

INVITED REVIEW

Ecological importance of sedges: a survey of the Australasian Cyperaceae genus *Lepidosperma*

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- **Background** Sedges (Cyperaceae) form an important ecological component of many ecosystems around the world. Sword and rapier sedges (genus *Lepidosperma*) are common and widespread components of the southern Australian and New Zealand floras, also occurring in New Caledonia, West Papua, Borneo, Malaysia and southern China. Sedge ecology is seldom studied and no comprehensive review of sedge ecology exists. *Lepidosperma* is unusual in the Cyperaceae with the majority of species occurring in dryland habitats.
- **Scope** Extensive review of ecological literature and field observations shows *Lepidosperma* species to be important components of many ecosystems, often dominating understorey and sedge-rich communities. For the first time, a detailed ecological review of a Cyperaceae genus is presented.
- **Conclusions** *Lepidosperma* species are long-lived perennials with significant abundance and persistence in the landscape. Speciation patterns in the genus are of considerable interest due to complex biogeographical patterns and a high degree of habitat specificity. Potential benefits exist for medicinal products identified from several *Lepidosperma* species. Over 178 organisms, including 26 mammals, 42 birds, six reptiles, five amphibians, eight arachnids, 75 insects, three crustaceans and 13 fungi, are found to be dependent on, or making use of, *Lepidosperma* species. A significant relationship exists between *Lepidosperma* species and the moth genus *Elachista*. Implications for the conservation and ecology of both sedges and associated species are discussed.

Key words: *Lepidosperma*, Cyperaceae, Schoeneae, sedge, ecology, fire, mammals, birds, reptiles, insects, spiders, fungi.

INTRODUCTION

‘Owing to the lack of detailed information, much more study is necessary before our knowledge of the part played by the Cyperaceae in the make-up of the communities can be adequately assessed in relation to other important families.’ (Diels, 1906, transl. 2007)

Sedges (Cyperaceae) are a large, cosmopolitan family of global ecological and economic significance (Simpson and Inglis, 2001). Sedges form a major component of most wetland vegetation units around the world and make an enormous contribution to nutrient cycling and habitat formation in these ecosystems (Harper, 1992; Chambers *et al.*, 2008). *Carex*, with up to 2000 species, is one of the world’s largest genera with a distribution and great significance in wetlands and seasonally damp habitats around the world (Govaerts *et al.*, 2007; Waterway and Starr, 2008). *Cyperus*, with around 600 species, is another well-known genus that includes important economic and horticultural species (Goetghebeur, 1998; Simpson and Inglis, 2001). *Cyperus papyrus* is the earliest known plant used for making paper, in use as early as 3000 BC, and continuing in common use until 200 AD. Papyrus largely replaced animal skin parchments and stone for writing and had a profound impact on human society, being

instrumental in the development of efficient communication systems (Parkinson and Quirke, 1995; Newton, 2009).

Many species of Cyperaceae tribe Schoeneae occur in dryland habitats that are only seasonally damp (e.g. woodland and heath communities; Goetghebeur, 1998). This is an unusual habitat in a family that is predominantly comprised of genera and species which occur in wetlands and damp areas. A summary of habitat preference or specificity is presented for *Lepidosperma* species in Table 1. Temperate Australia and Africa both have a large number of dryland sedges, particularly in the genera *Afrotrilepis*, *Carpha*, *Caustis*, *Coleochloa*, *Costularia*, *Cyathochaeta*, *Gahnia*, *Lepidosperma*, *Mesomelaena*, *Microdracoides*, *Schoenus*, *Tetraria* (*sensu lato*, *s.l.*), *Tetrariopsis* and *Tricostularia* (Goetghebeur, 1998; Linder, 2003; Shane *et al.*, 2005; Helme and Trinder-Smith, 2006; Slingsby and Verboom, 2006). A smaller number of genera and species occupy dryland habitats in central and northern Africa and South America where they are often found on granite inselbergs (Haines and Lye, 1983; Goetghebeur, 1998; Porembski, 2006; Beentje and Ghazanfar, 2010). The predominance of dryland species in these bioregions suggests the possibility of different patterns of speciation relative to the younger geological landscapes common in the northern hemisphere (Hopper, 2009; Lambers *et al.*, 2010).

TABLE 1. Ecological niche occupied by *Lepidosperma* species; records are based on notes from herbarium voucher specimens and personal observations

| Niche | <i>Lepidosperma</i> species |
|---|---|
| Hygrophilous (moisture-loving) | <i>L. australe</i> , <i>L. chinense</i> , <i>L. effusum</i> , <i>L. elatius</i> (in part), <i>L. filiforme</i> (in part), <i>L. forsythii</i> , <i>L. gladiatum</i> (in part), <i>L. limicola</i> , <i>L. longitudinale</i> , <i>L. persecans</i> (in part), <i>L. quadrangulatum</i> , <i>L. rostratum</i> , <i>L. striatum</i> , <i>L. tetraquetrum</i> (strict rheophyte?), <i>L. sp.</i> Blackwood (R. Davis 7696), <i>L. sp.</i> Bluff Knoll robust (G.J. Keighery 12595), <i>L. sp.</i> Z dark sheath (P.G. Wilson 10177) |
| Petrophilous (rock-loving) | <i>L. amantiferrum</i> , <i>L. angustatum</i> , <i>L. avium</i> , <i>L. bungalbin</i> , <i>L. clipeicola</i> , <i>L. concavum</i> , <i>L. ferricola</i> , <i>L. ferriculmen</i> , <i>L. gibsonii</i> , <i>L. gracile</i> , <i>L. jacksonense</i> , <i>L. lyonsii</i> , <i>L. resinolum</i> , <i>L. rupestre</i> , <i>L. tuberculatum</i> , <i>L. tuberculatum</i> var. <i>grande</i> , <i>L. sp.</i> Billyacatting (S.D. Hopper 8630), <i>L. sp.</i> Blue Hills (A. Markey & S. Dillon 3468), <i>L. sp.</i> Giant Terete Culms (S.D. Hopper 8631), <i>L. sp.</i> Gosnells (A. Markey 1145), <i>L. sp.</i> Kambalda (A.A. Mitchell 5156), <i>L. sp.</i> Moresby Range (R.J. Cranfield 2751), <i>L. sp.</i> Mt Caudan (N. Gibson & M. Lyons 2081), <i>L. sp.</i> Mt Ragged (K. Newbey 7858), <i>L. sp.</i> Parker Range (N. Gibson & M. Lyons 2094), <i>L. sp.</i> Peak Charles fine (K. Newbey 5411), <i>L. sp.</i> Pigeon Rocks (H. Pringle 30237), <i>L. sp.</i> Wolga Rock (S.D. Hopper 6513) |
| Cremnophilous (cliff faces) | <i>L. evansianum</i> , <i>L. ferricola</i> (in part) |
| Arenophilous (sand-loving) | <i>L. canescens</i> , <i>L. carphoides</i> , <i>L. rigidulum</i> , <i>L. scabrum</i> |
| Seasonally xerophilous (areas of low water availability)/seasonally mesophilous (moderate growing conditions) | <i>L. asperatum</i> , <i>L. benthamianum</i> , <i>L. congestum</i> , <i>L. costale</i> , <i>L. curtisiae</i> , <i>L. diurnum</i> , <i>L. drummondii</i> , <i>L. filiforme</i> , <i>L. fimbriatum</i> , <i>L. flexuosum</i> , <i>L. gahnioides</i> , <i>L. globosum</i> , <i>L. humile</i> , <i>L. inops</i> , <i>L. laeve</i> , <i>L. latens</i> , <i>L. laterale</i> (in part), <i>L. leptophyllum</i> , <i>L. leptostachyum</i> , <i>L. lineare</i> , <i>L. neesii</i> , <i>L. neozelandicum</i> , <i>L. obtusum</i> , <i>L. oldfieldii</i> , <i>L. pauperum</i> , <i>L. perplanum</i> , <i>L. ptereres</i> , <i>L. pruinosum</i> , <i>L. pubisquamum</i> , <i>L. sanguinolentum</i> , <i>L. sieberi</i> , <i>L. squamatum</i> , <i>L. tenue</i> , <i>L. tortuosum</i> , <i>L. urophorum</i> , <i>L. ustulatum</i> , <i>L. viscidum</i> , <i>L. sp.</i> Archer Drive (S. Kern & R. Jasper LCH 18300), <i>L. sp.</i> Bandalup Scabrid (N. Eveleigh 10798), <i>L. sp.</i> Bluff Knoll scabrid (K.H. Rechinger 60431), <i>L. sp.</i> Carracarrup Creek (S. Kern <i>et al.</i> , LCH 16738), <i>L. sp.</i> Elverdton (R. Jasper <i>et al.</i> LCH 16844), <i>L. sp.</i> Gingin (M.A. Langley & P.M. Smith MAL 2193), <i>L. sp.</i> Hopetoun Road (S. Kern <i>et al.</i> LCH 16552), <i>L. sp.</i> Maydon (S. Kern, R. Jasper, H. Hughes LCH 17844), <i>L. sp.</i> Meckerling (R. Davis WW27-32), <i>L. sp.</i> Mt Burdett (M.A. Burgman & C. Layman MAB 3287), <i>L. sp.</i> Mt Chester (S. Kern <i>et al.</i> LCH 16596), <i>L. sp.</i> Mt Groper (K. Newbey 11808), <i>L. sp.</i> Mt Short (S. Kern <i>et al.</i> LCH 17510), <i>L. sp.</i> P1 small head (M.D. Tindale 166A), <i>L. sp.</i> Ravensthorpe (G.F. Craig 5188), <i>L. sp.</i> Saltbush Hill (K.R. Newbey 4118), <i>L. sp.</i> Shoemaker Levy (L. Ang & O. Davies 10815), <i>L. sp.</i> Steere River (S. Kern, R. Jasper, H. Hughes LCH 17764), <i>L. sp.</i> U1 big heads (A.S. George 11294), <i>L. sp.</i> Zuytdorp (G.J. Keighery & N. Gibson 1710) |
| Wet forests | <i>L. elatius</i> , <i>L. ensiforme</i> , <i>L. laterale</i> (in part), <i>L. persecans</i> , <i>L. sp.</i> Manypeaks large (R. L. Barrett RLB 2476), <i>L. sp.</i> Margaret River (B.J. Lepschi 1841) |
| Coastal dunes | <i>L. gladiatum</i> , <i>L. sp.</i> Coastal Dunes (R.J. Cranfield 9963) |
| Subalpine | <i>L. chinense</i> (in part), <i>L. filiforme</i> (in part), <i>L. inops</i> (in part), <i>L. tortuosum</i> (in part) |

