	n		a	C ₄	P	T, S, Ds, M	0.1–0.3								
		<i>Eragrostis stenostachya</i>	n		P	C ₄	P	T			0.2–0.3						
		<i>Eragrostis subtilis</i>	n		P	C ₄	P	D	0.2–0.3								
		<i>Eragrostis tenellula</i>	n		a	C ₄	P	T, S, D, Ds, M	0.2–0.3								
		<i>Eragrostis triquetra</i>	n		P	C ₄	P	S, Ds	0.2–0.3								
		<i>Thellungia advena</i>	n		P	C ₄	P	S	0.3–0.4								
	Uniolinae	<i>Uniola</i> sp. (Palm Grove P.I.Forster PIF23666) [cv.]	n	I/CH	P	C ₄	R	S								1.6–1.8	
				I/CL												0.2–0.4	
				Ax/cl												0.2	
Zoysieae	Sporobolinae	<i>Sporobolus disjunctus</i>	n		P	C ₄	P	S	0.3								
Micrairoideae																	
Micraireae		<i>Eriachne armitii</i>	y	CH	a	C ₄	P	T, S, D, Ds					0.6–0.9				
				CL									0.2				
		<i>Eriachne axillaris</i>	n	CH	a	C ₄	P	T						Not seen			
				CL													
		<i>Eriachne basalis</i>	n	CH	a	C ₄	P	T, Ds						1.3–2.2			
				CL										0.4–0.6			
				Ax										0.3			
		<i>Eriachne insularis</i>	n	CH	P	C ₄	P	S					1.6–1.8				
				CL									0.3				
		<i>Eriachne pallescens</i>	n	CH	P	C ₄	P	T, S					1.5–2.0				
				CL									0.3–0.7				
		<i>Eriachne triseta</i>	y	CH	P	C ₄	P	T, S, Ds					2.5–2.8				
				CL									0.4				
		<i>Eriachne stipacea</i>	y	CH	P	C ₄	P	T, S, Ds					1.4–2.6				
				CL									0.3				

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Table 3. (Continued).

Subfamily or tribe	Subtribe	Species	R	Florets	L	P	T	C	1a	1b	1c	2a	2b	2c	2d	3a	3b
		<i>Eriachne vesiculosa</i>	n	CH	P	C ₄	P	T, Ds					1.1–2.9				
				CL									0.4–0.7				
		<i>Pheidochloa gracillima</i>	y	CH	a	C ₄	P	T					0.8–1.5				
				CL									0.1				
Oryzoideae																	
Ehrharteae		<i>Microlaena stipoides</i> [cv.]	y	CH	P	C ₃	P	S, M								1.6–4.9	
				CL												0.2–0.7	
				Ax/cl												0.1–0.2	
		<i>Tetrarrhena juncea</i>	n	CH	P	C ₃	P	S, M					2.8–3.0				
				CL									1.2–1.4				
Panicoideae																	
Paniceae	Incertae sedis	<i>Walwhalleya prolata</i> [cv.]	n		P	C ₃	P	S, Ds, M	0.9–1.7								
		<i>Ancistrachne uncinulata</i> [cv.] ^D	n		P	C ₃	P	S, M	1.5–2.3								
		<i>Ancistrachne maidenii</i> [cv.] ^D	n	CH	P	C ₃	R	M								1.4–1.6	
				Ax/cl												0.2–0.4	
	Boivinellinae	<i>Echinochloa turneriana</i>	n		a	C ₄	P	S, D, Ds	1.0–1.1								
		<i>Entolasia stricta</i> [cv.]	n		P	C ₃	P	S, M	0.8–1.0								
		<i>Entolasia</i> sp. aff. <i>whiteana</i> [cv.]	n	CH	P	C ₃	P	S						1.6–1.8			
				Ax/cl										1.0–1.3			
		<i>Entolasia whiteana</i> [cv.]	n		P	C ₃	P	S, M	0.8–1.0								
		<i>Ottochloa gracillima</i> [cv.]	n		P	C ₃	P	S, M	0.4–1.0								
	Cenchrinae	<i>Uranthoecium truncatum</i>	n		a	C ₄	R	D, Ds	0.5–0.6								
	The cleistogamy group ^D	<i>Calyptochloa cylindrosperma</i> [cv.]	y	CH	P	C ₃	RP	Ds								2.5–2.6	
				Ax/cl												0.6	
		<i>Calyptochloa gracillima</i> [cv.]	y	CH	P	C ₃	RP	S								1.5–2.0	
				Ax/cl												0.3–0.7	
		<i>Calyptochloa johnsoniana</i> [cv.]	y	CH	P	C ₃	RP	S								3.0–3.1	
				Ax/cl												0.3	
		<i>Cleistochloa sclerachne</i> [cv.]	y	CH	P	C ₃	RP	T								2.1–2.2	
				Ax/cl												0.4–0.8	
		<i>Cleistochloa</i> sp. (Duaringa K.B.Addison 42) [cv.]	n	CH	P	C ₃	RP	S								2.5–3.7	

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Table 3. (Continued).

Subfamily or tribe	Subtribe	Species	R	Florets	L	P	T	C	1a	1b	1c	2a	2b	2c	2d	3a	3b
				CL												1.5–2.0	
				Ax/cl												1.3–1.8	
		<i>Cleistochloa subjuncea</i> [cv.]	y	CH		P	C ₃	RP S								1.5–2.8	
				Ax/cl												0.5	
		<i>Dimorphochloa rigida</i> [cv.]	y	CH		P	C ₃	RP S, M								1.6–2.5	
				Ax/cl												0.3–0.5	
		<i>Dimorphochloa</i> sp. (Charters Towers E.J.Thompson + CHA554) [cv.]	n	CH		P	C ₃	R S								2.5–2.9	
				Ax/cl												0.4–0.5	
		<i>Dimorphochloa</i> sp. (Miles E.J.Thompson EJ906) [cv.]	n	CH		P	C ₃	R S								2.1–2.3	
				Ax/cl												0.5–0.8	
		<i>Dimorphochloa</i> sp. (Mt Cooper R.J.Cumming 18623) [cv.]	n	CH		P	C ₃	R S								2.0–2.1	
				Ax/cl												0.5	
	Neurachninae ^D	<i>Neurachne munroi</i> [cv.]	n			P	C ₄	R D, Ds	1.5–2.0								
		<i>Neurachne muelleri</i>	n			P	C ₄	R D, Ds	0.8–1.0								
		<i>Neurachne queenslandica</i>	n			P	C ₃	R S	4.8								
		<i>Thyridolepis michelliana</i> [cv.]	y	1/CH ^C		P	C ₃	R D, Ds	1.0–2.0								
				2/CH ^C					0.2–0.5								
				2/CL ^C					0.2–0.5								
		<i>Thyridolepis multicaulis</i>	y	1/CH ^C		P	C ₃	R D	2.2–2.4								
				2/CH ^C					0.4–0.7								
				2/CL ^C					0.4–0.7								
		<i>Thyridolepis xerophila</i> [cv.]	y	1/CH ^C		P	C ₃	R S, D, Ds	1.2–1.6								
				2/CH ^C					1.2–1.6 or 0.3–0.7								
				2/CL ^C					0.3–0.7								
Andropogoneae	Incertae sedis	<i>Spathia neurosa</i> [cv.]	y	ss		a	C ₄	R Ds	0.3–0.6								
				ps					1.4–2.0								
	Arthraxoninae	<i>Arthraxon australiensis</i> [cv.]	n			a	C ₄	D T	1.7–2.2								
		<i>Arthraxon hispidus</i>	n			a	C ₄	D S, M	0.6–0.9								
	Andropogoninae	<i>Bothriochloa biloba</i>	n			P	C ₄	R M	0.9–1.8								

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Table 3. (Continued).

Subfamily or tribe	Subtribe	Species	R	Florets	L	P	T	C	1a	1b	1c	2a	2b	2c	2d	3a	3b
		<i>Bothriochloa decipiens</i> (both varieties)	y		P	C ₄	R	S, D, Ds	0.9–1.3								
		<i>Bothriochloa macra</i>	n		P	C ₄	R	M	0.9–1.8								
		<i>Clausospicula extensa</i> [cv.]	n		a	C ₄	R	T		1 × 0.8–1.2 ^A							
										2 × 0.5–0.6							
		<i>Cymbopogon gratus</i>	n		P	C ₄	RF	S, Ds	0.9–1.4								
		<i>Cymbopogon procerus</i>	n		P	C ₄	RF	T	0.9–1.3								
		<i>Dichanthium queenslandicum</i> [cv.]	n	ss	P	C ₄	R	S	1.1–1.3								
				ps					1.8–2.5								
		<i>Dichanthium sericeum</i> subsp. <i>humilius</i> [cv.]	n	CH	a	C ₄	R	T, S, D, Ds	0.3–0.7								
				CL					0.2–0.7								
		<i>Dichanthium sericeum</i> subsp. <i>polystachyon</i> [cv.]	n	CH	a	C ₄	R	T, S, Ds	0.6–0.9								
				CL					0.4–0.9								
		<i>Dichanthium sericeum</i> subsp. <i>sericeum</i> [cv.]	y	CH	P	C ₄	R	T, S, D, Ds, M	0.5–1.2								
				CL					0.4–1.0								
				ps					0.6–1.3								
		<i>Schizachyrium crinizonatum</i> [cv.]	y	CH	a	C ₄	RF	T, Ds					1.0–1.1				
				CL									0.4				
		<i>Schizachyrium dolosum</i>	y	CH	a	C ₄	RF	T					1.0–1.1				
				CL									0.4				
		<i>Schizachyrium fragile</i> [cv.]	y	CH	a	C ₄	RF	T, S, D, Ds					1.5–2.4				
				CL									0.3				
		<i>Schizachyrium occultum</i> [cv.]	y	CH	a	C ₄	RF	T, S					1.4–1.5				
				CL									0.3				
		<i>Schizachyrium pachyarthon</i>	y	CH	a	C ₄	RF	T, S					1.4–1.9				
				CL									0.3–0.5				
		<i>Schizachyrium perplexum</i> [cv.]	y	CH	a	C ₄	RF	T, Ds					1.1–1.4				

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Table 3. (Continued).

Subfamily or tribe	Subtribe	Species	R	Florets	L	P	T	C	1a	1b	1c	2a	2b	2c	2d	3a	3b
				CL									0.2				
		<i>Schizachyrium pseudoulalia</i> [cv.]	y	CH	a	C ₄	RF	T, S, Ds					0.8–1.0				
	Ischaeminae			CL									0.3–0.4				
		<i>Ischaemum fragile</i>	n	CH	a	C ₄	R	T, S					2.6–2.7				
				CL									0.5–0.8				
		<i>Ischaemum rugosum</i>	n		P	C ₄	R	T, S	1.1–1.7								
	Rottboelliinae	<i>Elionurus citreus</i> [cv.]	n	CH	a	C ₄	RF	T, S, Ds				1.8–2.2					
				CL								0.6–0.8					
		<i>Elionurus purpureus</i> [cv.]	n	CH	a	C ₄	RF	S				0.9–1.1					
				CL								0.8					
		<i>Mnesithea formosa</i>	n		a	C ₄	R	T, S, Ds		0.3–0.9							
	Sorghinae	<i>Vacoparis laxiflorum</i>	n		a	C ₄	P	T, S, Ds		0.8–1.5							
Arundinelleae		<i>Garnotia stricta</i>	y		P	C ₄	P	T	0.5–0.6								
Pooideae																	
Tritceae	Hordeinae	<i>Australopyrum pectinatum</i>	n		P	C ₃	P	M	1.3–2.5								
Poeae	Agrostinae	<i>Dichelachne crinata</i>	y	CH	P	C ₃	P	S, M				0.9–1.2					
				CL								0.3–0.5					
		<i>Dichelachne hirtella</i>	n	CH	P	C ₃	P	M				1.9					
				CL								0.6					
		<i>Dichelachne inaequiglumis</i>	y	CH	P	C ₃	P	M				1.0–1.2					
				CL								0.3–0.6					
		<i>Dichelachne micrantha</i>	y	CH	P	C ₃	P	S, M				0.8–1.2					
				CL								0.4					
		<i>Dichelachne montana</i>	n	CH	P	C ₃	P	S, M				0.5–0.7					
				CL								0.3–0.5					
		<i>Dichelachne parva</i>	n	CH	P	C ₃	P	M				1.1					
				CL								0.5					
		<i>Dichelachne rara</i>	y	CH	P	C ₃	P	S, M				1.9					
				CL								0.7					
		<i>Dichelachne sieberiana</i>	y	CH	P	C ₃	P	M				2.2–2.5					
				CL								0.5					
Stipeae		<i>Austrostipa aristiglumis</i>	n	CH	P	C ₃	P	S, M				5.2–5.7					

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Table 3. (Continued).