Although less well known, the sword and rapier sedges, *Lepidosperma*, are a significant plant genus in many temperate ecosystems of Australasia and the genus also extends to South East Asia. The majority of literature, and thus the majority of this review, is focused on Australian and New Zealand species, but all species are included here. *Lepidosperma concavum* was among the earliest collections of Australian plants, that of Banks and Solander from Botany Bay in 1770 (Benson and Eldershaw, 2007). *Lepidosperma* species regularly dominate the understorey of a wide range of dryland habitats throughout their range and may also be important components of wetland and riverine environments in southern Australia and New Zealand (Specht, 1972; Atkinson, 1984, 2004; Fensham, 1989; Beard, 1990; Conn, 1993; Usback and James, 1993; Kirkpatrick, 1997; Pen *et al.*, 2000; Keith, 2004; Berkinshaw, 2009).

Taxonomic nomenclature has been reviewed by Barrett and Wilson (2012), with 73 validly named species currently published. An additional 41 putative species are currently listed as provisional polynomial taxa on the Western Australian Herbarium website FloraBase (1998 onwards) following the protocol outlined by Barker (2005). This listing provides legislative protection for taxa that are yet to be formally named. Taxonomic revision of the genus is currently underway by R. L. Barrett, K. L. Wilson, J. J. Bruhl and colleagues. With the total number of species in the genus estimated at well over 200,

Lepidosperma is one of the larger genera in the Australasian flora and the largest genus of Cyperaceae in the region (Barrett, 2012). In the global biodiversity hotspot of southern Western Australia, the genus is probably one of the five largest, behind *Acacia* and *Eucalyptus*, with similar numbers to *Grevillea* and *Styliidium* (Beard *et al.*, 2000; Hopper and Gioia, 2004; J. Wege, pers. comm.; R. L. Barrett unpubl. data). *Lepidosperma* belongs to Cyperaceae tribe Schoeneae and is most closely related to *Machaerina* (including *Baumea*), *Neesenbeckia* and *Tetraria p.p.* (*T. capillaris*; Verboom, 2006). *Lepidosperma* can be readily defined by the persistent, thickened, hypogynous scales at the base of the nutlet (Bruhl, 1995). The culms are scapose and the leaves are (spiro)dichous in arrangement.

Given the ecological predominance of the genus in many parts of its range and the poorly resolved taxonomy, a review was conducted to determine what is known about the genus *Lepidosperma*, and its relative importance in community ecology. Emphasis is placed on how other organisms relate to *Lepidosperma* species in a community ecology setting. The opportunity is also taken to correct the literature (where possible) with updated nomenclature for the *Lepidosperma* species involved, as names have commonly been misapplied and correct application of names can have important implications for conservation efforts. This review attempts to answer the questions of ‘are sedges important?’ and ‘do individual sedge species matter?’

METHODS

This paper primarily reviews knowledge available in reviewed scientific literature, books and academic theses. Additional unpublished observations are reported here for the first time. An introduction to the ecological attributes of *Lepidosperma* is given where those attributes may be applicable to understanding the conservation implications for management of ecological communities containing *Lepidosperma* species. Details are then provided of the organisms that are known to have ecological associations with the genus *Lepidosperma*. Incidental co-occurrence is largely ignored; however, co-occurrence is considered significant when *Lepidosperma* species are a characteristic component of the ecosystem, or specifically mentioned as a species of significance.

Nomenclature follows the original sources unless otherwise indicated by an alternative name. While attempts have been made to ensure that all names listed here are current, some may now be considered synonyms or placed in alternative genera. Application of names in *Lepidosperma* follows Barrett and Wilson (2012).

ECOLOGICAL CHARACTERISTICS

Habitat specificity

Some *Lepidosperma* species show marked geological specificity and numerous endemic species have been located on banded ironstone formations (Gibson and Lyons, 1998a, b, 2001; Gibson, 2004a, b; Barrett, 2007a; Gibson *et al.*, 2007, 2010; Fig. 1), granite outcrops (McKenzie *et al.*, 2004; Fig. 2), dolerite outcrops (Wilson, 1994) and numerous other geological formations, usually on shallow soils (Barrett, 2007b; Barrett *et al.*, 2009; R. L. Barrett pers. obs., Fig. 3).

Lepidosperma species are common components of vegetation containing rare plant species (e.g. Lynch, 1999; Benson and Allen, 2007; Bell, 2008; Stack *et al.*, 2008). They also occur in intrinsically rare habitats (Gibson *et al.*, 2000, 2007). Temperate Australian peat soils are largely derived from rushes and sedges, including *Lepidosperma*, and are an important habitat for many species including *Sphagnum*. These ecosystems are increasingly threatened by land-use activities and climate change (Whinam *et al.*, 2001) and are poorly represented in conservation reserves (Specht *et al.*, 1995). A lichen species (*Heterodea muelleri*) that was considered extinct in New Zealand was recently located on the Chatham Islands where it grows in association with *Lepidosperma australe* (de Lange, 2009).

The ecological distribution of *Lepidosperma* species is detailed in Table 1: 16 are hygrophilous (moisture-loving), 29 are petrophilous (rock-loving), two are cremnophilous (cliff-loving), four are arenophilous (sand-loving), 58 are generalist seasonally xerophilous (areas of low water availability)/seasonally mesic (moderate growing conditions), six are from wet forests, two occur on coastal sand dunes and four extend to subalpine zones. Most *Lepidosperma* species are seasonally xerophilous, such as the widespread *L. sanguinolentum* in southern Western Australia, which grows on extensive sandplains from Ravensthorpe on the south coast, north to Geraldton on the west coast, and inland to Queen Victoria Spring on the edge of the Queen Victoria Desert. A broad

view of xerophyly is taken here to include habitats that are seasonally mesic, but have a longer seasonally xeric period, including woodlands and heath habitats. In the south western interzone of Western Australia, *Lepidosperma* species are commonly restricted to rock outcrops, where they may be locally common on granite or banded ironstone formations (Barrett, 2007a). Species such as *L. bungalbin*, *L. gibsonii*, *L. jacksonense* and *L. lyonsii* all grow on isolated rocky ranges in the Western Australian Goldfields and Murchison districts, surviving there by means of increased runoff from sporadic rainfall events (Barrett, 2007a). In the Die Hardy Ranges, north of Southern Cross, Western Australia, *L. ferricola* grows in fissures on banded ironstone cliff faces, occupying a niche also occupied by rare species of *Tetratheca* (Elaeocarpaceae) (Barrett, 2007a; Butcher *et al.*, 2007). *Lepidosperma avium* is a relictual species endemic to the Everard Ranges in the arid north-west of South Australia (Wilson, 1994; Barrett, 2012). *Lepidosperma laterale* (*s.l.*) is a very widespread species complex which occurs in woodlands and forests from eastern regions of South Australia, throughout much of Victoria and Tasmania, and north along the Great Dividing Range and coastal areas of New South Wales and Queensland, extending as far as the Iron Range on Cape York Peninsula, spanning 31 degrees in latitude and 43 degrees in longitude (Barrett and Wilson, 2012). This species complex also occurs in New Zealand and New Caledonia, presumably as a result of long-distance dispersal events.

Lepidosperma species can be numerous and particularly common around granite outcrops, often dominating the understorey (Ashton and Webb, 1977; Hopper *et al.*, 1997; Pigott and Sage, 1997; Hunter and Clarke, 1998; McKenzie *et al.*, 2004). Granite rocks may act as important refugial habitats, largely due to their ability to ‘harvest’ small quantities of water, forming water-accumulating microsites and thus providing a relatively stable ecosystem in areas that may otherwise have unpredictable or low rainfall (York Main, 1997). Water accumulation zones on and around rock outcrops provide important habitats for a large number of *Lepidosperma* species. Granite outcrops in eastern Australia also act as ‘islands’ for speciation (McGann, 2002) and locally endemic *Lepidosperma* species are now coming to light on inselbergs on the New England Tableland (J. J. Bruhl and R.L. Barrett, pers. obs.). A similar pattern is also observable in southwestern Australia (R. L. Barrett and S. D. Hopper, pers. obs.).

Wilson (1986) reviewed the Australian Cyperaceae occurring in alpine zones but did not list any *Lepidosperma* species. *Lepidosperma chinense*, *L. filiforme*, *L. inops* (*s.l.*) and *L. tortuosum* all occur in subalpine zones over parts of their respective ranges. Horsnell *et al.* (2009) record *Lepidosperma ‘viscidum’* as being both a xerophyte and a hygrophyte, occurring in areas containing wetlands that were subject to salinization along the south coast of Western Australia. It is most likely that they are actually referring to two currently unnamed taxa with affinity to *L. squamatum* that have distinct habitat preferences (R. L. Barrett, pers. obs.). Many additional species are yet to be formally named, the majority of which are petrophilous or generalist xerophilous species. A few species of *Lepidosperma* are hygrophilous and these are often better studied, as wetland habitats are more



FIG. 1. (A) *Lepidosperma* sp. Honman Ridge (R. L. Barrett & M. Wallace RLB 4120) on banded ironstone formation, Honman Ridge, Great Western Woodlands, Western Australia. (B) Roots of *Lepidosperma gibsonii* that were growing under a flat slab of banded ironstone, Mount Gibson, Western Australia. (C) *Lepidosperma gibsonii* growing in massive banded ironstone.

regularly threatened than xeric habitats, and these species are discussed here in more detail. More studies of the xerophilous species are required to balance our understanding of the genus.

Lepidosperma australe regularly grows in seasonally waterlogged soils where the roots have been recorded to be continuously under water for up to 270 d without any apparent

detrimental effects (Johnson, 1972). Lloyd *et al.* (2000) suggest that *L. australe* is most abundant in ecotone sites near seasonally wet areas, although it also extends beyond the wet margins onto dune slacks (Roxburgh *et al.*, 1994). Robertson *et al.* (1991) consider *L. australe* to be an early colonizer species on the margins of lakes. It grows with other

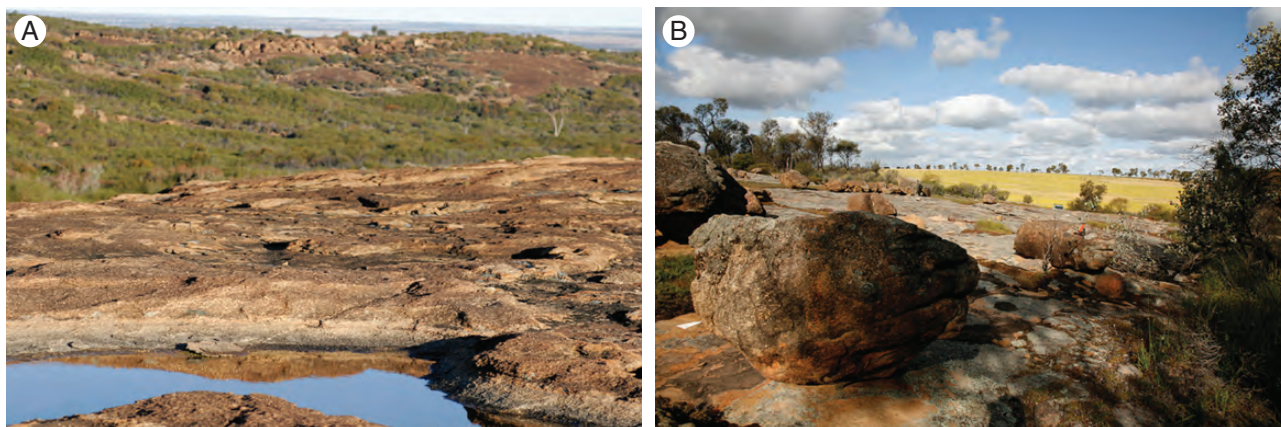


FIG. 2. Granite outcrops providing rich habitats and refuge areas for *Lepidosperma* species in the wheatbelt of Western Australia. (A) Chiddarcooping Nature Reserve. (B) Gathercole Nature Reserve.

sedges and promotes the accumulation of soil and litter at the lake margin, eventually providing a suitable substrate for larger shrubs and trees. *Lepidosperma filiforme* is a common component of sedgeland in Tasmania (Harris and Kitchener, 2005) and *L. neozelandicum* is common in wet heathlands (gumlands) in the far north of New Zealand (Clarkson *et al.*, 2011). *Lepidosperma longitudinale* is found in areas of impeded drainage across southern Australia where it may form very dense stands, dominating the understorey (Brown *et al.*, 1982); however, it only tolerates partial seasonal inundation (Froend *et al.*, 1993). *Lepidosperma longitudinale*, *L. gladiatum* and in some cases *L. effusum* and *L. persecans* are common species in numerous wetlands of national significance in Australia (Usback and James, 1993; Jacobs, 1999). Fringing vegetation such as dense communities of *L. effusum* and *L. tetraquetrum* serve to slow water flow during flood events and provide stability to the margins of waterways (Pen, 1999).

Lepidosperma elatius is a common species in wet forests in south-eastern Australia. In a study of flood-maintained vegetation patterns in south-eastern Tasmania, Wintle and Kirkpatrick (2007) found that *L. elatius* occurs in depositional areas of drainage lines where it plays an important role in trapping debris and sediment. *Lepidosperma* species occurring in swamp habitats can be significant contributors to the development of peat soils due to their high biomass production (Green *et al.*, 1988).

Perhaps due to their local dominance and habitat or substrate specificity, *Lepidosperma* species have often been found to be important defining members of plant communities (e.g. Kirkpatrick, 1981; Griffin *et al.*, 1983; Atkinson, 1984; Fensham, 1989; Groves, 1999; Tozer, 2003; Keith, 2004; Harris and Kitchener, 2005; Hunter and Bell, 2007; Craig *et al.*, 2008; Sandiford and Barrett, 2010). Bridgewater (1978) proposed a vegetation alliance ‘Lepidospermion’ on coastal dunes in Victoria where *Lepidosperma* species are prominent and Adam *et al.* (1989) recognized a similar vegetation association in New South Wales. There is some evidence that community boundaries may be particularly influenced by phosphorus concentrations in the soil (Ashton, 1976), and Hogg and Kirkpatrick (1974) demonstrated a

specific association of *L. laterale* with dolerite and mudstone in Tasmania. Brown *et al.* (1982) found that *L. filiforme* in south-western Tasmania is most common at sites with low soil pH, although tolerant of a wide soil pH range (4.3–8.7), while *L. longitudinale* is usually found in locations with a pH of about 7.5.

Chemistry and medicinal properties

There has been very limited investigation of the chemical properties of *Lepidosperma* tissues. Aplin and Cannon (1971) assessed three Western Australian *Lepidosperma* species and found that they lacked alkaloids. Kukkunen (1971) identified six different flavonoid compounds in *L. concavum* but did not identify the individual compounds present. Williams and Harborne (1977) conducted a survey of flavonoid chemistry in Cyperaceae and found that *L. tortuosum* contained quercetin. In further studies, Harborne *et al.* (1985) surveyed 16 *Lepidosperma* species for the presence of flavonoids and found that flavonols were common in *Lepidosperma* species and included some yellow aurone pigments and an anthocyanin-type pigment, carexidol. Harborne *et al.* (1985) considered that *Lepidosperma* can be well characterized chemically by the presence of tricetin, quercetin and isorhamnetin, while mostly lacking luteolin and aurones, the latter being present rarely in some species. Pigmentation can play an important role in photoprotection, a factor especially important in species occupying xeric environments (Steyn *et al.*, 2002). Flavonoids play particular roles in plant defence, often deterring herbivores from feeding on the plants (Simmonds, 2001; Morimoto and Komai, 2006). The presence of two potentially allelopathic chemicals (cyperotundone and α -cyperone) has been explored in *Cyperus rotundus* by Morimoto and Komai (2005) but it is unknown whether these chemicals are more widespread in the Cyperaceae and whether they might be found in *Lepidosperma* species.

Naturally derived pharmaceutical products remain the primary source of new medicinal drugs and analysis of new plant-derived compounds remains an important part of modern medical research (Newman *et al.*, 2008). Gott



FIG. 3. (A) A rare cremonophytic species, *Lepidosperma evansianum*, at Wentworth Falls in the Blue Mountains National Park, New South Wales. (B) The widespread *Lepidosperma filiforme* partly covered by a summer snowfall on the summit of Mount Field in the Tasmanian highlands. (C) *Lepidosperma* sp. Southern Granite beside a gnamma (vernal pool) on Mt Lindesay, near Denmark, Western Australia. (D) *Lepidosperma congestum* and *L. viscidum* in windswept coastal heath south of Port Lincoln, South Australia.

(1993) reported the traditional use of the stem bases of *L. gladiatum* and *L. viscidum* for use against colds by Aboriginal people in South Australia. This has been investigated by Semple *et al.* (1998) and Palombo and Semple (2001) who investigated the antibacterial properties of these species, finding that extracts of *L. gladiatum* and *L. viscidum* were both active against a range of Gram-positive bacteria. Palombo and Semple (2002) conducted further tests with the most active species, *L. viscidum*, and found activity against methicillin-resistant *Staphylococcus aureus* (MRSA) and partial activity against vancomycin-resistant *Enterococcus* (VRE). Meilak and Palombo (2008) investigated *L. viscidum* for potential activity against *Mycobacterium fortuitum* and *M. smegmatis* but no significant effect was found. A significant amount of work has been undertaken to isolate stilbenes, including chemical analogues of resveratrol, from *Scleria*

holoschoenus (Abdel-Mogib *et al.*, 2001) and a number of *Carex* species (see González-Sarrías *et al.*, 2011). Resveratrol is a well-known constituent of red wine that has shown benefits in reducing the risk of heart disease and possesses anti-cancer and anti-ageing properties (González-Sarrías *et al.*, 2011). Recently, novel stilbenes have also been isolated from a *Lepidosperma* species in South Australia and their potential medical benefits are the subject of ongoing research (Duke *et al.*, 2012).

Nutrient acquisition

Cyperaceae are recognized for their ability to colonize a diverse range of habitats. Their prevalence in dry shrublands and woodlands in Australia may in part be explained by their ability to extract phosphorus from nutrient-poor soils.

Cluster roots were first described in Cyperaceae by Renner (1935). The production of these specialized root structures in *Carex* is documented by Selivanov and Utemova (1969) who confused them for mycorrhizal structures. Lamont (1974, 1981, 1982, 1983, 1984) further defined the root type as 'dauciform roots' and characterized their ability to enhance nutrient uptake in *Cyathochaeta*, *Gahnia*, *Lepidosperma* and *Schoenus*. More recent work has shown that many genera and species in Cyperaceae tribes Schoeneae (including *Lepidosperma*) and Cariceae have the ability to develop such dauciform roots and they may be present in all species in the tribe Schoeneae (Raab *et al.*, 1999; Shane and Lambers, 2005; Shane *et al.*, 2005; Yano *et al.*, 2011).