Subfamily or tribe	Subtribe	Species	R	Florets	L	P	T	C	1a	1b	1c	2a	2b	2c	2d	3a	3b
				CL									0.5–1.0				
		<i>Austrostipa bigeniculata</i> ^A	y	CH		P	C ₃	P	S, M				3.3–4.4				
				CL									0.8–2.8				
		<i>Austrostipa densiflora</i>	n	CH		P	C ₃	P	S, M				2.6–2.8				
				CL									0.5–0.8				
		<i>Austrostipa flavescens</i> ^A	y	CH		P	C ₃	P	S, M				0.8–3.2				
				CL									0.4–0.9				
		<i>Austrostipa mollis</i> ^A	y	CH		P	C ₃	P	S, M				3.2–4.7				
				CL									0.6–2.5				
		<i>Austrostipa pubescens</i>	n	CH		P	C ₃	P	S, M				5.2–6.2				
				CL									0.9–1.5				
		<i>Austrostipa rudis</i>	n	CH		P	C ₃	P	S, M				3.2–4.8				
				CL									0.3–1.0				
		<i>Austrostipa semibarbata</i> ^A	y	CH		P	C ₃	P	M				2.6–6.1				
				CL									1.0–1.9				
		<i>Austrostipa scabra</i>	n	CH		P	C ₃	P	S, D, Ds				0.9–1.5				
				CL					S, D, Ds				0.6–1.0				
		<i>Austrostipa setacea</i> [cv.]	n	CH		P	C ₃	P	S, D, Ds				1.7–1.8				
				CL									0.4–0.5				
		<i>Austrostipa stuposa</i> ^A	y	CH		P	C ₃	P	DS, M				4.0–6.0				
				CL									0.4–2.0				

Subfamily or tribe taxonomy follows Soreng *et al.* (2017). Subtribe taxonomy follows Soreng *et al.* (2017) except Neurachninae. Species nomenclature follows Brown and Bostock (see <http://data.qld.gov.au/dataset/censusof-the-queensland-flora-2020/>, accessed 16 June 2021). [cv.], cultivated; R, recorded by Culley and Klooster (2007); n, no; y, yes. Florets of spikelets with multiple staminate florets: 1, basal floret of spikelet in terminal inflorescence; 2, second floret; CH, terminal chasmogamous anthers; CL, terminal cleistogamous anthers; Ax, axillary inflorescence; ch, axillary chasmogamous spikelet; cl, axillary cleistogamous spikelet; L, life cycle: a, annual; p, perennial. P, photosynthetic pathway. T, terminal inflorescence type: P, panicle; D, digitate racemes; RP, spike-like panicle (sometimes reduced to a raceme); R, raceme; RF, spatheolate racemes in fascicles. C, climate zone: T, equatorial to tropical; S, subtropical; D, desert; Ds, semi-desert (grassland); M, temperate. CL type 1, monomorphic CL anthers: 1a, species with inflorescences comprising CH-only, CL-only or a mixture of CH and CL spikelets; 1b, CH and CL on separate plants; 1c, species with amphigamous inflorescences. CL type 2, dimorphic CL anthers: 2a, species with inflorescences comprising CH-only, CL-only or a mixture of CH and CL spikelets; 2b, CH and CL on separate plants; 2c, amphigamous with axillary inflorescences; 2d, amphigamous with CL inflorescences on short leafy branches. CL type 3, Amphigamous CL with dimorphic spikelets: 3a, with axillary dimorphic spikelets; 3b, cleistogenes present.

^ACH plants not seen.

^BAstrebla species have up to nine fertile florets, only basal floret recorded here.

^CTerminal spikelet in inflorescence consisting of heterogeneous florets.

^DSee Thompson and Fabillo (2021).

For each CL species, the following were recorded: taxonomic distribution, life cycle, photosynthetic pathway according to Watson and Dallwitz (1992), type of terminal inflorescence, and geographic distribution by climate zones, modified from climate classification of Australia by the Bureau of Meteorology (BOM; <http://www.bom.gov.au/climate/how/newproducts/images/zones.shtml>, accessed 27 February 2020; Table 3, Fig. 2). Three of the climatic zones were subdivided in order to accommodate biogeographic diversity in Australian grasses found during this study, viz. tropical: western (T1) and eastern (T2); semi-desert: northern (Ds1), eastern (Ds2), southern (Ds3) and western (Ds4); and temperate: eastern (M1), Tasmania (M2) and western (M3). Maps of the frequency of genera and species by subfamily and tribe were developed from The Australasian Virtual Herbarium (see <http://avh.ala.org.au/occurrences>, accessed January 2021) and BRI herbarium specimen records (Fig. 3 and 4). Distribution records for each species were

tallied for each of the climatic zones and are summarised in Fig. 3.

Diagrammatic representations of hypothetical relationships of the CL types were developed for the taxa within each of the five Australian subfamilies (Appendix 1). The individual diagrams were used to establish an overall CL relationship diagram (Fig. 5).

In total, 33 species from 11 genera in 5 sub-families were chosen as representative examples of the types of CL discovered and are described below (Table 4). The observations made from herbarium specimens and cultivated plants for these examples provide the framework for the model of relationships between the CL types (Fig. 5 and Appendix 1). Information relating to amphigamous species worldwide was gathered from examination of herbarium specimens and the literature (Table 2). The taxonomic distribution of grass CL worldwide was gathered from the literature, mainly from Campbell *et al.* (1983) and Watson and Dallwitz (1992) (Table 5).

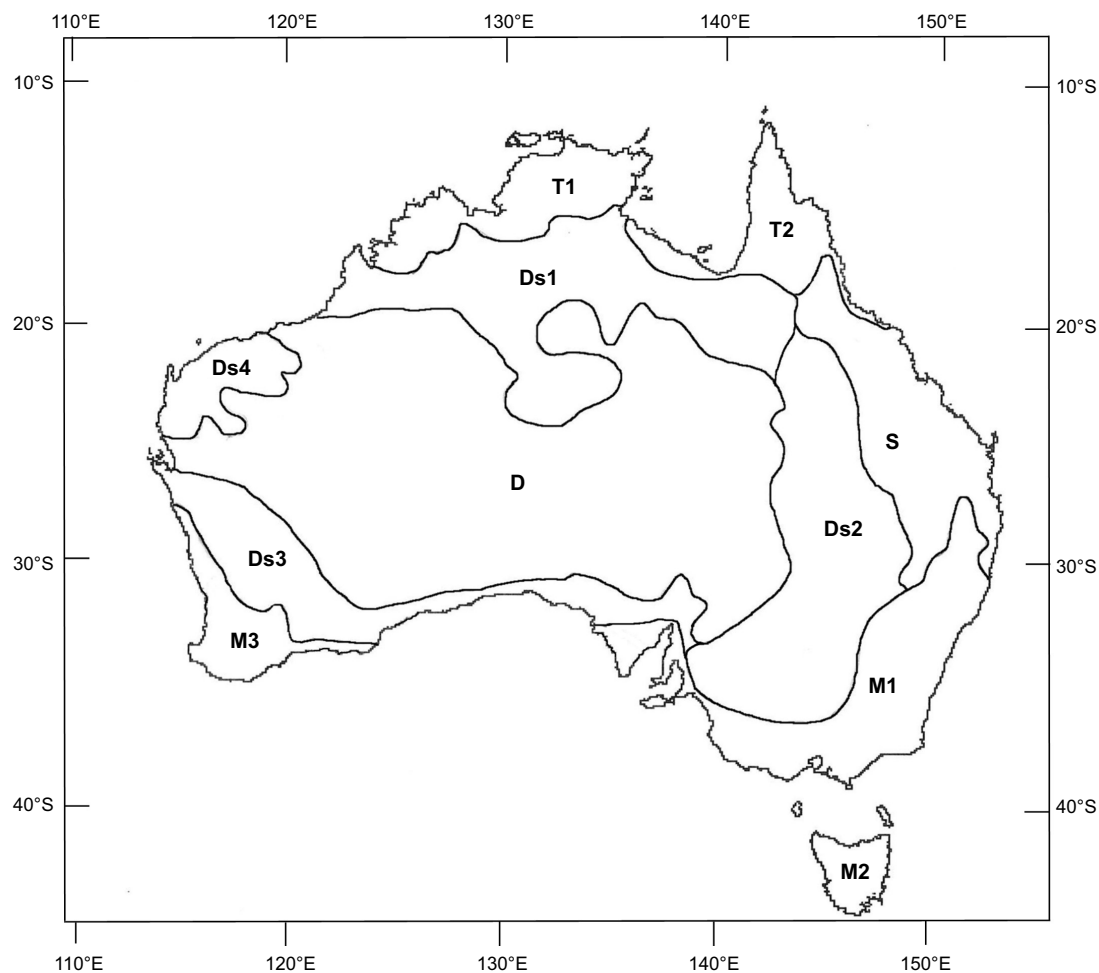


Fig. 2. Climatic zones of Australia modified from Bureau of Meteorology (BOM, see <http://www.bom.gov.au/climate/how/newproducts/images/zones.shtml>, accessed 27 February 2020). T, equatorial to tropical; S, subtropical; D, desert; Ds, semi-desert; M, temperate.

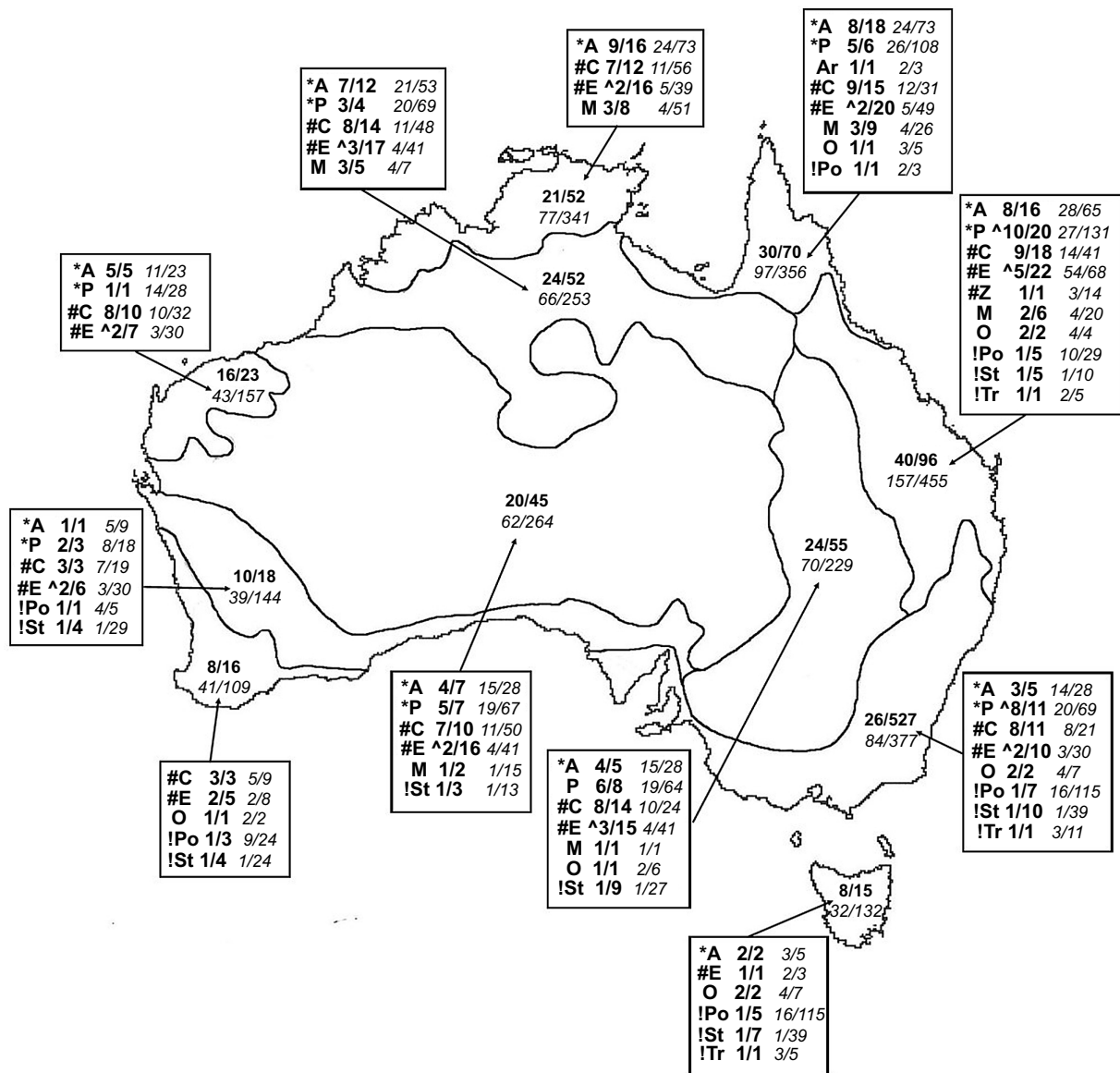


Fig. 3. Taxonomic and geographic distribution by climatic zones for Australian native grasses manifesting cleistogamy (CL). Totals for genera and species of CL grasses and all Australian grasses (indicated by 12/13 and 12/13 respectively) are shown within the polygons for each climatic zone and boxes show taxonomic breakdowns for CL taxa. Circumflexes (^) indicate genera with multiple CL types. Taxonomic breakdown: #, Subfamily Chloridoideae; C, tribe Cynodonteae; E, tribe Eragrostoideae; Z, tribe Zoysieae; M, subfamily Micrairoideae; O, subfamily Oryzoideae; asterisks (*), subfamily Panicoideae; A, tribe Andropogoneae; Ar, tribe Arundinelleae; P, Paniceae; exclamation marks (!), subfamily Pooideae; Po, tribe Poeae; St, tribe Stipeae; Tr, tribe Triticeae.

Results

Three broad groups of CL types were defined, viz. Type 1 monomorphic CL anthers, Type 2 dimorphic CH and CL anthers and Type 3, amphigamous CL with dimorphic spikelet, and with ten subgroups (Table 6). Amphigamy in Australian grasses is represented by several combinations of inflorescence types (Fig. 1). Terminal inflorescences can vary from open panicles or reduced panicles to racemes in combina-

tion with axillary inflorescences varying from reduced panicles to few-flowered racemes. Basal inflorescences are rare in Australian grasses and are possessed by two species of *Enneapogon* Desv. ex P.Beauv. and one species of *Eriachne* R.Br having single- to few-flowered racemes and few-flowered racemes to reduced panicles respectively.

Fig. 5 shows hypothetical morphological relationships for the 10 subgroups of CL types for the twelve subfamilies represented in Australia. The core of the relationships is

based on plants that are CH-only, CL-only and combined CH and CL on different plants of the same species. In its simplest expression, the CH and CL anthers are the same size (CL Type1).

Of the 997 native grasses from 151 genera recorded in Australia, 135 species from 46 genera were found to have some form of CL (Tables 3 and 5). These figures represent 14% of all species there and 30% of the genera, compared to 3 and 11% worldwide respectively (Table 5). However, there are disproportions in the distribution of taxonomic, geographic, life cycle, physiological and morphological

aspects of CL species (Tables 5 and 7). In total, grasses worldwide and in Australia are placed predominantly in three subfamilies, viz. Chloridoideae, Panicoideae and Pooideae, in approximately similar proportions (Table 5). The taxonomic distribution of CL is also predominated by these subfamilies, but worldwide proportionately more CL species occur in Pooideae (Table 5).