The dauciform roots of *Lepidosperma* are among the largest produced in the Cyperaceae (Lambers *et al.*, 2006; Fig. 4). Production of dauciform roots in *Lepidosperma* is induced by low availability of phosphorus and results in the production of elongated cells that release carboxylates in an exudative burst (Shane *et al.*, 2006). Carboxylates promote the release of soil-bound phosphorus (Shane *et al.*, 2005; Watt and Weston, 2009). The full range of conditions is yet to be determined (Miller, 2005; Shane *et al.*, 2005; Playsted *et al.*, 2006) and Bakker *et al.* (2005) found that the addition of phosphorus did not influence the production of dauciform roots in *Schoenus nigricans*.

In addition to dauciform roots, some *Lepidosperma* species also commonly develop sand-binding roots that can serve to stabilize surrounding soil and aid water uptake and retention (Dodd *et al.*, 1984). The ecological role of these sand binding roots has been explored in detail for the morphologically similar *Lyginia barbata* (Anarthriaceae; Shane *et al.*, 2009, 2010, 2011). Similar studies should be undertaken in *Lepidosperma* and allied genera.

While studying the natural abundance of nitrogen in *Banksia* woodland ecosystems, *Lepidosperma* sp. Coastal Dunes was shown to have a relatively low level of shoot nitrate reductase (about 40 pkat. per g f. wt) and corresponding low $\delta^{15}\text{N}$ (about 1; Pate *et al.*, 1993; Pate, 1994; as *L. angustatum*). Nitrate is an important macronutrient and plays a vital role in growth (Crawford and Glass, 1998). The

low level of shoot nitrate reductase found by Pate *et al.* (1993) may indicate that *Lepidosperma* species preferentially use organic nitrogen as found for the Arctic sedge *Eriophorum vaginatum* by Chapin *et al.* (1993).

Bowman *et al.* (1986) studied mineral and nutrient uptake and mobilization by plants across a landscape in south-western Tasmania, finding that *L. filiforme* had foliar concentrations of $113 \mu\text{g g}^{-1}$ phosphorus, $4100 \mu\text{g g}^{-1}$ potassium, $950 \mu\text{g g}^{-1}$ sodium, $950 \mu\text{g g}^{-1}$ calcium and $540 \mu\text{g g}^{-1}$ magnesium. This species was able to withdraw 93 % of phosphorus and potassium, 58 % of sodium and 18 % magnesium prior to leaf senescence. Such a high level of internal nutrient recycling means that *Lepidosperma* species are well adapted to survival in low-nutrient soils.

Studies by Jones (1968) suggested that the addition of fertilizer to natural stands of *L. sieberi* (as *L. concavum*) had no significant impact on growth rate over two years. However, results of studies on the effect of overstorey thinning and fertilization for *L. urophurum* suggest that many respond positively to the addition of fertilizer (Bauhus *et al.*, 2001). Bridle and Kirkpatrick (2003) investigated the impacts of human and animal waste on plant growth and found that the addition of urine increased the cover of *L. sieberi* (as *L. concavum*).

Ultramafic/serpentine substrates

Serpentine soils are derived from ultramafic parent rock. They are defined by the presence of extreme mineral concentrations, commonly low calcium, phosphorus and potassium, and high magnesium and nickel (Nagy and Proctor, 1997). Plants occurring on these ultramafic/serpentine substrates often have specific adaptive strategies to deal with mineral toxicity and nutrient deprivation (Nagy and Proctor, 1997; Proctor, 2003). Relatively little is known about floristic communities on ultramafic soils in Australia, despite the presence of a number of species endemic to these communities (Gibson *et al.*, 1992). There is considerable interest in the flora of ultramafic soils in southern Western Australia, particularly on Bandalup Hill, near Ravensthorpe. This hill and the associated Ravensthorpe Range show very high levels of floristic



FIG. 4. Dauciform roots of *Lepidosperma longitudinaline* (western form), from Bold Park, Western Australia (photos: Mike Shane).

diversity with a high level of local endemism and rarity (Kern *et al.*, 2008). A detailed assessment of *Lepidosperma* taxa from the Ravensthorpe Range and Bandalup Hill showed that 42 species should be recognized from this area, only five of which are currently named (Barrett *et al.*, 2009). About half of these taxa are locally endemic and 18 of these require conservation assessments to determine whether they should be listed as rare or threatened (Barrett *et al.*, 2009). This geographical region has by far the highest diversity for the genus *Lepidosperma*, and also has a large number of species in genera such as *Eucalyptus* and *Melaleuca* (Kern *et al.*, 2008). The Ravensthorpe Range has a very diverse and complex geological history and this is thought to be one of the reasons for the range's high levels of floristic diversity. Kruckeberg (1986) has suggested that unusual geologies may often act as opportunities for speciation as plants adapt to particular substrates and become unfit outside their particular niche. Speciation across geological boundaries may occur even with continued outcrossing if the out-crossed progeny from the alternative geological parent fail to survive. As a result, a number of closely related species may be found in unusually close proximity in geologically diverse locations (Heslop-Harrison, 1964).

An unidentified *Lepidosperma* species from south-east Queensland was found to grow effectively in metal-rich soils, absorbing significant amounts of copper and arsenic, and some silver, cadmium, molybdenum, lead and zinc (Ashley *et al.*, 2003). *Lepidosperma australe* has been recorded as a significant gold-accumulating species in New Zealand where it may have potential as an indicator species for gold prospecting (Ward and Brooks, 1978).

Lepidosperma laterale and *L. perteres* are locally common in ultrabasic massifs of New Caledonia (Jaffré, 1974). Within New Caledonia, *L. pauperum* and *L. perplanum* are both restricted to ultrabasic soils, while *L. perteres* is not restricted to specific soil types (Morat *et al.*, 1986). Nutrient acquisition varies with soil type, with Jaffré (1976) demonstrating that *L. perteres* is able to take up significantly higher amounts of nitrogen and potassium from ferrous soils than from brown soils in New Caledonia. The uptake of manganese from ferrous soils was ten-fold greater than that from brown soils while uptake of magnesium from ferrous soils was significantly reduced. There was also a ten-fold reduction in the uptake of silicon from ferrous soils (Jaffré, 1976).

Fire and disturbance response

Long-term survival in ecosystems prone to disturbance or environmental fluctuations is primarily determined by the ability to persist and reproduce. Plants that have the ability to resprout following disturbance events such as fire or grazing tend to allocate greater resources to below-ground biomass than to sexual reproduction, with lower seedling recruitment rates but long generation times (Bond and Midgley, 2003). These characteristics are true of most *Lepidosperma* species. All *Lepidosperma* species are clonal perennials and most have been observed in the field by the author. These observations have shown that clones vary in size, from around 5–10 cm for *L. inops* to over 10 m for *L. gladiatum*. These clones provide a robust resource to

withstand disturbance events and periods of low rainfall. Explicit data on the age of individual clones are not available, but assessment of clone size against annual growth rates suggests that plants of most species probably live for at least 50 years, and some clones are estimated to be in excess of 100 years old (R. L. Barrett, pers. obs.). Such longevity of individuals and resilience to disturbance means that *Lepidosperma* species can survive with very low recruitment rates and persist in some extreme environments. Given their persistence, they can form a very significant and stable component of the ecosystems in which they occur.

Specht (1981) classifies *Lepidosperma* species as evergreen hemicryptophytes. Almost all Australian *Lepidosperma* species that have been observed post-fire have shown capacity to resprout from rhizomes, with vegetative growth rapidly re-establishing or exceeding pre-fire biomass (Bradstock *et al.*, 1997; Ashton, 2000; Barrett, 2000; Hopper, 2000; Brown *et al.*, 2002; Morrison, 2002; R. L. Barrett, pers. obs.). In *Lepidosperma*, rhizome resources are often sufficient for flowering to occur in the first year following fire (Hopper, 2003; provided the burn season allows for floral initiation and development). Long-term monitoring of *L. elatius* in wet forests at Wallaby Creek in Victoria revealed a significant increase in density over a period of 50 years in response to the maturation and eventual decline of the eucalypt canopy in the absence of fire (Ashton, 2000). *Lepidosperma limicola*, a common species in sedge swamps in the Gibraltar Range of New South Wales, was equally abundant in burnt and unburnt sites (Williams and Clarke, 2006). In contrast, it should be noted that some populations of *L. filiforme* (?= *L. flexuosum*) in the Sydney region appear to be killed by fire, regenerating only from seed (Kubiak, 2009; R. L. Barrett and K. L. Wilson, pers. obs.). This is possibly due to the relatively shallow rhizomes and habitat in dense heath that is likely to promote hot fires (R. L. Barrett and K. L. Wilson, pers. obs.).

While able to resprout following fire, a form of *L. laterale* from north-eastern Queensland montane heath communities significantly decreased in abundance following fire, probably due to biomass reduction in a nutrient-limited environment limiting short-term recovery (Williams *et al.*, 2005). Careful fire management was advised to ensure that fire frequency did not have a detrimental impact on this species. Correct classification of the fire response of each species is essential for sustainable management, particularly for rare or ecologically critical species (Gill and Bradstock, 1992). Cary and Morrison (1995) found that *L. laterale* is one of the few species in sandstone communities in the Sydney region that is able to tolerate high fire frequency (<5 years between fires). Adult plants are able to reproduce and seedlings are able to recruit and persist under these conditions, which may be promoting germination. *Lepidosperma laterale* also increased in cover following fire on Fraser Island, more so after low- rather than high-frequency fires (Spencer and Baxter, 2006).

Lepidosperma leptostachyum declined in abundance by at least 20 % under a variety of fire regimes in jarrah forest near Manjimup in Western Australia (Burrows and Wardell-Johnson, 2003). They suggested this decline was possibly due to decreasing rainfall patterns. This species has

relatively shallow rhizomes that are often close to the litter layer and there may be a high level of mortality for this reason, particularly from hot fires. They also showed a decline in abundance of *L. squamatum* (*s.l.*) following spring fires that had an interval of 7–9 years.

Lepidosperma perteres from New Caledonia is rhizomatous and is able to resprout vigorously following fire, often dominating post-fire maquis vegetation (Jaffré *et al.*, 1998). However, it may be negatively affected by frequent fires, which can promote the dominance of other plant species (McCoy *et al.*, 1999). The prevalence of *L. chinense* in some grasslands in Hong Kong is also attributed to the promotion of fire in these areas (Kadoorie Farm and Botanic Garden, 2003).

Tozer and Auld (2006) measured the degree of leaf scorch in *L. neesii* in the Sydney region following fire. Their study showed that fire penetration was always less than the depth of the meristematic tissue, thus allowing the plants to resprout following fire. *Lepidosperma neesii* shows very strong preference for seasonally dry sites with low shade cover, decreasing in abundance in dry shaded areas, decreasing further in moist open areas and becoming very sparse in moist shaded areas (Tozer and Bradstock, 2003). This pattern of habitat preference corresponds to litter levels that provide fuel for fires.

Some *Lepidosperma* species are readily able to recover from disturbance. Ough (2001) found that *L. elatius* recovered with equal frequency following both clear-fell logging and wildfire, although total cover of this species was lower in the wildfire site. Partial habitat disturbance due to the development of log removal tracks for timber harvesting in Tasmanian forests had little impact on the density of *L. sieberi* (as *L. concavum*; Williamson and Neilsen, 2003). In contrast, Loyn *et al.* (1983) found that in East Gippsland, *L. laterale* increased in abundance following fire, but decreased in abundance in areas harvested for timber. Density of *L. leptostachyum* plants declined following logging operations in south-western Western Australia (Burrows *et al.*, 2002). In urban locations, *Lepidosperma* species can show remarkable resilience. Rose and Fairweather (1997) found that *L. filiforme*, *L. laterale* and *L. lineare* (as *L. gunnii*) were all able to persist in the long term in urban bushland invaded by *Pitopsis undulatum* and numerous other weeds, while many other native species were significantly declining in abundance.

In areas of northern New South Wales that were previously used for plantation forestry of *Eucalyptus grandis*, but are now included in conservation estates, control of weeds in the understorey led to a significant increase in the density of the persistent species *L. laterale* (Cummings and Reid, 2008). Control of the invasive species bitou bush (*Chrysanthemoides monilifera* ssp. *rotundata*) in native bushland on coastal dunes in New South Wales led to an increase in cover of *L. laterale* though there were some short-term detrimental effects of herbicide spraying (Vranjic *et al.*, 2011). Burrows and Wardell-Johnson (2003) suggest that *L. squamatum* (*s.l.*) disappears from long-unburnt tall karri (*Eucalyptus diversicolor*) forest, probably due to shading, although it may persist in the seed bank.

While some forms of disturbance are not overly detrimental, in the Buller District of New Zealand, grazing and trampling

has resulted in the elimination of *L. australe* from dairy farms around the wetlands of the Kongahu Swamp (Sorrell and Partridge, 1999). Pelton and Conran (2002) found that vegetation rolling for firebreak construction in sandy heath communities in South Australia had a negative impact on two significant indicator species, *L. carphoides* and *L. laterale*.

While investigating energy content and flammability of common forest species in Tasmania, Dickinson and Kirkpatrick (1985) found that *L. laterale* had an energy content of around 20 000 J g⁻¹, an ash content (excluding silica) of 7–10 % and a silica content of 10 %, making them one of the least significant components of flammable material in the forest.

Germination and dormancy

Cyperaceae ‘seeds’ are technically a nutlet, the fruit comprising more than one carpel, but only a single seed, but as they are very small and one-seeded, they are sometimes referred to incorrectly as an achene (J. J. Bruhl, pers. comm.). Bruhl (1991) has confirmed that the thickened persistent scales at the base of the nutlet are in fact a perianth. Nutlet production is first dependent on inflorescence development. In *Lepidosperma*, the inflorescences are initiated during winter, with immature buds developing at this time, then undergoing a period of stasis over summer, maturing and flowering within weeks of breaking rains the following autumn (or occasionally after heavy summer rains) (R. L. Barrett, pers. observ.). This pattern is strong in the Western Australian species, but the timing is not as consistent in eastern Australian species (K. L. Wilson and J. J. Bruhl, pers. obs.). *Lepidosperma* spikelets are bisexual, with hermaphrodite flowers, most species developing several basal sterile bracts, followed by a functionally male flower and terminated by a bisexual flower (Bruhl *et al.*, 1992; Bruhl, 1995; Goetghebeur, 1998). Spikelets are protogynous, the lower functionally male flower developing first, followed by the stigma of the bisexual flower, the stamens of the bisexual flower either developing later or remaining only partially developed (R. L. Barrett, pers. obs.). A few species such as *L. jacksonense* produce two bisexual flowers per spikelet (Barrett, 2007a). All species are considered to be wind-pollinated and population genetic studies suggest that they are primarily outcrossing (M. D. Barrett and M. Wallace, unpubl. data).

Potential nutlet production varies greatly between species of *Lepidosperma*, from 1–4 spikelets per inflorescence in *L. tortuosum* to over 1000 spikelets per inflorescence in *L. elatius* (Wheeler and Bruhl, 2000; R. L. Barrett, pers. obs.). Almost all species produce a single nutlet per spikelet; however, a few species have been observed to consistently produce two nutlets per spikelet (e.g. *L. jacksonense*, Barrett, 2007a). In *Lepidosperma* species, nutlets develop to approximately full size in a matter of weeks following fertilization (R. L. Barrett, pers. obs.). These nutlets do not necessarily develop fully, with Wheeler and Bruhl (2000) finding that many nutlets appeared ‘full’ but were in fact lacking a developed embryo, a condition sometimes indicated by wrinkling of the nutlet surface (more prominent with age). Consistent winter rainfall is required to allow embryo fill, so with inflorescence development, two good seasons of rainfall are

required for good nutlet development (R. L. Barrett, pers. obs.). This can be a rare combination in arid areas at the edge of the distribution of the genus (R. L. Barrett, pers. obs.).

Embryos were found to be small, only 0.12 mm long in *L. clipeicola* and only 0.40 mm long in *L. elatius* and *L. laterale*, and matched the *Schoenus*-type embryo morphology (Wheeler and Bruhl, 2000). Vanhecke (1974) studied the embryos of *L. chinense*, *L. laterale* (s.l.), *L. longitudinale* and *L. sieberi* (as *L. squamatum*) and found a similar size variation, from 0.20 to 0.32 mm long. The embryos are described as being asymmetric, with well-developed, S-shaped vascular tissue and with the germinal pore towards the base and to the side (Vanhecke, 1974). Of the four species currently held in the Millennium Seed Bank, seed weight (per thousand) ranges from 3.38 g for *L. laterale* to 7.05 g for *L. urophorum* (Royal Botanic Gardens Kew, 2008). These relatively small nutlets are more likely to be removed by ants (Westoby *et al.*, 1990).

Only those nutlets naturally released from the inflorescence were considered developed by Wheeler and Bruhl (2000), an observation generally supported by Kodym *et al.* (2010). Pollen viability was very high (90–95 %) while nutlet viability was very low for *L. clipeicola* (0.5 %), and higher for *L. elatius* (72 %) and *L. laterale* (62 %), although no fruits were germinable due to an inability to overcome dormancy mechanisms (Wheeler and Bruhl, 2000).

In most *Lepidosperma* species, nutlets do not readily germinate without specific dormancy-breaking methods (Bell *et al.*, 1993; Kodym *et al.*, 2010; Dixon, 2011). Kullmann (1981) recorded some germination for *L. gladiatum* in pot trials, with seedlings emerging between 53 and 72 d after sowing. Many broad studies of natural germination rates have found very low recruitment for *Lepidosperma* species, even in cases where they are common components of the ecosystem (Lunt, 1997; Wang, 1997; Pettit and Froend, 2001; Fisher *et al.*, 2009). Roche *et al.* (1997) found low levels of nutlet viability and no germination of *Lepidosperma* species was achieved from smoke treatments or non-smoke controls. Penman *et al.* (2008) found a significant germination response to heat treatment and a marginally significant germination response to smoke treatment for *L. laterale* from near Eden in New South Wales. Enright *et al.* (1997) found an occasional germination response to smoke in *L. laterale* from the Grampians National Park, western Victoria. Wills and Read (2002) found a germination response to heat treatment for *L. sieberi* (as *L. concavum*) from Gippsland, Victoria. Ward *et al.* (1997) found no response to heat or smoke in nutlets of *L. tenue* (= *L. leptostachyum*) from un-mined jarrah forest. However, they noted that the nutlets were collected in summer and as most fertile nutlets fall in late spring, they may have been using infertile nutlets. Physical disturbance of the soil seed bank of *L. gladiatum*, a species of coastal sand dunes, has been observed to promote increased germination (K. W. Dixon, pers. comm.).

Nutlet removal and dispersal

Lepidosperma nutlets have persistent hypogynous scales at the base that act as an elaiosome for ant dispersal (Berg, 1975; Barton, 1994). Local dispersal is probably due to ants

(which collect fallen nutlets) and birds (which take nutlets directly from the inflorescence), with long-distance dispersal most likely attributable to birds. Berg (1975) suggests that myrmecochory is a very important component in the distribution of these species and in maintaining habitat diversity. The hypogynous scales at the base of the nutlets of *L. australe* can become quite spongy and Edgar (1970) and Thorsen *et al.* (2009) suggest that this aids dispersal of the nutlets by water (hydrochory).

ECOLOGICAL ASSOCIATIONS

The nature of ecological associations can vary greatly. This section of the review attempts to detail the current knowledge of ecological associations for the genus *Lepidosperma*. Most recorded associations are with larger animals that have been well studied (mammals and birds in particular), although there are also a significant number of associations with insects and fungi recorded in the literature. This review attempts to assess the relative importance of *Lepidosperma* species to all organisms that are recorded in association with them. Current research suggests that a significant number of *Lepidosperma* species are short-range endemics (with a total range of less than 100 km²) (e.g. Barrett *et al.*, 2009). Where these species are hosts for species-specific taxa such as Elachistine moths (Kaila, 2011), these species will also be intrinsically rare and all the more vulnerable to climatic fluctuations and ecosystem disturbance.