More than half of all CL Australian grasses have CL Type 1. Choroid and panicoid grasses represent 77% of all Australian CL species in nearly equal proportions compared to both groups representing 24 and 37% of all Australian

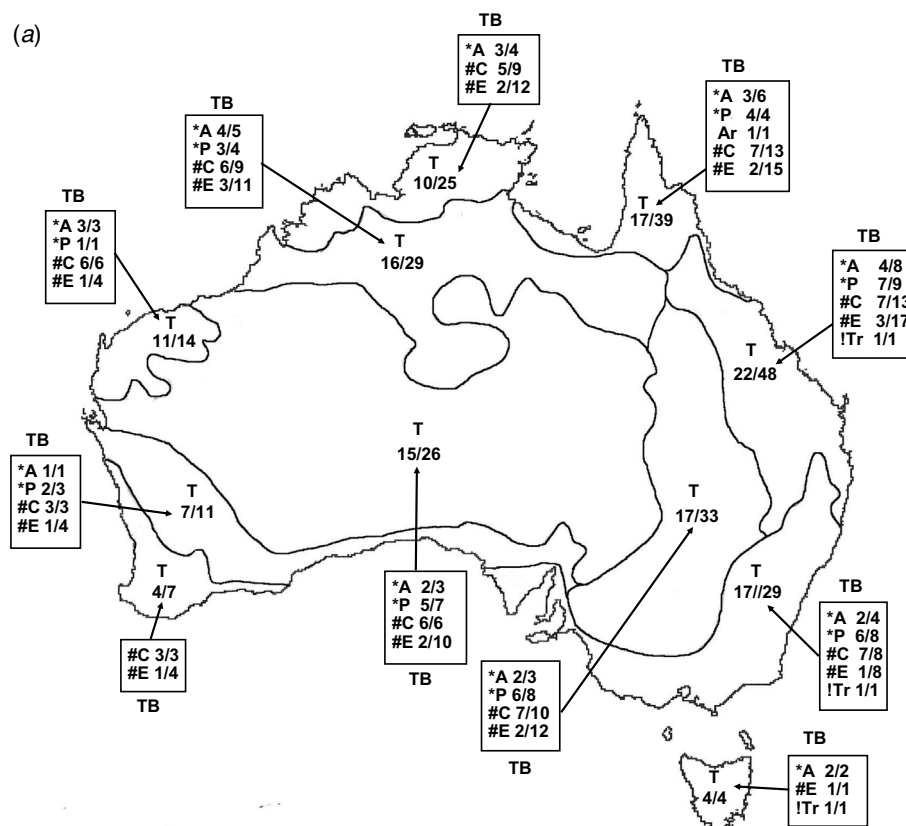
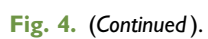
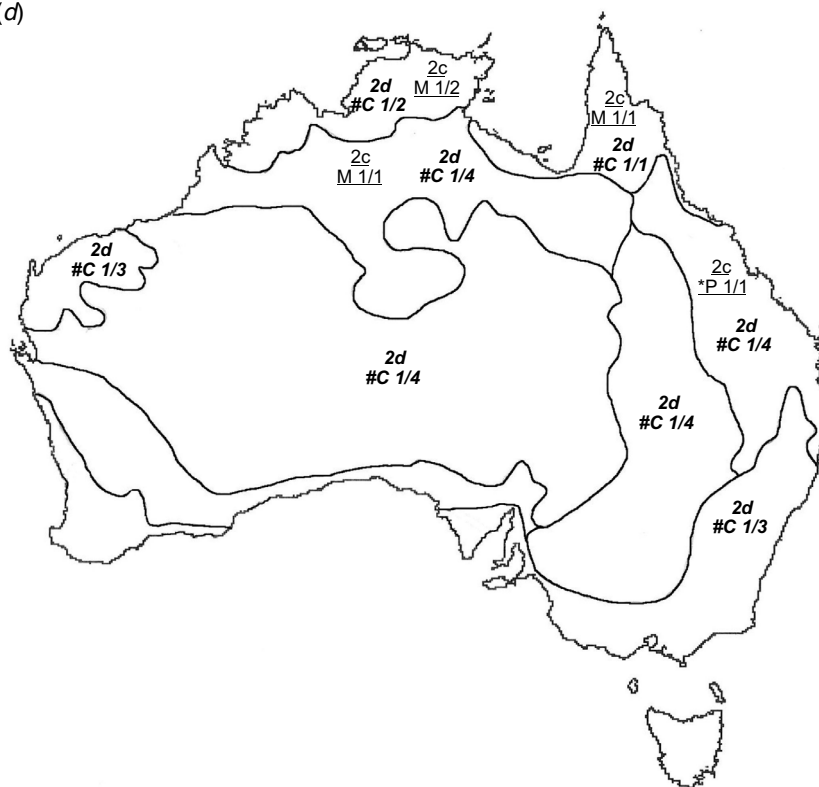


Fig. 4. Taxonomic and geographic distribution by climatic zones for the types of cleistogamy (CL) found in Australian native grasses. Totals (T) and taxonomic breakdown (TB) by genera and species for each CL type are shown within the polygons for each climatic zone and boxes show taxonomic breakdowns by tribes. (a) Type 1, monomorphic CL anthers. **Type 1a**, species with inflorescences comprising chasmogamous (CH)-only, CL-only or a mixture of CH and CL spikelets. (b) **Type 1b**, CH and CL on separate plants. **Type 1c**, species with amphigamous inflorescences. (c, d) Type 2, species with dimorphic CL anthers. (c) **Type 2a**, species with inflorescences comprising CH-only, CL-only or a mixture of CH and CL spikelets; **Type 2b**, species with amphigamous CL with axillary inflorescences. (d) **Type 2c**, species with CH and CL on separate plants. **Type 2d**, species with amphigamous inflorescences, CL spikelets on short leafy branches. (e) Type 3, species with amphigamous CL with dimorphic spikelets. **Type 3a**, species with axillary dimorphic spikelets; **Type 3b**, species with cleistogenes. Taxonomic breakdown: hash symbol (#) Subfamily Chloridoideae; C, tribe Cynodonteae; E, tribe Eragrostoideae; Z, tribe Zoysieae; M, subfamily Micrairoideae; O, subfamily Oryzoideae; asterisks (*), subfamily Panicoideae; A, tribe Andropogoneae; Ar, tribe Arundinelleae; P, Paniceae; exclamation marks (!), subfamily Pooideae; Po, tribe Poeae; St, tribe Stipeae; Tr, tribe Triticeae



(d)



(e)

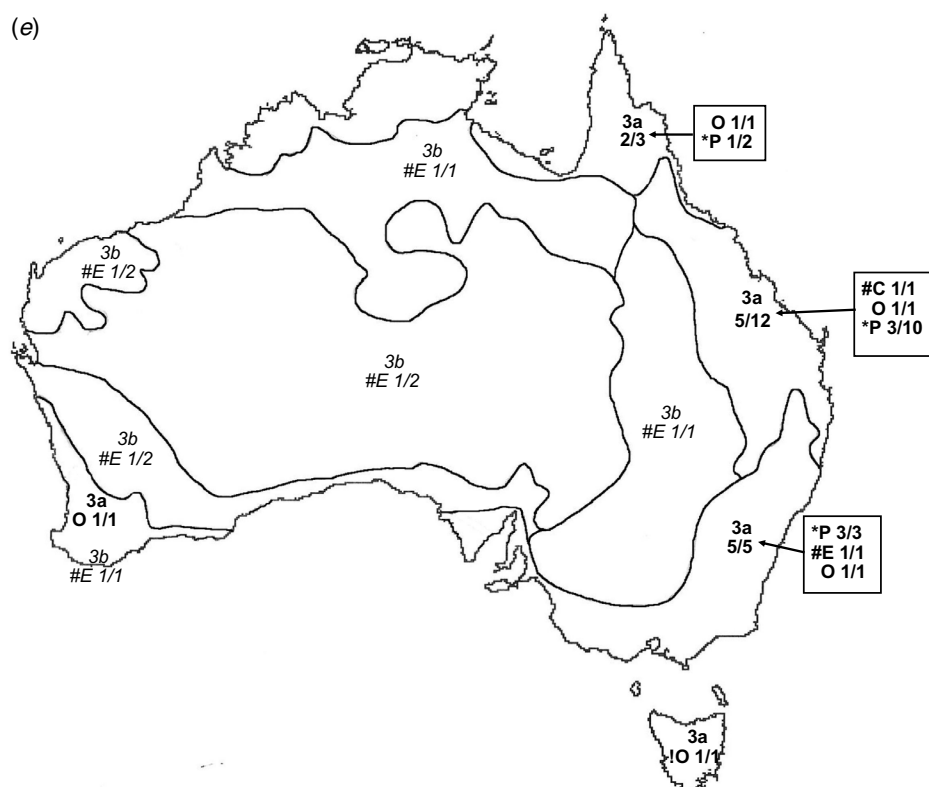
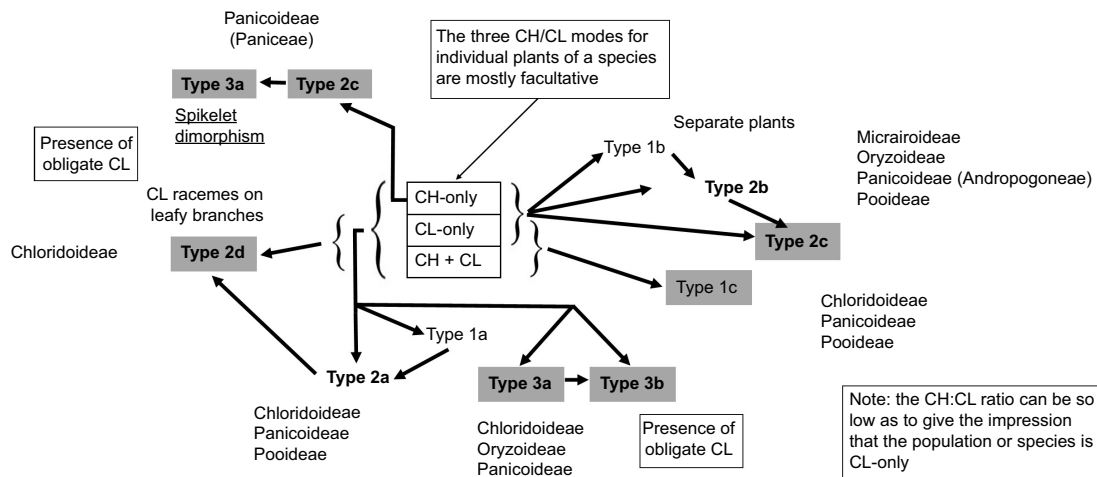


Fig. 4. (Continued).



Legend
Types of CL in Australian grasses

1. Monomorphic CL anthers

- 1a Species with CH and CL in the same terminal inflorescences
- 1b Species with CH and CL on separate plants
- 1c Species with **amphigamous** inflorescences

2. Dimorphic CL anthers

- 2a Species with CH and CL in the same terminal inflorescences
- 2b Species with CH and CL on separate plants
- 2c Species with **amphigamous** axillary CL racemes
- 2d Species with **amphigamous** CL inflorescences on short leafy branches

3. Amphigamous CL with dimorphic spikelets

- 3a Species with dimorphic axillary spikelets
- 3b Cleistogenes present

Fig. 5. Hypothetical morphological relationships of the types of cleistogamy (CL) in Australian grasses. The model shows relationships of variations on the three pollination modes, CH-only, CL-only and CH and CL combined in the same inflorescence, with the simplest known form central with radiating increasing complexity. Taxonomic distribution is shown with representative subfamilies indicated adjacent to each CL subtype. CH, chasmogamous. The distribution of the various forms of amphigamy is highlighted.

Poaceae respectively (Table 5). Chloridoid and panicoid grasses have the broadest range of CL types, with some of the types overlapping (Table 5). Geographic distribution and taxonomic diversity of CL types are highest in the subtropics and semi-desert of Australia (Fig. 3 and 4, Table 7). Two CL types, 2d and 3b, are found only in semi-desert and desert and are represented by the chloridoid genera, *Astrelba* F.Muell. and *Enneapogon* Desv. ex P.Beauv. and the latter is the only Australian genus known with species that exhibit differentiated basal CL spikelets hidden in the leaf sheaths, cleistogenes.

The taxonomic distribution of Australian CL species within the tribes and subtribes of subfamilies Chloridoideae and Panicoideae is restricted (Soreng *et al.* 2017; Table 5). In the Australian Chloridoideae, three of the four tribes and five of the ten subtribes contain CL species. Most of the CL in the Australian Chloridoideae are found in the tribes Cynodonteae and Eragrostoideae representing respectively 14 and 30% of all the Australian species in those tribes. There is a similar pattern in the Australian Panicoideae. Three of the four panicoid tribes and nine of the eighteen subtribes have CL species. The panicoid tribes Andropogoneae and Paniceae contain most of the CL species and represent respectively 18 and 13% of all the species in the two tribes.

CL in axillary and basal inflorescences can be obligate or facultative. Where it occurs in CL Type 3 it is obligate with few exceptions as found in *Enneapogon*. In CL Types 1 and 2, the axillary spikelets have facultative CL.

The geographic distribution of the taxa within Australian Poaceae shows distinct trends with highest frequencies along the tropical eastern coast (36% of species), subtropical eastern coast (46% of species) and temperate eastern coast (38% of species) (Fig. 3). The distribution of CL grasses follows a similar trend with 50% of species occurring in the tropical zone, 71% in the subtropical zone and 42% in the temperate zone (Fig. 3 and 4). Nearly 80% of all Australian CL species occur in the eastern coastal subtropical to tropical zones within the latitude range 10–30°S.

The composition of grass floras worldwide and in Australia with respect to photosynthetic pathway is distinctly different (Table 7). Australia has a greater proportion of C₄ grasses than worldwide. However, the proportions of CL species that are C₃ and C₄ are similar to those for the totals of C₃ and C₄ species for the world and Australia.