Mammal associations

Twenty-six mammal species in Australia have been recorded making use of *Lepidosperma* species as detailed in Table 2 and references cited there. Two are recorded as making use of *Lepidosperma* tussocks as nest sites, including Gilbert's potoroo (*Potorous gilbertii*) and the western ringtail possum (*Pseudocheirus occidentalis*). Seven *Lepidosperma* species form part of the diet of five mammal species: swamp rat (*Rattus lutreolus*), western grey kangaroo (*Macropus fuliginosus*), common wombat (*Vombatus ursinus*), the endangered quokka (*Setonix brachyurus*) and the introduced common fox (*Vulpes vulpes*). The habitat or occurrence of 24 mammal species is specifically recorded as being associated with *Lepidosperma* species. These include a number of small mammals that depend on dense cover for shelter. The *Lepidosperma* plants probably also provide habitat for the prey of many species, although this has not been specifically documented.

Dense stands of *Lepidosperma* species can form stable habitats that are important to the long-term survival of a number of rare and threatened mammal species. *Lepidosperma* species provide habitat for the critically endangered Gilbert's potoroo and endangered quokka (along with a number of Australia's rarest birds; see below). Both species are found in dense vegetation cover in long-unburnt areas where along with the dominant rush *Anarthria scabra*, *Lepidosperma* species form an important component of the understorey (Vetten, 1996; Courtenay and Friend, 2004). The potoroo's nesting sites are usually under a dense cover of sedges (Friend, 2008). This species was considered extinct for

TABLE 2. *Mammal species associated with Lepidosperma*

| Mammal species | <i>Lepidosperma</i> | Community type | Location | Part | Use | References |
|--|--|---|--|---------------|---------------------|------------|
| Gilbert's potoroo – <i>Potorous gilbertii</i> (CE) | <i>L. spp.</i> | Long-unburnt dense vegetation | Two Peoples Bay, Western Australia | – | Habitat, nesting | 1, 2, 3 |
| Gilbert's potoroo (CE) Quokka – <i>Setonix brachyurus</i> (V) | <i>L. gladiatum</i> | Fringing vegetation | Bald Island, southern Western Australia | – | Habitat, refuge | 4 |
| Long-nosed potoroo – <i>Potorous tridactylus</i> (V); Australian swamp rat – <i>Rattus lutreolus</i> | <i>L. laterale</i> | Sedgeland | SW Victoria | – | Habitat | 5 |
| Tasmanian bettong – <i>Bettongia gaimardi</i> subsp. <i>cuniculus</i> (E in Tasmania) | <i>L. longitudinale</i> | Sedgeland | Tasmania | – | Habitat | 6 |
| Eastern barred bandicoot – <i>Perameles gunnii</i> (V) | <i>L. laterale</i> | Open woodland | E Tasmania | – | Habitat | 7 |
| Eastern barred bandicoot (E) | Large <i>L. spp.</i> | Dense ground cover | S Victoria | – | Habitat | 8 |
| Pacific rat – <i>Rattus exulans</i> | <i>L. australe</i> | | Stewart Island, New Zealand | – | Habitat | 9 |
| Australian swamp rat; bush rat – <i>Rattus fuscipes</i> | <i>L. spp.</i> | Sedgeland | New South Wales | – | Habitat | 10 |
| Australian swamp rat | <i>L. filiforme, L. spp.</i> | Sedgeland | | Rhizomes | Food, habitat | 11, 12 |
| Broad-toothed rat – <i>Mastacomys fuscus</i> (NT) | <i>L. spp.</i> | Sedgeland | New South Wales, Victoria, Tasmania | – | Habitat | 13 |
| Smoky mouse – <i>Pseudomys fumeus</i> | <i>L. filiforme</i> | Sedgeland | | – | Habitat | 14 |
| New Holland mouse – <i>Pseudomys novaehollandiae</i> (V) | <i>L. sieberi</i> (as <i>L. concavum</i>), <i>L. filiforme</i> | | Tasmania | | Habitat | 14 |
| New Holland mouse (V) | <i>L. semiteres</i> | Sedgeland | S Victoria | – | Habitat | 15, 16, 17 |
| White-footed dunnart – <i>Sminthopsis leucopus</i> (V in Victoria); swamp antechinus – <i>Antechinus minimus</i> subsp. <i>maritimus</i> (NT in Victoria); other mammals | <i>L. filiforme, L. laterale, L. semiteres</i> | | Otway Ranges, Victoria | | Habitat | 18, 19, 20 |
| Brown antechinus – <i>Antechinus stuartii</i> | <i>L. urophorum</i> | Dense understorey | SE New South Wales | | | 21 |
| Kangaroo Island dunnart – <i>Sminthopsis aitkeni</i> (E) | <i>L. spp.</i> | Dense understorey | Kangaroo Island, SA | | | 22 |
| Western grey kangaroo – <i>Macropus fuliginosus</i> | <i>L. tenue</i> (?= <i>L. leptostachyum</i>), <i>L. angustatum</i> (= <i>L. sp. aff. squamatum</i>) | Jarrah forest | Perup area, Western Australia | Culms, leaves | Food | 23 |
| Western grey kangaroo; red-necked wallaby – <i>Macropus rufogriseus</i> | <i>L. carphoides</i> | | Grampians, Victoria | | Habitat (minor) | 24 |
| Parma wallaby – <i>Macropus parma</i> (R in New South Wales) | <i>L. limicola</i> | Sedge swamps | Gibraltar Range National Park, New South Wales | | Habitat (unusual) | 25 |
| Tammar wallaby – <i>Macropus eugenii</i> | <i>L. spp.</i> | Dense vegetation | | | Day shelter | 26 |
| Quokka (V) | <i>L. effusum</i> (? & <i>L. persecans</i>) | Wet forest | SW Western Australia | | Protective habitat | 27, 28 |
| Quokka (V) | <i>L. squamatum</i> (s.l.) & <i>L. tetraquetrum</i> | Wet forest | SW Western Australia | Culms, leaves | Food | 29 |
| Common wombat – <i>Vombatus ursinus</i> | <i>L. viscidum</i> | Mallee, heath | Messent Conservation Park, South Australia | Culms, leaves | Food | 30 |
| Western ringtail possum – <i>Pseudocheirus occidentalis</i> (V) | <i>L. spp.</i> | Dense sedges | Western Australia | Tussocks | Nesting sites | 31 |
| Little pygmy possum – <i>Cercartetus lepidus</i> | <i>L. sieberi</i> (as <i>L. concavum</i>) | Dense understorey | Tooms, E Tasmania | | Habitat | 32 |
| Dibbler – <i>Parantechinus apicalis</i> (E) | <i>L. gladiatum</i> | Long-unburnt heath | WA Islands | | Habitat | 33 |
| Leadbeater's possum – <i>Gymnobelideus leadbeateri</i> (E) | <i>L. elatius</i> | Sedge-rich <i>Eucalyptus camphora</i> swamp (E) | Victoria | | Habitat association | 34 |
| Flute-nosed bat – <i>Murino florium</i> (R) | <i>L. laterale</i> | Open forest | N Queensland | | Habitat association | 35 |
| European fox – <i>Vulpes vulpes</i> | <i>L. gladiatum</i> | | Cape Woolamai, Victoria | Leaves | Food | 36 |

Abbreviations: V, Vulnerable; E, Endangered; CE, Critically Endangered; NT, Near Threatened; R, Rare. These categories refer to current National listings under the *Environment Protection and Biodiversity Conservation Act 1999* (the EPBC Act, Australia) unless otherwise specified. Geographical abbreviations: NZ, New Zealand; SA, South Australia; WA, Western Australia.

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around 100 years before being rediscovered near Two Peoples Bay on the southern coast of Western Australia (Sinclair *et al.*, 1996). Bald Island is a small Western Australian island with a large amount of fringing vegetation dominated by *L. gladiatum* (Abbott, 1980), a species that provides refugial habitat for the Gilbert's potoroo and quokka. *Lepidosperma* species, which dominate sedgeland or the understorey of woodlands, form a major habitat for a number of rare species including the Tasmanian bettong (*Bettongia gaimardi cuniculus*), a species now extinct on the mainland (Taylor, 1992), the eastern barred bandicoot (*Perameles gunnii*), New Holland mouse (*Pseudomys novaehollandiae*), Kangaroo Island dunnart (*Sminthopsis aitkeni*), white-footed dunnart (*Sminthopsis leucopus*) and the swamp antechinus (*Antechinus minimus* subsp. *maritimus*) (Table 2).

Within habitats dominated by sedges, further segregation of mammal species can be found. The swamp rat (*Rattus lutreolus*) and bush rat (*Rattus fuscipes*) are both found in sedgeland in New South Wales that includes *Lepidosperma* species. However, the behaviour of the swamp rat effectively excludes the bush rat from the wetter sedgeland habitats (low, open vegetation dominated by Cyperaceae and Restionaceae) dominated by different *Lepidosperma* species (Lunney, 2008). The swamp rat is the only species recorded eating the rhizomes of a *Lepidosperma* species (*L. filiforme*) providing the marsupial rat with an important food resource (Braithwaite *et al.*, 1978; Cockburn, 1981). Evergreen sedges can be an important dietary component for animals such as the western grey kangaroo, particularly once annual plant species have senesced (Shepherd *et al.*, 1997). Under drought conditions, the rare species *L. rupestre* is heavily grazed by kangaroos in the Kalbarri Gorge, Murchison River (R. L. Barrett, R. D. Phillips and A. Faber, pers. obs.).