Of Australian CL grasses, more than twice as many are perennial as are annual. Further research is required to determine the relative proportions of these life cycles in all grasses in Australia and worldwide.

Table 4. Eleven cleistogamous (CL) grass genera by subfamily and tribe selected as examples of the types of expression of CL found in Australia with corresponding categories by various authors.

Parameter	Chloridoideae (Eragrostideae)			Panicoideae (Andropogoneae)				Panicoideae (Paniceae)	Micrairoideae (Eriachneae)		Pooideae (Stipeae)
Genus	<i>Astrebla</i>	<i>Enneapogon</i>	<i>Uniola</i> sp.	<i>Clausospicula</i>	<i>Dichanthium</i>	<i>Schizachyrium</i>	<i>Spathea</i>	<i>Thyridolepis</i>	<i>Eriachne</i>	<i>Pheidochloa</i>	<i>Austrostipa</i>
Habitat	Mostly subtropical to tropical arid grasslands on clay plains	Arid temperate to tropical landscapes	Subtropical semi-desert woodlands on sandstone hills	Tropical woodlands on well drained alluvium	Very broad range; mesic to arid temperate and tropical landscapes	Mostly tropical over a broad range of landscapes	Subtropical to tropical arid grasslands on clay plains	Semi-desert shrublands and woodlands on a variety of soils with low water holding capacity	Mostly tropical, coastal only to semiarid to arid	Tropical seasonal soakage areas	Mostly temperate to subtropical and semi-desert to desert; a broad range of landscapes
Authors											
Hackel (1906)	CL-only [2]	Facultative [1]	Dimorphic species [1]	–	–	–	–	–	–	–	–
Campbell et al. (1983)	Sheath fertilisation [2]	Sheath fertilisation, cleistogenes [4]	–	–	Sheath fertilisation [1]	Sheath fertilisation [7]	Sheath fertilisation [1]	No category	No category	No category	Sheath fertilisation
Connor (1979)	CL and CH	CL and CH	–	–	–	CL and CH	CL-only	–	CL and CH; CL only	CL-only	CL and CH
Watson and Dallwitz (1992)	Exposed-CL or CH	Exposed-CL or CH ± hidden cleistogenes	Exposed-CL or CH	Exposed-CL	Exposed-CL or CH	Exposed-CL or CH	Exposed-CL	Exposed-CL or CH	Exposed-CL or CH	Exposed-CL	Exposed-CL
Culley and Klooster (2007)	Dimorphic [2]	Dimorphic [4]	–	–	Dimorphic [1]	Dimorphic [7]	Dimorphic	Complete [1] dimorphic [2]	Dimorphic	Dimorphic [1]	Dimorphic
This study											
CL type	Dimorphic CL anthers [4]	Monomorphic CL anthers dimorphic CL anthers amphigamous CL [6]	Amphigamous CL [1]	Monomorphic CL plants [1]	Monomorphic CL anthers [2 and 3 subspecies]	Dimorphic CL plants [7]	Dimorphic CL anthers [1]	Dimorphic CL anthers [3]	Amphigamous CL with dimorphic anthers dimorphic CL plants [8]	Dimorphic CL plants [1]	Dimorphic CL plants [11]
CL and CH presence	Same plant; facultative CH	Same plant	Same plant			Different plants	Same plant; facultative CH	Same plant	Same or different plants	Different plants	Different plants
Inflorescences	Terminal only: spikelets with CH or CL florets and spatheolate CL racemes.	Mixed CH or CL in terminalonly; amphigamous; clandestine CL axillary; cleistogenes	Amphigamous – terminal and clandestine axillary	Terminal-only	Terminal sometimes axillary	Fascicles: CH on elongated peduncles	Fascicles: CL racemes partly or totally enveloped by spatheoles; CH racemes on elongated peduncles	Terminal only	Terminal and rarely basal	Terminal only	Terminal only

(Continued on next page)

Table 4. (Continued).

Parameter	Chloridoideae (Eragrostideae)			Panicoideae (Andropogoneae)				Panicoideae (Paniceae)	Micrairoideae (Eriachneae)		Pooideae (Stipeae)
Genus	<i>Astrebla</i>	<i>Enneapogon</i>	<i>Uniola</i> sp.	<i>Clausospicula</i>	<i>Dichanthium</i>	<i>Schizachyrium</i>	<i>Spathea</i>	<i>Thyridolepis</i>	<i>Eriachne</i>	<i>Pheidochloa</i>	<i>Austrostipa</i>
Spikelets	Heteromorphic: basal spikelets longest; facultative CH and CL, and obligate CL	Varies by species: monomorphic; heteromorphic; facultative CL and obligate CL	Dimorphic: terminal facultative CL axillary obligate CL	Monomorphic	Monomorphic	Monomorphic	Monomorphic	Monomorphic	Dimorphic	Monomorphic	Monomorphic
Fertile florets	Heteromorphic: distal obligate CL florets, proximal facultative CH florets	Heteromorphic	Heteromorphic	Monomorphic	Monomorphic	Monomorphic	Monomorphic	Monomorphic	Monomorphic	Monomorphic	Monomorphic
Anthers	Both CH and CL heteromorphism	Varies by species: monomorphic; monomorphic and dimorphic; heteromorphic	Heteromorphic within spikelets; dimorphic across inflorescences	Dimorphic CH ^A	Monomorphic	Dimorphic	Dimorphic	Dimorphic	Dimorphic	Dimorphic	Dimorphic
Caryopsis morphology	Both CH and CL heteromorphism	Varies by species: monomorphic heteromorphic	Heteromorphic across florets dimorphic across inflorescences	Monomorphic ^A	Monomorphic	Monomorphic	Monomorphic	Monomorphic	Monomorphic	Monomorphic	Monomorphic
Diaspore	All florets united	Varies by species: terminal spikelet only; axillary spikelets with or without disarticulating culm; plus cleistogene	Terminal florets and retained axillary spikelet	Floret	Spikelet	Spikelet	Floret	Spikelet	Floret	Floret	Spikelet

^AOnly CL spikelets seen.

CH, chasmogamous; [n], number of species recorded by author.

Table 5. Tallies of grass genera (g) and species (s) showing taxonomic distribution of cleistogamy (CL), worldwide and Australia.

Sub-family	PP	Worldwide						Australia											
		Total (g/s)				CL (g/s)				Total CL (g/s)									
		(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	CL types (g/s)								(n)	(%)
Anomochlooideae	C ₃	2/4	0.3/0.03	0/0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aristidoideae	C ₄	3/367	0.4/3	1/4	1/1	1/59	0.7/6	0	0	0	0	0	0	0	0	0	0	0	0
Arundinoideae	C ₃	14/40	2/0.3	0/0	0	4/13	2.6/1	0	0	0	0	0	0	0	0	0	0	0	0
Bambusoideae	C ₃	125/1670	16/15	1/4	1/1	3/3	2/0.3	0	0	0	0	0	0	0	0	0	0	0	0
Chloridoideae	C ₃	2/3	0.3/0.03	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	C ₄	122/1599	16/14	26/63	32/20	26/244	22/24	11/40	1/1	2/5	1/1	0	0	1/4	1/1	1/2	15 (3 ^A)/54	33/39	
Danthonioideae	C ₃	19/292	3/3	1/21	1/7	3/44	2/4	0	0	0	0	0	0	0	0	0	0	0	0
Micrairoideae	C ₃	6/126	0.8/1	0	0	2/18	1.3/2	0	0	0	0	0	0	0	0	0	0	0	0
	C ₄	2/58	0.3/0.5	2/4	3/1	2/48	1.3/5	0	0	0	0	2/7	1/2	0	0	0	2 (1 ^A)/9	4/7	
Oryzoideae	C ₃	19/115	3/1	3/4	4/1	5/13	3.3/1	0	0	0	0	1/1	0	0	1/1	0	2/2	4/1	
Panicoideae	C ₃	52/493	7/4	6/27	7/8	19/45	12.7/4	6/9	0	0	0	0	1/1	0	4/11	0	10 (1 ^A)/21	22/17	
	C ₄	185/2748	24/24	16/56	20/17	60/299	40.7/29	10/16	3/3	0	1/2	2/8	0	0	0	0	15 (1 ^A , 1 ^B)/29	33/21	
Pharioideae	C ₃	3/12	0.4/0.1	0/0	0	2/3	0.7/0.3	0	0	0	0	0	0	0	0	0	0	0	0
Pooideae	C ₃	202/3968	26/34	25/137	31/43	18/210	10.7/20	1/1	0	0	1/8	1/11	0	0	0	0	3/20	7/15	
Puelioideae	C ₃	2/11	0.3/0.1	0/0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total		768/11506		82/321		151 ^B /997		27 (1 ^B)/66	4/4	2/5	3/11	6/27	2/3	1/4	6/13	1/2	46 (6 ^A , 1 ^B)/135		

Worldwide total data and taxonomy from [Watson and Dallwitz \(1992\)](#) and [Soreng et al. \(2017\)](#). Worldwide CL data from [Campbell et al. \(1983\)](#) and taxonomy adjusted according to [Soreng et al. \(2017\)](#). Australian total data from B. K. Simon and Y. Alfonso, AusGrass (see <http://ausgrass2.myspecies.info/>). PP, photosynthetic pathway. CL types: 1, monomorphic CL anthers: 1a, species with inflorescences comprising CH only, CL only or a mixture of CH and CL; 1b, CH and CL on separate plants; 1c, species with amphigamous inflorescences; Dimorphic CL anthers: 2a, species with inflorescences comprising CH only, CL only or a mixture of CH and CL; 2b, CH and CL on separate plant; 2c, amphigamous with axillary inflorescences; 2d, amphigamous with CL inflorescences on short leafy branches; Amphigamous CL with dimorphic spikelets; 3a, with axillary spikelet dimorphism; 3b, cleistogenes present.

^ASome genera have multiple expressions of CL.

^BSome genera have C₃ and C₄ species.

^CSome species occur in more than one climatic zone; distribution data from The Australasian Virtual Herbarium (see <http://avh.ala.org.au/occurrences>).

The distribution of types of terminal inflorescences found in types of CL grasses also shows disproportionalities (Table 7). CL grasses with a reduced inflorescence such as a raceme represent 27% of all CL Australian species, whereas racemes are represented by 11% of Australian grasses overall. By contrast, 75% of CL species have panicles and 81% of all Australian species have panicles.

Cultivated plants from CL caryopses of species of *Austrostipa* S.W.L.Jacobs and J.Everett and *Schizachyrium* that have CL Type 2b produced CL-only inflorescences; however, it is unknown whether the CH caryopses from these species produce CH-only plants. Both CH and CL caryopses from species with CL Types 1a and 2a appear from cultivation trials to produce plants with inflorescences of all three possibilities, viz. spikelets CH-only, CL-only or a mixture of CH and CL.

The light condition trial using cultivated plants provided mixed results. C₃ genera including *Calyptochloa* and *Dimorphochloa* were similar in producing CL inflorescences in both full sun and partial shade. The C₄ species of *Enteropogon* differed by the partial-shade plants mostly producing fewer inflorescences. The C₄ grasses

Arthraxon, *Clausospicula* and *Spathia* strongly favoured full-sun conditions.

Discussion

The three broad categories of CL types, viz. (1) monomorphic CL anthers, (2) dimorphic CL anthers and (3) amphigamy with dimorphic spikelets, with the ten subtypes are discussed below using examples representative of each type. These examples contribute new information relating to grass CL and provide the foundation for this study. The examples also enable comparison with other authors' classifications of CL types presented in Table 4, thereby permitting an understanding of the impact of the new information on the review of classification of grass CL in Australia.

(1) Monomorphic CL anthers

This category is defined by species having CH and CL anthers of the same size. Monomorphic CL anthers are usually found in species with only terminal inflorescences, but several

Table 6. Classification of types of cleistogamy (CL) found in Australian grasses.

Type of CL	Spikelet fertilisation mode according to inflorescence position			Number of species
	Terminal	Axillary	Basal (or subterranean)	
1. Monomorphic CL anthers (CH and CL anthers the same size)				
1a. Monomorphic anthers in the same terminal inflorescences	CH-only, CL-only or a mixture of CH and CL	Absent	Absent	66
1b. Monomorphic CL anthers with CH and CL only on separate plants	CH and CL on separate plants	Absent	Absent	4
1c. Monomorphic CL anthers with amphigamy	CH-only, CL-only or a mixture of CH and CL	CL-only; CH and CL spikelets similar	CL-only	5
2. Dimorphic CH and CL				
2a. Dimorphic CL anthers in the terminal inflorescence	CH-only, CL-only or a mixture of CH and CL	Absent	Absent	11
2b. Dimorphic CL anthers only on separate plants	CH and CL on separate plants	Absent	Absent	27
2c. Amphigamous with axillary CL inflorescences	CH-only or CL-only	CL-only if present; CH and CL spikelets similar	CL-only if present	3
2d. Amphigamous with CL inflorescences terminal on short leafy branches	Of two types: (i) mixed CH and CL in racemes overtopping plant. (ii) CL-only in racemes on short branches	Absent	Absent	4
3. Amphigamous CL with dimorphic spikelets				
3a. Amphigamous CL with dimorphic axillary spikelets	CH-only	CL-only if present; CH and CL spikelets similar or dissimilar	Absent	15
3b. Amphigamous CL with cleistogenes ^A	CH-only, CL-only or a mixture of CH and CL	CL-only or with some CH present; CH and CL spikelets similar	CLeistogenes ^A present	2
3c. Amphigamous CL with rhizanthogenes (not present in Australia)	CH-only	Absent	Rhizanthogenes ^B present	0

CH, chasmogamous.

^ACleistogene, CL spikelets born at the base of the plant usually hidden in the leaf sheaths, with differentiated morphology from the terminal CH spikelets.

^BRhizanthogene, subterranean CL spikelets born on rhizomes usually with differentiated morphology from the terminal CH spikelets, species of *Amphicarpum* Kunth (from south-eastern North America) can bear rhizanthogenes with gradational variation in morphology varying from similar to the CH terminal spikelets to strongly differentiated.

species are amphigamous. The CL spikelets are usually interspersed with CH spikelets in the same inflorescence in various proportions, sometimes influenced by environmental factors (Campbell *et al.* 1983; Bell and Quinn 1985; Philipson 1986; Bell and Quinn 1987; Culley and Klooster 2007). Soil moisture, light intensity and time of year have been found to influence the presence of CL in *Dichanthium clandestinum* (L.) Gould. CH and CL spikelets can occur without apparent pattern in the same inflorescence or in different parts of the same inflorescence (Hitchcock and Chase 1915; Burbidge 1941; Campbell *et al.* 1983; Bell and Quinn 1985; Philipson 1986; Bell and Quinn 1987; Morrone *et al.* 2007). Hackel (1906) referred to this category as ‘facultative cleistogamous species’.

Of the 135 Australian grasses recorded with CL ~55% have monomorphic CL anthers (Table 5). Of the new records of CL since Culley and Klooster (2007), 45% relate to species with

monomorphic CL anthers, although Culley and Klooster (2007) did not use this category. Discussed below are examples of the three subtypes of monomorphic CL anthers where the CH and CL spikelets are: (a) in the same inflorescence, e.g. *Dichanthium* Willmet, *Enneapogon*, *Spathia* and *Thyridolepis* (Nees) S.T.Blake; (b) on separate plants, e.g. *Clausospicula* Lazarides; (c) with amphigamy, e.g. *Ectrosia* R.Br. and *Eragrostis* N.M.Wolf.

(1a) Monomorphic anthers in the same terminal inflorescences

Dichanthium

Dichanthium comprises ~16 species worldwide, with five native to Australia, one with three subspecies (Watson and Dallwitz 1992; Simon 2002). *Dichanthium sericeum* (R.Br.) A.Camus. is the only species that has been recorded with

Table 7. Distribution of types of cleistogamy (CL) found in Australian grasses (AG) by various categories.

Category		Percentage of all AG	Number of species by CL type										
			1a	1b	1c	2a	2b	2c	2d	3a	3b	T	% CL
Life cycle	Annual	24	21	4	2	2	9	3	0	0	0	41	30
	Perennial	77	45	0	3	8	18	0	4	15	2	96	70
Terminal inflorescence type	Panicle	81	36	2	5	8	19	2	0	1	2	75	55
	Digitate	5	14	0	0	0	0	0	0	0	0	14	10
	Spike-like panicle	1	0	0	0	0	0	0	0	9	0	9	7
	Raceme	11	15	2	0	0	1	0	4	5	0	27	20
	Fasciculate	2	2	0	0	2	7	0	0	0	0	11	8
Climatic zone	Tropical	41 ^A	19	3	4	1	14	1	0	1	0	43	31
	Subtropical	40 ^A	31	3	3	6	15	1	0	10	0	69	52
	Desert	25 ^A	27	0	2	0	4	1	4	0	2	40	29
	Semi-desert	43 ^A	35	3	4	1	10	0	4	1	1	59	43
	Temperate	40 ^A	19	0	1	8	4	0	0	3	0	35	26

Climatic zones adopted from BOM (<http://www.bom.gov.au/climate/how/newproducts/images/zones.shtml>, accessed 27 February 2020). PP, photosynthetic pathway. CL types: Monomorphic CL anthers: 1a, species with inflorescences comprising CH only, CL only or a mixture of CH and CL; 1b, CH and CL on separate plants; 1c, species with amphigamous inflorescences. Dimorphic CL anthers: 2a, species with inflorescences comprising CH only, CL only or a mixture of CH and CL; 2b, CH and CL on separate plant; 2c, amphigamous with axillary inflorescences; 2d, amphigamous with CL inflorescences on short leafy branches. Amphigamous CL with dimorphic spikelets: 3a, with axillary spikelet dimorphism; 3b, cleistogenes present.

^ASome species occur in more than one climatic zone; distribution data from AVH (<http://avh.ala.org.au/occurrences>, accessed January 2021).

CL until now, but without mention of subspecies (Campbell *et al.* 1983; Yu *et al.* 2000). Whalley *et al.* (2013) recorded 65% CL for *D. sericeum* subsp. *sericeum*. The latter subspecies is a short-lived perennial growing in a variety of habitats, whereas the other two subspecies have been recorded as annuals mostly found in grasslands on heavy clay soils. *Dichanthium queenslandicum* B.K.Simon, a rare perennial, has not been recorded with CL before this study and also mostly inhabits grasslands on clayey soils.

Inflorescences of plants of the CL species of *Dichanthium* can occur in either of three states of spikelets, viz. CL-only, CH-only, or a mixture of both CH and CL (Table 8). Furthermore, in mixed CH and CL panicles, two sets of ranges for CH and CL anthers were found and these ranges more or less match the ranges for CH-only and CL-only (Table 9).

Enneapogon

Enneapogon consists of 30 species worldwide (Watson and Dallwitz 1992). Fifteen are endemic to Australia and one Australian species extends into New Guinea (Weiller and Lazarides 2005). Four Australian species have been reported with CL (Hubbard 1937; Burbidge 1941).

Three types of CL were recorded for the five Australian species of *Enneapogon* with CL (Tables 2 and 10). Two species have monomorphic CL anthers, viz. *Enneapogon asperatus* C.E.Hubb., and *Enneapogon eremophilus* Kakudidi. *E. asperatus*, as reported by Burbidge (1941), has CL in the proximal primary branch of the terminal inflorescence enveloped by the leaf sheath with the remainder of the

inflorescence exerted, and CH. This specific form of CL is very rare in grasses, although Campbell *et al.* (1983) in the broad sense, referred to it as ‘Type 1. Sheath fertilisation’, where the inflorescence or spikelets, at least initially, are held within the leaf sheaths of the upper portions of inflorescence culms. A variation on clandestine CL inflorescences can be found in the panicoid genus *Dichantherium* (Hitch. and Chase) Gould from North America where the CL spikelets with dimorphic anthers are produced periodically and hidden in the leaf sheaths (Freckmann and Lelong 2003).

Spathia

Spathia is a monospecific genus with close affinity to *Dichanthium*, differing by the slightly thinner texture of the glumes and the colour of their indumentum (Blake 1944a). *S. neurosa* has been reported as an annual with a restricted occurrence mostly in north-western portions of the black soil plains of the Mitchell Grass Downs in the hot arid tropics of Australia (Lazarides 1970; Silcock *et al.* 2014).

The circumscription of *S. neurosa* was based on one specimen (Ewart and Davies 1917; Blake 1944a). Since then, 27 additional accessions, including seven by Blake, have been contributed to Australian herbaria. Observations from these specimens support the description by Blake (1944a) in terms of the anthers being only CL and 0.5 mm long, except for three specimens that Blake did not see. Two had male pedicellate spikelets with large anthers and one had most racemes enveloped by spatheoles as well as a single elongated inflorescence culm, but the raceme had

Table 8. Comparison of anthers in *Spathia neurosa* and the Australian cleistogamous (CL) species of *Dichanthium*. Chasmogamous (CH).

Character		<i>Spathia neurosa</i>	<i>Dichanthium queenslandicum</i>	<i>Dichanthium sericeum</i> subsp.		
				<i>humilius</i>	<i>polystachyon</i>	<i>sericeum</i>
Presence of enlarged spatheoles		Mostly	Absent	Absent	Sometimes present	Sometimes present
Anthers in sessile spikelet	Number	2	2	2	2	2
	CH length (mm)	0.3–0.5	1.1–1.3	0.3–0.7	0.6–0.9	1.1–1.2
	CL length (mm)	0.3–0.5	1.1–1.3	0.2–0.7	0.4–0.9	0.3–1.0
Anthers in pedicellate spikelet	Number	0 or 2	0 or 2	0	0 or 2	0 or 2
	Length (mm)	1.4–2.0	2.0–2.5	0	0.6–0.9	0.6–1.3

Table 9. Composition of the terminal inflorescences, with anther lengths (mm), for chasmogamous (CH) and cleistogamous (CL) spikelets of *Dichanthium sericeum* subsp. *sericeum* and *Enneapogon cylindricus*.

Species	Spikelet composition of terminal inflorescence					
	CL-only	CH-only	Mixture of CH and CL			
			A		B	
			CH	CL	CH	CL
<i>Dichanthium sericeum</i> subsp. <i>sericeum</i>	0.3–0.6	1.1–1.2	0.5–0.7	0.4–0.6	1.1–1.2	0.8–1.0
<i>Enneapogon cylindricus</i>	0.3–0.4	0.4 or 0.7–1.3	0.2–0.6	0.2–0.6	0.9–1.2	0.3–0.9

Both species have two categories, A and B, of anther lengths in inflorescences of plants where CH and CL spikelets occur together.

Table 10. Chasmogamous (CH) and cleistogamous (CL) anther lengths (mm) for three Australian species of *Enneapogon* by inflorescence location.

Inflorescence types on the same plant	<i>Enneapogon avenaceus</i>			<i>Enneapogon caerulescens</i>		<i>Enneapogon cylindricus</i>	
	CH		CL	CH	CL	CH	CL
Terminal (panicle)	ft: 1	0.5–0.7	0.2–0.5	0.2–0.7	0.2–0.5	0.2–1.3	0.2–0.8 (–1.2)
	ft: 2	0.3–0.4	0.3–0.6	0.2 (very uncommon)	0.3–0.4 (uncommon)	ft: 2–4: sterile	
	ft: 3	0.2–0.3	0.2–0.3	ft: 3–6: sterile			
	Or sterile or absent						
Axillary ^A (raceme)	Absent		Absent	0.3–0.6 ft: 2–3: sterile (uncommon)	0.4–1.0 (uncommon)	0.2–0.4 (–0.8) ft: 2–4: sterile	
Basal ^A (reduced raceme; spikelets = cleistogenes)	Absent		Absent	0.2–0.3ft: 2–3: sterile (uncommon)	Absent	0.2–0.4ft: 2–3: sterile (occasional)	

ft, floret, with successive positions (1–6) from base to apex.

^AInflorescence enveloped by leaf sheath.

disarticulated. By contrast, plants cultivated for this study from CL caryopses produced three kinds of racemes on:

1. Short inflorescence culms enveloped by the spatheoles with sessile spikelets CL-only, anthers 0.3–0.6 mm long, and pedicellate spikelets empty with or without a lemma,
2. Short or partially elongated inflorescence culms with sessile spikelets mostly CL with pedicellate spikelets male, anthers 1.4–2.0 mm long, and
3. Usually elongated inflorescence culms exerted from the spatheoles with sessile spikelets with monomorphic CH and CL anthers, and male pedicellate spikelets male with large anthers and the lemma present (Table 8).

Thyridolepis

Thyridolepis is an Australian endemic genus consisting of three perennial species from semiarid to arid parts of Australia (Blake 1972; B. K. Simon and Y. Alfonso, AusGrass: Grasses of Australia, ver. 1.0, see <http://ausgrass2.myspecies.info/>, accessed 15 June 2020). Blake (1972) recorded two species with CL.

Species of *Thyridolepis* have spikelets with male or empty lower florets and hermaphrodite upper florets that are mostly CL. CH and CL anthers in the upper florets have a similar size range, whereas anthers in the lower florets are much larger. Cultivated plants of *Thyridolepis xerophylla* (Domin) S.T.Blake produced spikelets with CH upper florets, with

anthers of two sizes, 1.2–1.6 mm long and 0.3–0.7 mm long, the former being similar to the lower floret and the latter being similar to the CL anthers.

Other genera

Heslop-Harrison (1961) reported the role of the glume pit in control of CL in *Bothriochloa decipiens* (Hack.) C.E.Hubb. By contrast, other grasses with pitted glumes, including the naturalised species, *Bothriochloa insculpta* (Hochst. ex A.Rich) A.Camus and *Bothriochloa pertusa* (L.) A.Camus, have not been observed with CL. Furthermore, examination of herbarium specimens for this study showed that the two varieties of *B. decipiens* differ in the abundance of CL-only inflorescences and the ratio of CL:CH in mixed CH and CL inflorescences. In *Bothriochloa decipiens* var. *decipiens* (Hack.) C.E. Hubb, CL is common, whereas in *Bothriochloa decipiens* var. *cloncurrans* (Domin) C.E.Hubb., CL is uncommon.

Cymbopogon Spreng. is a tropical and subtropical genus of ~40 species with no CL having been recorded before this study (Soenarko 1977; Campbell *et al.* 1983; Culley and Klooster 2007). CL has been recorded for the first time in *Cymbopogon gratus* Domin and *Cymbopogon procerus* (R.Br.) Domin. CL was found to be an occasional occurrence mixed with CH in the same inflorescence in some herbarium specimens of both species.

Field collections of *Entolasia whiteana* C.E.Hubb. following a period of erratic rainfall showed some differences in inflorescences on plants in the same population. The affected panicles were much reduced in size and all spikelets were CL.

Australian species in the chloridoid genera *Tripogon* Roem. and Schult. and *Sporobolus* R.Br. were also found for this study to have monomorphic cleistogamous anthers in the same inflorescence. *Tripogon loliiformis* (F.Muell.) C.E.Hubb., known by the common name five-minute grass, and other members of the genus are known as resurrection plants for their ability to recover after complete dehydration (Gaff and Latz 1978; Tothill and Hacker 1983; Lazarides 1992). *Sporobolus disjunctus* R.Mills ex B.K.Simon is the only known Australian species in the genus to be CL. Some North American species of *Sporobolus* have been recorded with amphigamy and CL (Hitchcock and Chase 1915; Campbell *et al.* 1983). Specimens of *Sporobolus cryptandrus* (Torr.) A.Gray and *S. vaginiflorus* (Torr. ex A.Gray) Alph. Wood examined for this study included CL-only and CH-only on separate plants. Further research is required to determine if these American species match CL Type 1b.