The western ringtail possum is usually found in areas with good coverage of *Lepidosperma* species in the understorey and may nest on the ground where these sedges are particularly dense (de Tores, 2008a). The endangered dibbler (*Parantechinus apicalis*) survives in long-unburnt heath communities where it is not especially habitat-specific, but does inhabit *L. gladiatum* thickets on islands in Western Australia (Bencini *et al.*, 2001). The flute-nosed bat (*Murino florium*), a rare species from northern Queensland, is occasionally found in habitats with an understorey containing *L. laterale* (s.l.) (Kutt and Schulz, 2000). It is unlikely that this plant species is of any particular importance to the bat in these locations, but it is possible that the sedge provides habitat for insects on which the bat feeds. It is interesting that the introduced fox (*Vulpes vulpes*) has been recorded as regularly consuming the leaves of *L. gladiatum* on Cape Woolamai, Victoria (Norman, 1971).

Bird associations

Forty-three bird species in Australia and New Zealand have been noted making use of *Lepidosperma* species (Table 3, and references cited there). Thirteen are recorded as making use of *Lepidosperma* tussocks as nest sites. These records include the little penguin (*Eudyptula minor*) and short-tailed shearwater (*Puffinus tenuirostris*), with *L. gladiatum* in Western Australia and *L. laterale* in Tasmania providing protective

cover and stability for sandy burrow substrates. Eleven bird species noted as nesting among *Lepidosperma* species are mainly found in coastal thickets and dense forest understorey vegetation. These birds include the endangered western whipbird (*Psophodes nigrogularis leucogaster* and *nigrogularis*), Mt Lofty Ranges subspecies of the southern emu-wren (*Stipiturus malachurus intermedius*), rufous bristlebird (*Dasyornis broadbenti*) and the vulnerable noisy scrub-bird (*Atrichornis clamosus*, Fig. 5). The actual *Lepidosperma* species involved is not specified in most records, although pilotbirds (*Pycnoptilus floccosus*) are recorded as nesting in *L. elatius* and noisy scrub-birds in *L. sp.* Manypeaks Large (R. L. Barrett RLB 2476) (recorded as *L. longitudinale* or *L. persecans*). Four of the birds nesting in *Lepidosperma* species have also been noted to incorporate *Lepidosperma* leaf material in their nest construction (the rufous bristlebird, pilotbird, noisy scrub-bird and western whipbird). The noisy scrub-bird is known to utilize *L. effusum*, *L. gladiatum*, *L. sp.* Manypeaks Large (R. L. Barrett RLB 2476) and the unusual *L. tetraquetrum*, which has rigid, four-angled culms that are flattened for nest construction (S. Comer, pers. comm.).

Ten *Lepidosperma* species form part of the diet of 12 bird species: emu (*Dromaius novaehollandiae*), southern emu wren (*Stipiturus malachurus*), three finch/firetail species and seven parrots, including the endangered New Zealand kakapo (*Strigops habroptilus*). The record of emus eating the nutlets of *L. carphoides* is particularly interesting, as emus are noted long-distance dispersers of plant species (e.g. Calviño-Cancela *et al.*, 2006; He *et al.*, 2008). The habitat or occurrence of a further 17 bird species is specifically recorded as associated with *Lepidosperma* species; these include many small forest understorey insectivores, including the grey fantail (*Rhipidura fuliginosa*) and four fairy wren species (*Malurus* spp.) as well as endangered ground-layer birds such as the spotted quail-thrush (*Cinlosoma punctatum anachoreta*) and western bristlebird (*Dasyornis longirostris*). It is also of interest that there are no records of a number of granivorous birds such as doves and pigeons feeding on *Lepidosperma* fruit, but this may be due to a lack of precise observations at the right time of year rather than an absence of utilization.

Reptile associations

Lepidosperma clipeicola is an important habitat plant for an arboreal snake, Stephens' banded snake (*Hoplocephalus stephensii*). This snake spends a great deal of its foraging time in the culms of *L. clipeicola* (Fitzgerald *et al.*, 2002a, b). Prey species of this threatened snake are regularly caught while among dense stands of *L. clipeicola* culms and maintenance of healthy populations of this sedge are important for the long-term survival of the snake (Fitzgerald *et al.*, 2004).

The federally endangered Blue Mountains water skink (*Eulamprus leuraensis*) inhabits swamps dominated by sedges including *L. limicola*, and protection of these habitats is critical for the long-term survival of the skink (Keith and Benson, 1988; LeBreton, 1996; NPWS, 2001). Along with the helmeted honeyeater (*Lichenostomus melanops* subsp. *casidix*), the vulnerable swamp skink (*Egernia coventryi*) is

TABLE 3. Bird species associated with *Lepidosperma*

| Bird species | <i>Lepidosperma</i> | Community type | Location | Part | Use | References |
|---|---|---------------------------------|-----------------------------------|------------------|---------------------------------------|---|
| Emu – <i>Dromaius novaehollandiae</i> | <i>L. carphoides</i> | Heath | Victoria | Fruit | Food | 1, 2, 3 |
| Burrow-nesting seabirds – penguins, shearwaters, petrels and gulls | <i>L. gladiatum</i> | Islands, coastal dunes | Michaelmas Is., Western Australia | Sward | Nest habitat stability / cover | 4 |
| Short-tailed shearwater – <i>Puffinus tenuirostris</i> ; Little penguin – <i>Eudyptula minor</i> | <i>L. laterale</i> | Coastal dunes | Cape Queen Elizabeth, Tasmania | – | Nest habitat stability/cover | 5 |
| Australasian bittern – <i>Botaurus poiciloptilus</i> (E) | <i>L. effusum</i> | Lake edges | Lake Muir, Western Australia | – | Habitat | 6 |
| White-throated treecreeper – <i>Cormobates leucophaea</i> ; superb fairy-wren – <i>Malurus cyaneus</i> ; grey shrike-thrush – <i>Colluricincla harmonica</i> ; grey fantail – <i>Rhipidura fuliginosa</i> | <i>L. laterale</i> | Vegetation community boundaries | Southern Victoria | – | Habitat | 7 |
| Red-browed finch – <i>Neochmia temporalis</i> | <i>L. carphoides</i> <i>L. tetraquetrum</i> | Creeklines, heath | SW Western Australia | Fruit | Food | 8, 9, 10, 11, 12 |
| Beautiful firetail – <i>Stagonopleura bella</i> ; red-eared firetail – <i>Stagonopleura oculata</i> | <i>L. angustatum</i> , <i>L. gladiatum</i> , <i>L. persecans</i> | Forest, coastal vegetation | SW Western Australia | Fruit | Food | 9, 13, 14, 15, 16 |
| Red-eared firetail | <i>L. angustatum</i> | Coastal vegetation | Southern Western Australia | Fruit | Habitat, food | 17, 18 |
| Western bristlebird – <i>Dasyornis longirostris</i> (E) | Large <i>L. spp.</i> | | Southern Western Australia | – | Habitat | 15, 19, 20, 21, 22 |
| Eastern bristlebird – <i>Dasyornis brachypterus</i> (E) | <i>L. forsythii</i> | Unburnt habitats | | – | Habitat | 23 |
| Rufous bristlebird – <i>Dasyornis broadbenti</i> (E) | <i>L. [elatius]</i> , <i>L. laterale</i> , <i>L. gladiatum</i> <i>L. sp.</i> | Coastal areas | Victoria | Swards | Habitat, nest material | 22, 24, 25, 26 |
| Pilotbird – <i>Pycnoptilus floccosus</i> | <i>L. elatius</i> | Wet forests | Southern Victoria | Tussocks,leaves | Preferred habitat, nest site/material | 27, 28, 29, 30 |
| Ground parrot – <i>Pezoporus wallicus</i> | <i>L. sp.</i> | Heath | SE Australia | Fruit | Food | 31, 32 |
| Ground parrot | <i>L. filiforme</i> | Heath | Tasmania | Fruit | Food | 33, 34 |
| Western ground parrot – <i>Pezoporus flaviventris</i> (E) | Unnamed sp. (as <i>L. brunonianum</i>) | Heath | Western Australia | Fruit | Food | 35, 36 |
| Crimson rosella – <i>Platycercus elegans</i> | <i>L. laterale</i> <i>L. spp.</i> | Various Gardens | SE Australia | Fruit | Food | 34, 37, 38 |
| Eastern rosella – <i>Platycercus eximius</i> | <i>L. laterale</i> | | SE Australia | Fruit | Food | 34, 39 |
| Orange-bellied parrot – <i>Neophema chrysogaster</i> (juveniles) (CE) | <i>L. filiforme</i> | | SE Australia | Fruit | Food | 34, 40 |
| Orange-bellied parrot (CE) | <i>L. spp.</i> <i>L. gladiatum</i> | <i>L. sedgelandis</i> | South Australia | Fruit | Habitat, food | 41 |
| Turquoise parrot – <i>Neophema pulchella</i> | <i>L. laterale</i> | | SE Australia | Fruit | Food | 34, 42 |
| Kakapo – <i>Strigops habroptilus</i> (E in New Zealand) | <i>L. australe</i> | | Codfish, Stewart Is., New Zealand | Culms | Food | 43 |
| Noisy scrub-bird – <i>Atrichornis clamosus</i> (V) | <i>L. sp.</i> Many peaks Large (R. L. Barrett R-LB 2476) (as <i>L. longitudinale</i> or <i>L. persecans</i>); <i>L. effusum</i> , <i>L. gladiatum</i> , <i>L. tetraquetrum</i> | Dense shrubland, wet gullies | East of Albany, Western Australia | Tussocks, leaves | Nest site and material | 15, 44, 45, 46, 47, 48, 49, S. Comer, pers. comm. |
| Western whipbird – <i>Psophodes nigrogularis</i> subsp. <i>leucogaster</i> & subsp. <i>nigrogularis</i> (V) | <i>L. spp.</i> | | | Tussocks | Nest site, nest material | 50, 51, 52, 53 |
| Superb fairy-wren – <i>Malurus cyaneus</i> ; splendid fairy-wren – <i>M. splendens</i> ; southern emu-wren – <i>Stipiturus malachurus</i> | | Swamp margins | | – | Habitat | 49 |
| Superb fairy-wren | Large species | | | Tussocks | Nest site | 54, 55 |
| Variiegated fairy-wren – <i>Malurus lamberti</i> | <i>L. spp.</i> | Wet gullies | | | Habitat | 56 |