(1b) Monomorphic CL anthers with CH-only and CL-only on separate plants

Three annuals were recorded with monomorphic CH and CL anthers on separate plants, *viz.* two andropogonoid,

Clausospicula extensa and *Vacoparis laxiflorum* (Bailey) Sprangler., and one chloridoid, *Acrachne racemosa*. No specimens of *A. racemosa* and *C. extensa* were observed with CH anthers and some specimens of *A. racemosa* had reduced axillary CL panicles. It is considered to be likely that *C. extensa* and *A. racemosa* are species with a rare incidence of CH plants, as is the case for *Pheidochloa gracillima* S.T.Blake discussed below. Further research on the breeding system of *A. racemosa* and *C. extensa* is required, including field collections and observations from cultivated plants.

Clausospicula

Clausospicula is a monotypic genus with affinities to *Cymbopogon* Spreng, *Dichanthium*, *Schizachyrium* and *Spathia* Ewart and Archer (Soreng *et al.* 2017). Lazarides *et al.* (1991) considered *C. extensa* to be solely CL from the four specimens cited. Eleven accessions from Australian herbaria were examined for this study and all were found to be CL-only. Plants cultivated over a 4-year period were found to be CL-only with anthers of two sizes, namely one large and two smaller, 0.8–1.2 and 0.5–0.6 mm long respectively.

C. extensa has been temporarily placed in this category, pending further evidence.

(1c) Monomorphic CL anthers with amphigamy

Several species with monomorphic CL anthers in the terminal inflorescences have axillary or basal inflorescences that are CL-only or CL and CH. Species with CL-only basal inflorescences include *Eragrostis concinna* (R.Br.) Steud, and *Eragrostis fallax* M.Lazarides. Species with basal or axillary inflorescences with mixed CH and CL include *Ectrosia danesii* Domin, *Eragrostis basedowii* Jedwabnick and *Eragrostis stenostachya* (R.Br.) Steud.

(2) Dimorphic CL anthers

Campbell *et al.* (1983) recognised various types of dimorphism, with categories being based on what prevents the grass floret from opening, including the leaf sheath (where the inflorescence is enveloped by the sheath), spikelet modifications, or the soil. Culley and Klooster (2007) used a single category of 'dimorphic' representing ~87% of total CL in grasses; however, their category of dimorphic CL includes other types of CL as defined in the current study (Table 1). Dimorphic CL anthers as defined here refer to CL and CH on the same or different plants of the same species where the CH and CL anthers have differences, including length, width or shape. Nine genera within four subfamilies with dimorphic CL plants are represented in Australia. Four subtypes are recognised on the basis of CH and CL on separate plants or the position of amphigamous inflorescences on the same plant. *Astrebla*

F.Muell., *Austrostipa*, *Eriachne*, *Pheidochloa* S.T.Blake and *Schizachyrium* are discussed below.

(2a) Dimorphic CL anthers in the terminal inflorescence

Terminal inflorescences of species with dimorphic CL anthers can comprise CH-only, CL-only or a mixture of CH and CL spikelets. Three genera were recorded for this category, viz. *Dichelachne* Endl., *Elionurus* Humb. and Bonpl. and *Enneapogon*.

Enneapogon

Enneapogon avenaceus (Lindl.) C.E.Hubb. had not been recorded with CL before this study. Spikelets have up to three (usually two) heteromorphic fertile florets, with diminishing size of anthers, stigmas and caryopses from proximal to distal florets (Table 10). The proximal florets have dimorphic CL and the distal florets have monomorphic CL. Spikelets disarticulate readily at maturity and the diaspore is composed of the united florets as are the spikelets in the terminal inflorescences in other species of *Enneapogon*.

(2b) Dimorphic CL anthers only on separate plants

Four genera with dimorphic CL anthers on separate plants are discussed below. Typically, herbarium specimens examined comprised CL-only plants, and CH plants were usually very uncommon.

Austrostipa

CL has been recorded for 11 of the 62 predominantly perennial species of *Austrostipa* (syn. *Stipa* L.) (Townrow 1978; Vickery *et al.* 1986; Jacobs *et al.* 1989; Jacobs and Everett 1996). The information provided by Townrow (1978) indicates that the breeding systems of the Tasmanian species can range from CH-only, to partially CL to whole inflorescences CL or CH. The Tasmanian species have CL and CH anthers with two smaller than the other and the CH larger than the CL (Townrow 1978). Examination of herbarium specimens showed that at least some CL species have whole inflorescences CH or CL. However, it is not known what ratio of CH:CL occurs in a natural population and whether the same plants have the capacity to switch breeding system in response to environmental influences.

Austrostipa scabra (Lindley) S.W.L.Jacobs and J.Everett was propagated from CL caryopses and cultivated over several generations. Plants were found to be CL-only. *A. scabra* differs from most other *Austrostipa* by the caryopsis elongating beyond the apex of the palea thereby exposing the stylar base with the CL anthers entangled in the stigmas that subsequently detaches.

Eriachne

Eriachne R.Br. is a genus of 48 species in Australia, of which 3 were reported with CL by Lazarides *et al.* (2005) and now updated to 9 species (Table 3). Six species of *Eriachne* were assessed as having dimorphic CL plants, although several species need further investigation pending examination of additional specimens.

Pheidochloa

Pheidochloa S.T.Blake is a monospecific endemic genus from northern tropical Australia (Blake 1944b; Weiller 2005). *Pheidochloa gracilis* S.T.Blake is a small delicate annual mostly found in damp habitats. Blake (1944b) considered *P. gracilis* to be 'very evidently cleistogamous' and contextualised this condition with the small anthers found in three species of the allied genus, *Eriachne*.

Of the many herbarium specimens examined, most consisted of numerous CL plants with anthers 0.1 mm long, and only a few sheets included some CH plants with anthers 0.8 mm long.

Schizachyrium

Schizachyrium is a genus of ~60 tropical species with seven recorded for Australia (Simon 1989; Watson and Dallwitz 1992; B. K. Simon and Y. Alfonso, AusGrass, see <http://ausgrass2.myspecies.info/>). Sixteen species of *Schizachyrium* have been recorded with CL worldwide (Campbell *et al.* 1983). Blake (1974) provided descriptions of seven Australian species and in his generic diagnosis reported sessile spikelets to be commonly CL. He described the CH spikelets of *Schizachyrium dolosum* S.T.Blake as having larger anthers on long inflorescence culms exerted from tightly convolute spatheoles.

All of the Australian species of *Schizachyrium* have dimorphic CL plants with dimorphic anthers. Inflorescences are fascicles consisting of spatheolate terminal racemes on numerous short branches. Most specimens examined had racemes comprising CL spikelets on short inflorescence culms completely to partially enveloped by the spatheole, often gaping at maturity for some species. Conversely, CH-only racemes were found on elongated inflorescence culms and exerted from the spatheole. However, some specimens of species such as *Schizachyrium occultum* S.T.Blake had CL spikelets in racemes on elongated inflorescence culms exerted from the spatheole. This syndrome of CH racemes on elongating inflorescence culms was also found in *Astrebla* and *Spathia*.

Five species of *Schizachyrium* were cultivated for this study from CL caryopses and all of the numerous plants propagated from 2016 to 2020 had racemes enveloped by the spatheole with CL-only spikelets. A hypothesis from this finding and from cultivation of *Austrostipa* species is that caryopses from dimorphic CL plants produce only CL plants. No CH caryopses were found on herbarium specimens to be able to test a similar hypothesis with CH-only plants because the

CH spikelets disarticulate freely as soon as they are ripe, unlike the CL spikelets that are usually retained until the spatheole gapes during drying.

(2c) Amphigamous with axillary CL inflorescences

Two Australian grasses, viz. *Eriachne basalis* Lazarides and *Entolasia* sp. aff. *whiteana*, have been recorded with amphigamous CL without or with only minor spikelet dimorphism. *E. basalis* has a mixture of CH and CL spikelets in the terminal panicles and reduced basal panicles or single CL spikelets. *E. sp. aff. whiteana* is an undescribed species known from a single location in semiarid central Queensland. The terminal spikelets are CH-only and a little shorter than the axillary CL spikelets.

(2d) Amphigamous with CL inflorescences terminal on short leafy branches

Astrebla

Astrebla (Mitchell grasses) is an Australian endemic genus of four perennial species from semi-arid to arid grasslands considered to be an important asset to the grazing industry (Breakwell 1923; Everist 1935; Orr 1975; Nightingale and Weiller 2005). *Astrebla* spp. and Mitchell grasslands have been studied and written about more extensively than any other Australian grasses. Mitchell grasslands grow on heavy cracking clay soils prone to drying out rapidly in a tropical to subtropical climate with erratic summer rainfall and high evaporation rate, and frequent drought. Growth and flowering responses to rain, including at particular periods of the year, have been reported in several studies (Everist 1935, 1951; Roe 1941; Allen 1963; Everist 1964; Jozwik 1970; Jozwik *et al.* 1970; Williams and Roe 1975; Scanlan 1983; Hunter 1989; Orr 1991; Orr and Evenson 1991a, 1991b). Mitchell grasses produce two kinds of shoots in response to rain, innovation shoots following rainfall events of >50 mm and only short leafy branches on tillers generated following rain of ~15 mm (Everist 1964; Jozwik *et al.* 1970).

There has been little documentation on the breeding system of *Astrebla*. Hackel (1906) recorded two species of *Astrebla*, viz. *Astrebla pectinata* (Lind.) F.Muell. ex Benth and *Astrebla lappacea* (Lind.) Domin (Hackel (1906) as *Astrebla triticoides* Muell.), as being CL-only. Three other publications used the information from Hackel (1906) to classify CL in *Astrebla* spp. in different ways (Connor 1979; Campbell *et al.* 1983; Culley and Klooster 2007). Bailey (1878) referred to 'the palea empty or with rudimentary flower' for *A. pectinata*. Orr (1998) referred to *Astrebla* as autogamous. Nightingale and Weiller (2005) did not classify the form of CL but considered three of the species to have it, with *Astrebla squarrosa* C.E.Hubb. being the exception. Whalley *et al.* (2013) considered the breeding

system of *A. lappacea* to be 'mostly inbreeding with a small degree of cross-breeding'. Jozwik (1970) speculated that apomixis could be present in *Astrebla*, although Whalley *et al.* (2013) considered it unlikely.

In this study, the racemes of the four species of *Astrebla* can be totally or partially CL, depending on rainfall. CH occurs in the racemes produced on innovative shoots. Plants continue to flower as the soil dries out and then produce CL racemes, or only CL racemes are present following rainfall events of ~15 mm. Plants of *A. lappacea* and *A. pectinata* were found to bear two types of racemes, usually relatively long ones on the innovation shoots with elongated inflorescence culms and shorter ones on lateral branch shoots with short inflorescence culms. This dimorphism in racemes size and position represents an expression of facultative amphigamy. The shorter racemes were found to be less common for *A. squarrosa* and *A. elymoides*. The long racemes exceed the perimeter of the foliage, with the inflorescence culm exerted from the spatheoles and at least apical spikelets bearing proximal CH florets. The short racemes are produced at the perimeter of the foliage on the same plants as the long racemes or can occur alone. The short racemes are CL-only and are at first enveloped by the spatheoles and then gape at maturity. Inflorescences on herbarium specimens of species of *Astrebla* commonly consist entirely of CL-only racemes. It is therefore understandable why Hackel (1906) thought that the two species of *Astrebla* he cited were CL-only, given that he saw only the shorter racemes.

Astrebla species display both anther dimorphism and heteromorphism (Fig. 1, 6 and 7). All racemes consist of heteromorphic spikelets, with the longest ones at the base. Racemes that bear CH florets have obligately CL spikelets at least in the lower third of the raceme. Also, CH-bearing racemes frequently have some spikelets with up to three of the proximal florets aborted or sometimes damaged by an insect larva. Both CH and CL spikelets comprise several heteromorphic florets with heteromorphic anthers and caryopses smallest in the apical floret (Fig. 6, Table 11). Proximal florets can be CH or CL but the distal florets are obligately CL (Table 11). Anther size also varies within an individual floret, with one of the anthers being ~15–20% longer than the other two (Fig. 7). The morphology of spikelets from racemes exerted from the spatheoles of *Astrebla* spp. has similarities to *Enneapogon avenaceus* (Table 10).

Field survey showed that racemes on short tillers bearing CL-only spikelets can be continuously produced through the growing season or in a few more or less even-aged groups, presumably dependent on the suitability of soil moisture levels. Plants of *A. lappacea* and *A. pectinata* observed in the Camooweal area, north-western Queensland, had three age groups of CL-only racemes, two of the age groups coinciding with rainfall of 204 mm in December 2015 (annual average 63 mm) and 157 mm in March 2016 (annual average 56 mm; <http://www.bom.gov.au/climate/data/>, accessed 27 February 2020), and the third group,



Fig. 6. Caryopses of *Astrebla squarrosa* from cleistogamous (CL) and chasmogamous (CH) spikelets, each with six successive fertile florets showing heteromorphic caryopses, anthers and stigmas. The third floret (3) provides a comparison of CH and CL dimorphism of anthers and stigmas. From Thompson EJT1045 (BRI). Photo: E. J. Thompson. Scale bar: 2 mm.



Fig. 7. Cleistogamous (CL) caryopses of *Astrebla pectinata* from the proximal florets of spikelets from two different age groups of spatheolate CL racemes on the same plant showing entwined stigmas and anthers. (a) A pair of caryopses from spikelets from racemes produced early in the season. (b) A pair of caryopses from spikelets from younger racemes produced late in the season; anthers are smaller than those from the corresponding florets of the older spikelets. From Thompson EJT1085 (BRI). Photo: E. J. Thompson. Scale bar: 1 mm.

represented by relatively few racemes, from the previous season. The three age groups were distinguishable by the colour of the spikelets, green, straw-coloured and greyish ones from the previous season. The green racemes had immature caryopses with anthers 0.2–0.3 mm long and the mature ones had anthers 0.4–0.7 mm long (Fig. 6). No CH spikelets were seen in the collections of *A. pectinata* at that time. Similar observations were made from specimens collected from the Winton area following major rainfall events in March and July 2016.

Field observations also showed that dispersal of diaspores in *Astrebla* is most commonly shortly after maturity or sometimes release of the diaspores can be delayed. In *Astrebla*, the diaspore consists of the united florets, unlike many other chloridoid grasses that disarticulate between the florets. Release of CL spikelets can be inhibited by the spatheole and spikelets can be retained on the plants for several months after maturity, providing an aerial component to the seed bank. In specimens examined for this study, the retained spikelets had CL caryopses in the most distal one to three fertile florets and the proximal florets were empty.

From limited pot-cultivation nursery trials with plants propagated from CL caryopses, plants of *A. lappacea* and *A. pectinata* produced a few racemes with some CH spikelets and CL-only respectively, and *A. elymoides* and *A. squarrosa* did not produce any inflorescences.

(3) Amphigamy with dimorphic CL spikelets

This category refers to species that have two or more types of inflorescences in different positions (terminal, axillary or basal, or subterranean) on the same plant, with corresponding spikelet dimorphism (Quinn 1998). Spikelets in terminal inflorescences can be CH-only, CL-only or a combination of CH and CL; axillary spikelets are predominantly CL-only, with inflorescences consistently reduced compared to the terminals; and spikelets at the base and subterranean are CL-only, with inflorescences comprising a single spikelet or raceme of up to several spikelets. Chase (1918) referred to the CL spikelets at the base of the plant as cleistogenes and compared them to the spikelets in the terminal inflorescences of some North

Table 11. Chasmogamous (CH) and cleistogamous (CL) anther lengths (mm) for florets from terminal spikelets of species of *Astrebula*.

Floret	<i>Astrebula elymoides</i>		<i>Astrebula lappacea</i>		<i>Astrebula pectinata</i>		<i>Astrebula squarrosa</i>	
	CH	CL	CH	CL	CH	CL	CH	CL
1	2.8 ^A	0.3–1.0	1.7–1.8 ^A	0.3–0.6	1.2–1.9 ^A	0.1–0.9	1.9–2.5 ^A	0.8–1.2
2	1.3 ^B	0.1–0.4	1.0 ^C	0.2–0.7	1.9 ^C	0.1–0.6	2.1–2.4 ^C	0.7–1.3
3	Absent	0.3 or usually absent	↑	0.2–0.7	↑	0.1–0.3	1.5–1.8 ^C	0.4–1.0
4		↑		0.1–0.3 or empty		0.1 or empty	1.3 ^B	0.3–1.1
5				0.1–0.3, empty or vestigial		Empty or vestigial	↑	0.3–0.6 ^D or empty
6			Absent	Empty, vestigial or absent	Absent	Vestigial or absent		0.2–0.7 ^D or empty or vestigial
7		Absent		Vestigial or absent		↑	Absent	Empty or vestigial
8						Absent		Usually absent; also empty or vestigial
9				Absent				Usually absent or vestigial

Floret positions 1–9 from base to apex.

^ALow sampling because of the commonly aborted or occasionally attached by an insect larva, accompanying second floret less prone to insect larva attack.

^BLow sampling because of the low frequency of CH racemes in BRI collections.

^CFloret uncommon to be CH, usually CL.

^DCaryopses of distal florets (5–9) nearly always present even when florets 1–4 aborted or insect attached.

American grasses. However, there is variation in the degree of differentiation between the spikelets from the three types of inflorescences (Table 10).

Approximately 65 species, less than 0.5% of grasses worldwide, have been recorded as amphigamous with CL anther dimorphism (Table 2). This breeding system has been referred to variously, including cleisto-chasmogamic floral dimorphism (Frankel and Galun 1977), multiple strategies (Lloyd 1984), CL heteromorphic reproductive pattern (Cheplick and Clay 1989), structural dimorphism (Plitmann 1995), mixed mating (Goodwillie *et al.* 2005; Oakley *et al.* 2007), reproductive dimorphism (Cheplick 2007) and dimorphic CL (Albert *et al.* 2011).

In this study, species with amphigamous dimorphic CL have been subdivided into three categories, *viz.* with dimorphic axillary spikelets without cleistogenes, with cleistogenes, or with rhizanthogenes. In all cases known, cleistogenes and rhizanthogenes are obligately CL and in most cases axillary CL is obligate whereas CL in terminal inflorescences is facultative or absent. Phenology of CL axillary inflorescences usually precedes terminal inflorescences.

(3a) Amphigamous CL with dimorphic axillary spikelets

Six Australian grass genera, one chloridoid (*Uniola* sp.), one oryzoid (*Microlaena* R.Br.) and four panicoid ('the cleistogamy group') have been recorded with dimorphic axillary CL spikelets (Clifford 1962; Connor and Matthews 1977; Thompson and Fabillo 2021) (Tables 5 and 7). The

degree of difference between the terminal and axillary spikelets of the taxa varies from relatively small to distinctive (Table 2). Species in 'the cleistogamy group' share unique morphology and the group consists of 11 putative species from *Calyptochloa* C.E.Hubb., *Cleistochloa* s.l., *Dimorphochloa* s.l. and *Ancistrachne maidenii* (Hamilton) Vickery that all occur predominantly in shady habitats, mostly on shallow sandy soils derived from sandstone (Thompson and Fabillo 2021; Table 3). The species occur within the latitude range 5–36°S, covering tropical, subtropical and temperate climate zones, with only *Cleistochloa subjuncea* C.E.Hubb. occurring in all three zones. *Calyptochloa*, *Cleistochloa*, *Dimorphochloa* and *A. maidenii* rarely produce caryopses in the terminal inflorescences and when present have always been found to be CH. From observation of cultivated plants, species in *Cleistochloinae* always produce axillary CL spikelets before the terminal inflorescences appear mostly in summer and autumn and in some species only axillary spikelets were produced.

The proportion of caryopses produced in terminal and axillary inflorescences varies with the taxa. *Uniola* sp. (Palm Grove P.I. Forster PIF23666) produces most caryopses in the terminal inflorescences. Herbarium specimens and cultivated plants of *Microlaena stipoides* (Labill.) R.Br. from Queensland were rarely found with axillary spikelets.

Uniola sp. (Palm Grove P.I. Forster PIF23666)

Uniola L. s.s. consists of two species from North America and West Indies growing on coastal sand dunes (Yates

1966, 2003; Watson and Dallwitz 1992). *Uniola* sp. (Palm Grove P.I. Forster PIF23666) is a caespitose perennial growing in woodlands on well-drained soils derived from sandstone hills in central Queensland and known from five collections at BRI. The taxonomy of this rare species is uncertain, but it has affinity with *Uniola* s.s., with the laterally compressed spikelets and the distinctive paleas being two-keeled with wings. Notable differences between *Uniola* sp. (Palm Grove P.I. Forster PIF23666) and *Uniola* s.s. relate to the breeding system (amphigamous CL v. dimorphic CL plants), inflorescence type (raceme v. panicle) and diaspore dispersal mechanism (terminal spikelets disarticulating and axillary spikelets retained in sheath v. falling entire (the latter reported by Watson and Dallwitz 1992)).

The inflorescences of *Uniola* sp. (Palm Grove P.I. Forster PIF23666) comprise terminal racemes and single axillary spikelets different from the terminal ones. The terminal spikelets have up to three heteromorphic florets, of which the first and second are fertile with heteromorphic anthers and caryopses (Fig. 8). The first floret is CH or CL with dimorphic anthers, 1.6–1.8 and 0.4 mm long respectively, and the second floret is CL-only with anthers 0.2 mm long. The axillary spikelets occur at several nodes where they are hidden within the leaf sheath and are obligate CL with anthers 0.2 mm long. Axillary spikelets typically consist of a single fertile floret but have also been found to be multi-floreted. This type of variation in the axillary spikelet resembles that found in *Danthonia spicata* (L.) Beauv., also having spikelets with a single floret, or alternatively, an elongated rachilla bearing several florets (Weatherwax 1928).

Uniola sp. (Palm Grove P.I. Forster PIF23666) overlaps in geographic distribution and similarity of landscape type with some species in 'the cleistogamy group' of panicoid grasses that have the CL Type 3a syndrome.

(3b) Amphigamous CL with cleistogenes

Enneapogon

Enneapogon caeruleus (Gaudich.) N.T.Burbidge and *Enneapogon cylindricus* N.T.Burbidge have three types of inflorescences; namely, terminal, axillary and basal. Both species have terminal panicles with three states of spikelets, CH-only, CL-only or a mixture of both CH and CL, similar to *Dichanthium sericeum* subsp. *sericeum* (Table 9). *E. cylindricus* differs from *E. caeruleus* by having dimorphic CH and CL anthers in the terminal panicles (Table 10). The axillary racemes, when present, are mostly enveloped by the leaf sheath but *E. cylindricus* occasionally has exposed apical spikelets that are CH. *E. caeruleus* and *E. cylindricus* are the only Australian grasses recorded with cleistogenes (Burbidge 1941; Connor 1979; Campbell et al. 1983; Watson and Dallwitz 1992; Weiller and Lazarides 2005; Culley and Klooster 2007). Clandestine



Fig. 8. Chasmogamous (CH) and cleistogamous (CL) spikelets and caryopses of *Uniola* sp. (Palm Grove P.I. Forster PIF23666) from the two types of inflorescences, terminal and axillary respectively on the same plant. (a) Multi-floreted CH spikelet from terminal raceme showing four florets, 3rd and 4th fertile. (b) Caryopses from third and fourth florets of terminal spikelet. (c) Solitary clandestine CL spikelet with a single floret removed from enveloping leaf sheath. (d) Caryopsis from axillary spikelet. All from Thompson MOR814 (BRI). Photos: E. J. Thompson. Scale bar: 2.5 mm.

axillary spikelets and cleistogenes are obligately CL. Cleistogenes are commonly absent or of low frequency in herbarium specimens of these two species, suggesting that their presence may be influenced by environmental factors. However, it is possible that cleistogenes are produced some time after the terminal inflorescences as is case in North American species of *Danthonia*, as reported by Chase (1918). Further field collections would be required to investigate the possibility of this temporal succession of CL spikelet production. The cleistogenes of species of *Enneapogon* differ from the terminal and axillary spikelets by having fewer florets, shorter lemma awns, smaller anthers and larger caryopses (Fig. 9). Despite these differences, these two Australian species of *Enneapogon* do not fit Chase's (1918) conundrum (postulates that the cleistogenes have morphology that gives them the appearance that they belong to species from another tribe) because both species have cleistogenes that are readily recognisable as belonging to *Enneapogon* but, speculatively, a different species.

Enneapogon caeruleus and *E. cylindricus* each have three types of diaspores corresponding to the different inflorescences. As for *Enneapogon desvauxii* Beauv. from Africa, the Americas and Asia, the axillary spikelets of *E. cylindricus* and *E. caeruleus* mostly remain trapped in the leaf sheath. However, in *E. cylindricus* and *E. desvauxii*, the tillers disarticulate at the lowest nodes, whereas the tillers do not disarticulate in *E. caeruleus* (Hitchcock

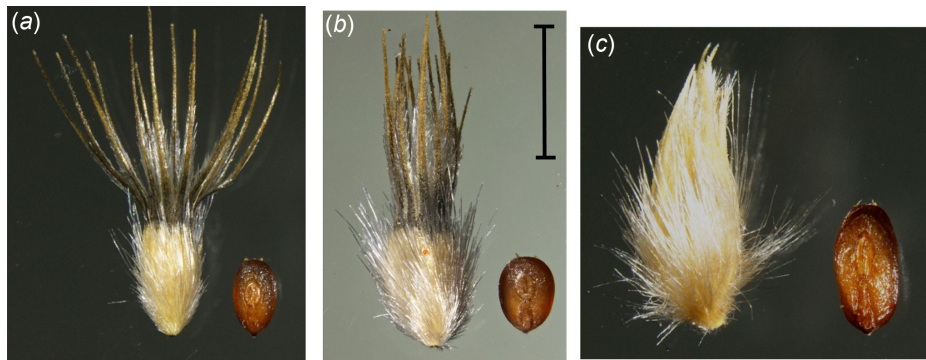


Fig. 9. Proximal florets and caryopses of *Enneapogon cylindricus* from the three types of inflorescence (amphigamy with terminal panicle, reduced axillary panicles and reduced basal raceme of one to several spikelets) on the same plant. The terminal panicles can be cleistogamous (CL)-only, chasmogamous (CH)-only or mixed CL and CH; axillary panicles have mostly clandestine CL spikelets with morphology similar to that of the terminal ones; basal spikelets are dissimilar to the terminals and axillaries and are CL-only (i.e. cleistogene). (a) Terminal. (b) Axillary. (c) Basal. All from Purdie 1454 (BRI). Photos: E. J. Thompson. Scale bar: 2 mm.

1936; Burbidge 1941; Chippindall 1955; Van Oudtshoorn 1999). The cleistogenes of the species of *Enneapogon* can potentially remain for some years at the base of the mother plant confined by multiple layers of old leaf sheaths or be released to disperse after disintegration of the mother plant. The cleistogenes of *Enneapogon* and other genera have been reported to germinate *in situ*, and thus grow out of the old plant (Poulter 1932; Chippindall 1955; Gibbs Russell *et al.* 1990). From the present study, it appears that cleistogenes continue to enlarge while attached to the living mother plant.

The occurrence of disarticulating tillers that function as a CL diaspore is very uncommon in Poaceae. Besides *Enneapogon*, it is known from the panicoid grass *Calypochloa gracillima* (C.E.Hubb.) E.J.Thomps. and B.K.Simon from Australia and American species of *Danthonia* (Darbyshire 2003; Thompson and Simon 2012). Most North American species of *Danthonia* produce three types of inflorescences that are all differentiated with corresponding spikelet dimorphisms. The terminal inflorescences have facultative CL. Cultivation trials by the author with *Danthonia sericea* over several years resulted in plants producing only terminal inflorescences that were CL-only or occasionally with a few CH spikelets. Axillary spikelets and cleistogenes were never produced, indicating the possibility of environmental influence.

(3c) Amphigamous CL with rhizanthogenes

Grasses that have amphigamy with subterranean spikelets, i.e. rhizanthogenes, are not represented in Australia. Nine species within five genera across four subfamilies have been recorded with rhizanthogenes and most species occur in relatively close geographical proximity in or near central America including Florida and Cuba, except *Libyella* Pamp., which occurs in northern Africa (Hitchcock 1950; Campbell *et al.* 1983; Clayton 1990; Watson and Dallwitz 1992; Table 2).

Overview

The three main categories of grass CL defined in this study have a strong overlap with those defined by other authors (Table 1). The study also concurs with other authors who did not accept that a species is likely to have CL-only as its only pollination system. It was found, during this study, that some Australian species have a very low occurrence of CH. However, species such as *Clausospicula extensa* Lazarides, not listed by Culley and Klooster (2007), and *Acrachne racemosa* (B.Heyne ex Roem. and Schult.) Ohwi, have been thought to be CL-only (Lazarides *et al.* 1991; Culley and Klooster 2007). Only CL-only material of *C. extensa* was observed in the relatively small number of specimens in herbarium collections and plants cultivated for this study. *A. racemosa* was also found to be CL-only in herbarium specimens. It is expected that cultivated plants propagated from CL-only plants would produce CL-only spikelets. Furthermore, it is considered likely that intensive field investigation would show CH-only plants in both of these species.

CL Types 1a and 2a include species with plants that bear inflorescences composed of spikelets in either of three modes, viz. CH-only, CL-only or a mixture of CH and CL. Observations from cultivated plants and herbarium specimens indicate that these modes are facultative. The three modes are central to understanding the relationships of the types of CL in Australian grasses (Fig. 5). Furthermore, the spectrum of expressions of CL represented in Australian species of the chloridoid genus *Enneapogon* provides an example of supporting evidence for the model. Australian species of *Enneapogon* exhibit several types of CL, including the following four occurrences:

- (a) The three modes in terminal inflorescences with or without anther dimorphism,

- (b) CL in the terminal inflorescence hidden in the basal branch that is enveloped by the leaf sheath,
- (c) Axillary racemes that can be CL-only or sometimes mixed CH and CL, and
- (d) Cleistogenes with modified spikelet characters (Table 10).

Both CH and CL morphs in Australian CL grasses can be obligate or facultative. The favourable conditions of the nursery in this study stimulated CH spikelets in *Spathia* previously thought to be CL-only. Similarly, field plants of *Astrebula* following good rainfall produce innovative shoots that bear spikelets with CH proximal florets, but the distal florets are always CL. Conversely, the nursery environment did not stimulate CH plants in species of *Schizachyrium* and *Austrostipa* propagated from CL caryopses. Also, species in 'the cleistogamy group' rarely produce caryopsis in the terminal inflorescences, with most being found in the axillary CL spikelets under field conditions as well as in the nursery.

Fifteen Australian grasses possess CL Type 3 with dimorphisms that correspond with the category of 'true CL' of Darwin (1877). The CL characters include dimorphisms in anthers, spikelets and inflorescences, but the degree of difference in the CH–CL characters can vary (Table 6). Two of these Australian species with Type 3 CL bear cleistogenes, but these basal CL spikelets do not completely match the syndrome described by Chase (1918) where the cleistogenes differ distinctly from the CH ones. Instead, in the Australian species with CL Type 3a, a different form of the Chase syndrome is expressed in that the spikelet peculiarities are found in terminal and axillary inflorescences (Fig. 1). The Australian CL Type 3 species have narrow taxonomic distribution, occurring in eight genera in subfamilies Chloridoideae, Oryzoideae and Panicoideae with 13 species in the latter. Fourteen species have C₃ photosynthetic pathway and predominantly occur in subtropical eastern Australia in woodlands on landscapes with shallow to skeletal soils. The three C₄ species are all chloridoid, of which two occur in open habitats in the desert and the third one in woodlands in the subtropics.

Aristida also presents anomalies in the geographic and environmental distribution of CL. Australian species of *Aristida* occupy a broad range of habitats, including extremely arid habitats; however, no form of CL has been recorded for any of the species. By contrast, four species in North America display CL including two species with amphigamous CL without spikelet dimorphism (Hitchcock 1924; Henrard 1929; Hitchcock 1950; Campbell *et al.* 1983).

This study also showed peculiarities in CH inflorescences more commonly associated with CL, especially with respect to the occurrence of axillary racemes and clandestine spikelets. Clandestine racemes or single spikelets are characteristic of dimorphic CL species, but they are very rare with CH-only grasses, e.g. *Cenchrus clandestinus* (Hochst. ex Chiov.) Morrone. CH axillary racemes occur in *Rottboellia cochinchinensis*, *Ischaemum fragile* R.Br. and

some species of *Thaumastochloa*, although some herbarium specimens of these species also have short lateral branches terminated by a raceme. Furthermore, some herbarium specimens of *Thaumastochloa major* S.T.Blake and *Thaumastochloa pubescens* (Benth.) C.E.Hubb. have dimorphic racemes with differentiated spikelets on the same plants. This type of raceme dimorphism represents a form of amphigamy being somewhat parallel to that found in *Astrebula*. De Koning *et al.* (1983) reported this dual inflorescence condition as 'heteromorphic spikes' for *T. major*. Cultivation trials over two growing seasons have shown a temporal aspect to the occurrence of these dimorphic inflorescences, i.e. they begin to appear towards the end on the growing season in autumn.

A further expression of diversity in taxa and adaptation to aridity occurs in resurrection grasses (Gaff and Latz 1978; Lazarides 1992). However, of the Australian genera, viz. *Eragrostiella* Bor, *Sporobolus* R.Br. and *Tripogon* (subfamily Chloridoideae), and *Micraira* F.Muell. (subfamily Micrairoideae), only *Sporobolus* and *Tripogon* are known to have species with CL.

CL morphology has played a role in the taxonomy of grasses. CL characters have been used in generic keys (Webster 1987; Simon 2002; Barkworth 2003). Presence of cleistogenes has been used to separate species of *Enneapogon* (Weiller and Lazarides 2005). CL morphology has also been shown to discriminate groups of genera (Thompson and Fabillo 2021).

Habitat specificity, combined with structural peculiarities in inflorescences, spikelets and florets, also occurs in relation to other types of breeding systems in Poaceae. The Australian dioecious genera *Pseudochaetochloa* A.Hitch., *Spinifex* L. and *Zygochloa* S.T.Blake express various degrees of dimorphism in male and female terminal inflorescences and spikelets, and occupy xeric habitats including rocky environments of various geology, coastal sand dunes and inland dunes respectively. A further example includes *Chionachne* R.Br., *Hygrochloa* Lazarides and *Thaurea* Pers., which have dimorphic spikelets in the same inflorescence on the same plant and usually a high level of habitat specificity, viz. clayey soil, wetlands and coastal dunes respectively.

Although the evolution of each of the CL types may have occurred independently, especially across the different taxa, the relationship model presented in Fig. 5 provides a starting point for understanding the taxonomic distribution of the diversity of CL morphology in grasses. In the absence of fossil records, the present-day geographic and taxonomic distributions of the CL types must form the basis for investigation of the evolution of grass CL (Fig. 3). Accordingly, one plausible driving force for some grass CL evolution is reproductive diversification in response to a climate with erratic rainfall with C₃ grasses more prevalent in shady habitats and C₄ grasses dominant in open habitats especially in the tropics and sub-tropics (Christie 1981;

Hattersley 1983, 1992; Conover and Sovonick-Dunford 1989; Osborne and Freckleton 2008). However, the presence, absence, range of CL types and geographic range of CL across species in some genera and complete absence of CL in other genera with sympatric species pose paradoxes about the evolutionary driving forces of CL in Australian grasses. The genus *Enneapogon* displays a spectrum of CL types, as mentioned above, but most of the species are CH-only and some species inhabit arid environments that overlap with the CL species. Furthermore, the chloridoid genus *Triodia* R.Br. comprises species, mostly from arid habitats with low water holding-capacity soils, that rarely produce seed and are CH-only, as was found by the author from examination of herbarium specimens and field observation (Burbidge 1953; Wright *et al.* 2014). Another example involves two C_4 andropogonoid genera that are frequently sympatric in semi-arid and tropical regions of Australia, viz. *Thaumastochloa* C.E.Hubb. with CH-only species and *Schizachyrium* with species having dimorphic CL on separate plants (Type 2b).

Conclusions

This study has provided further understanding of the taxonomic and geographic distributions of CL in Australian grasses. Information on CL breeding systems presented here broadens understanding of the taxonomy, ecology and management of several species, in particular Mitchell grasses that are important to the grazing industry. Furthermore, for most species that appear to be CL-only, it is likely that there is very low incidence of CH in the natural population or it is possible that localised environmental conditions trigger it. For some species the breeding system involves plants that are CH-only, CL-only or combined CH and CL. This information has enabled insight into hypothetical relationships of the types of CL in Australian grasses and has provided a new explanation for the possible origin of some CL categories. Responses to varying degrees of erratic rainfall offer a probable evolutionary driving force for at least some of the CL types found across the variation in taxonomic and geographic distributions and physiology of the species. By contrast, sympatric occurrences of CL and CH-only species in arid habitats provide a paradox for this notion. Besides this, the findings from this study have implications about the possible need for further investigation of grass CL in other parts of world.

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Data availability. Data used in this manuscript are presented in Table 3.

Conflicts of interest. The author declares that he has no conflicts of interest.

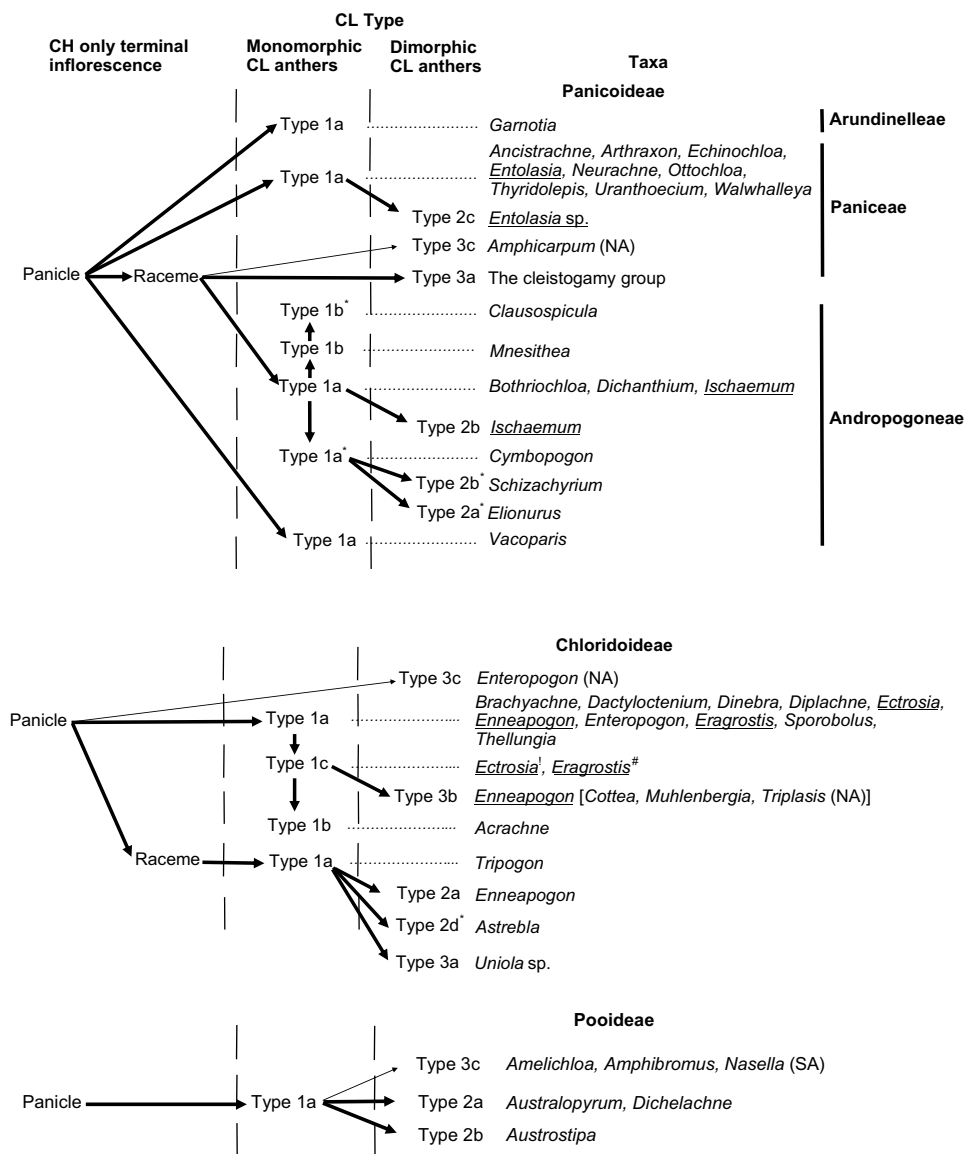
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Appendix I. Distribution of types of cleistogamy (CL) by species frequencies in Australia



CL types	Legend	Origin
Monomorphic anthers		
1a	Species with terminal inflorescences comprising CH only, CL only or a mixture of CH and CL	CA, Central America
1b	CH and CL on separate plants	NA, North America
1c	Species with amphigamous inflorescences	SA, South America
Dimorphic CH and CL anthers		
2a	Species with terminal inflorescences comprising CH only, CL only or a mixture of CH and CL	
2b	CH and CL on separate plants	
2c	Amphigamous with axillary inflorescences	
2d	Amphigamous with CL inflorescences on short leafy branches	
Amphigamous CL		
3a	With axillary spikelet dimorphism	
3b	Cleistogenes present	
3c	Rhizanthogenes present	
		Other
		* Spatheolate
		# <i>E. stenostachya</i> with axillary reduced spike-like panicle or raceme and other species with reduced axillary panicles
		! <i>E. danesii</i> with axillary racemes
		_____ indicates genus with more than one CL type