Continued

TABLE 3. *Continued*

| Bird species | <i>Lepidosperma</i> | Community type | Location | Part | Use | References |
|---|--|--|--------------------------|---------------------|-------------------------------------|------------|
| Blue-breasted fairy-wren – <i>Malurus pulcherrimus</i> | <i>L. sp.</i> | | Western Australia | Tussocks | Nest site | 57 |
| Red-winged fairy-wren – <i>Malurus elegans</i> | <i>L. effusum</i> , <i>L. longitudinal</i> , <i>L. persecans</i> , ? <i>L. tetraquetrum</i> | Dense <i>L. spp.</i> stands, stream & swamp margins | SW Western Australia | | Habitat | 49, 58, 59 |
| White-winged fairy-wren – <i>Malurus leucopterus</i> | <i>L. sp.</i> ; probably <i>L. gladiatum</i> | Coastal heath | SW Western Australia | | Occasional habitat | 49 |
| Mt Lofty Ranges southern emu-wren – <i>Stipiturus malachurus</i> subsp. <i>intermedius</i> (E) | <i>L. longitudinale</i> | Open wet forest | South Australia | Fruit, tussocks | Food, nest site | 60, 61 |
| Eyre Peninsula southern emu-wren – <i>Stipiturus malachurus</i> subsp. <i>parimeda</i> (V) | <i>L. viscidum</i> | Low woodland, mallee | South Australia | | Habitat | 62 |
| Striated fieldwren – <i>Calamanthus fuliginosus</i> | <i>L. spp.</i> | Regrowth understorey | | Tussocks | Occasional nesting | 63 |
| Striated Thornbill – <i>Acanthiza lineata</i> ; jacky winter – <i>Microeca fascians</i> ; crested shrike-tit – <i>Falcunculus frontatus</i> ; rufous whistler – <i>Pachycephala rufiventris</i> | | Forests | Bega, New South Wales | | Habitat | 64 |
| Spotted quail-thrush – <i>Cinlosoma punctatum</i> subsp. <i>anachoreta</i> (CE) | <i>L. semiteres</i> | Open eucalypt woodland | | | Habitat | 65 |
| Helmeted honeyeater – <i>Lichenostomus melanops</i> s- ubsp. <i>cassidix</i> (E); Lewin's rail – <i>Rallus pectoralis</i> (E); spotless crane – <i>Porzana tabuensis</i> ; southern emu-wren | <i>L. laterale</i> <i>L. spp.</i> | Sedge-rich <i>Eucal-</i> <i>yptus camphora</i> swamp | Victoria | | Co-occurrence, nes- ting habitat | 66, 67 |
| Yellow-throated honeyeater – <i>Lichenostomus flavicollis</i> | <i>L. sp.</i> | | N Tasmania | Tussocks, leaves | Nest site, nest material | 68, 69 |
| Spotted pardalote – <i>Pardalotus punctatus</i> | <i>L. spp.</i> | | | | Habitat | 64, 70 |

Abbreviations: V, Vulnerable; E, Endangered; CE, Critically Endangered. These categories refer to current National listings under the *Environment Protection and Biodiversity Conservation Act 1999* (the EPBC Act, Australia) unless otherwise specified.

References: 1. Quin, 1984. 2. Marchant and Higgins, 1990. 3. Davies, 2002. 4. Abbott, 1981. 5. Walsh *et al.*, 1997. 6. Lane *et al.*, 1996. 7. Berry, 2001. 8. Immelmann, 1962. 9. Immelmann, 1967. 10. Dell, 1965. 11. Read, 1987. 12. Read, 1994. 13. Immelmann, 1960. 14. Pepper, 1964. 15. Johnstone and Storr, 2004. 16. Higgins *et al.*, 2006. 17. Nichols *et al.*, 1982. 18. Bamford, 1989. 19. Smith and Moore, 1977. 20. McNee, 1986. 21. Smith, 1987. 22. Higgins and Peter, 2002. 23. Campbell, 1906. 24. Du Guesclin *et al.*, 1995. 25. Peter, 1999. 26. Baker, 2000. 27. Anon., 1908. 28. Howe, 1915. 29. Zwart, 1973. 30. Smith, 1984. 31. Meredith *et al.*, 1984; 32. Forshaw, 2002. 33. Bryant, 1994. 34. Higgins, 1999. 35. Barth, 2007. 36. Murphy *et al.*, 2011. 37. Lepschi, 1993. 38. Knight, 2000. 39. Rose, 1997. 40. Brown and Wilson, 1984. 41. Clarke, 2004. 42. Quin, 1990. 43. Wilson, 2004. 44. Webster, 1963. 45. Smith and Robinson, 1976. 46. Smith, 1985. 47. Danks *et al.*, 1996. 48. Smith, 1996. 49. Higgins *et al.*, 2001. 50. Howe and Ross, 1933. 51. Bryant, 1938. 52. Woinarski *et al.*, 1988. 53. Smith, 1991. 54. Dove, 1910a. 55. Dove, 1910b. 56. Schodde, 1996. 57. Brooker and Brooker, 2001. 58. Payne *et al.*, 1991. 59. Rowley *et al.*, 1988. 60. Littlely and Cutten, 1994. 61. Westphal *et al.*, 2003. 62. Pickett, 2002. 63. Dove, 1912. 64. Smith, 1984. 65. Garnett and Crowley, 2000. 66. Pearce and Minchin, 2001. 67. Turner and Rylah, 2003. 68. Dove, 1915. 69. Dove, 1917. 70. Higgins and Peter, 2002.



FIG. 5. Nest of the vulnerable noisy scrub-bird (*Atrichornis clamosus*) built in, and with leaves of, the rare sedge *Lepidosperma* sp. Manypeaks Large (R. L. Barrett RLB 2476), Manypeaks Range, Western Australia. (A) Female on 'runway' of nest (photo: Graeme Chapman). (B) Nest made primarily from sedge leaves (photo: Sarah Comer).

found in a sedge-rich *Eucalyptus camphora* swamp with *L. laterale*, a habitat that is listed as endangered in Victoria (Turner and Rylah, 2003). Three skink species are found in *Eucalyptus regnans* forest with an understorey including *L. elatius*: the southern forest cool-skink (*Niveoscincus coventryi*), the southern water skink (*Eulamprus tympanum*) and the trunk-climbing cool-skink (*Pseudemoia spenceri*) (Brown and Nelson, 1993). Reptile ecology is poorly understood in these forest ecosystems and habitat complexity is considered critical to maintaining animal diversity (Lindenmayer, 2009). Michael *et al.* (2010) have shown that many reptile species occurring on granite outcrops require specific rock structures and specific vegetation structures to maintain viable populations and this needs to be considered in the management of granite outcrops where *Lepidosperma* species are often prominent.

Amphibian associations

Lepidosperma concavum has been recorded as potential breeding habitat for the vulnerable green and golden bell frog (*Litoria aurea*) on Bowen Island in New South Wales (Osborne and McElhinney, 1996). The rare Nornalup frog (*Geocrinia lutea*) and Karri frog (*G. rosea*) can be found calling from stands of *L. effusum* and *L. tetraquetrum* (Wardell-Johnson and Roberts, 1993). Lea's frog (*Geocrinia leai*) often lays its eggs in sedges overhanging wetlands and waterways (Pen, 1999). The slender tree frog (*Litoria adelaidensis*) requires dense vegetation including sedges fringing waterways for protective habitat (Pen, 1999).

Insect associations

The presence or absence of butterflies and moths with species- or genus-specific plant associations can be useful indicators in ecological restoration projects (Lomov *et al.*, 2006). The three-spot skipper butterfly (*Motasingha trimaculata*) is dependent on

Lepidosperma and *Phlebocarya* (Haemodoraceae) species as larval food plants and female adults remain close to these food plants (Symon, 1980; Braby, 2000; Sands and New, 2002).

The moth genus *Elachista* has a number of species with larvae dependent on *Lepidosperma* species and Kaila and Ståhls (2006) indicated the possibility of species-specific inter-relationships with further studies of their taxonomy required. Kaila (2011) has now shown that there are indeed a large number of species-specific relationships between *Elachista* and *Lepidosperma*. At least 34 *Elachista* species depend on *Lepidosperma* species for their larval stage, forming distinctive mines in leaves (Fig. 6; Table 4). For many more species, the host plant remains unknown. Multiple *Elachista* species may utilize a single species of *Lepidosperma* by occupying different parts of the same leaf; however, in most cases, *Elachista* species are restricted to a single host species (Kaila, 2011). Due to the lack of taxonomic knowledge in the genus *Lepidosperma* and a lack of current identification tools, many of the host *Lepidosperma* species could not be fully identified by Kaila (2011) and a summary of the current taxonomy as far as can be interpreted is presented in Table 4. There are numerous moth species in tussock grasslands of New Zealand (including *Elachista* species) that have larval associations with Cyperaceae species, but the genera of Cyperaceae involved were usually not recorded, so the utilization of *Lepidosperma* species remains uncertain (White, 2002).

The magnificent sunmoth (*Synemon magnifica*) relies on *L. viscidum/L. concavum* (and possibly *L. laterale*) as a larval food plant with the larvae feeding on the rhizomes of the plant (Common and Edwards, 1981; Common, 1990; Zborowski and Edwards, 2007). The white-banded sunmoth (*Synemon directa*) is thought to breed on *L. gladiatum* (M. Williams, pers. comm.; ABRS, 2009). Larvae of the endangered graceful sunmoth *Synemon gratiosa* from the Perth region primarily feed on *Lomandra*, but is also reported to feed on *Lepidosperma* species (Burbidge, 2004). Larvae of

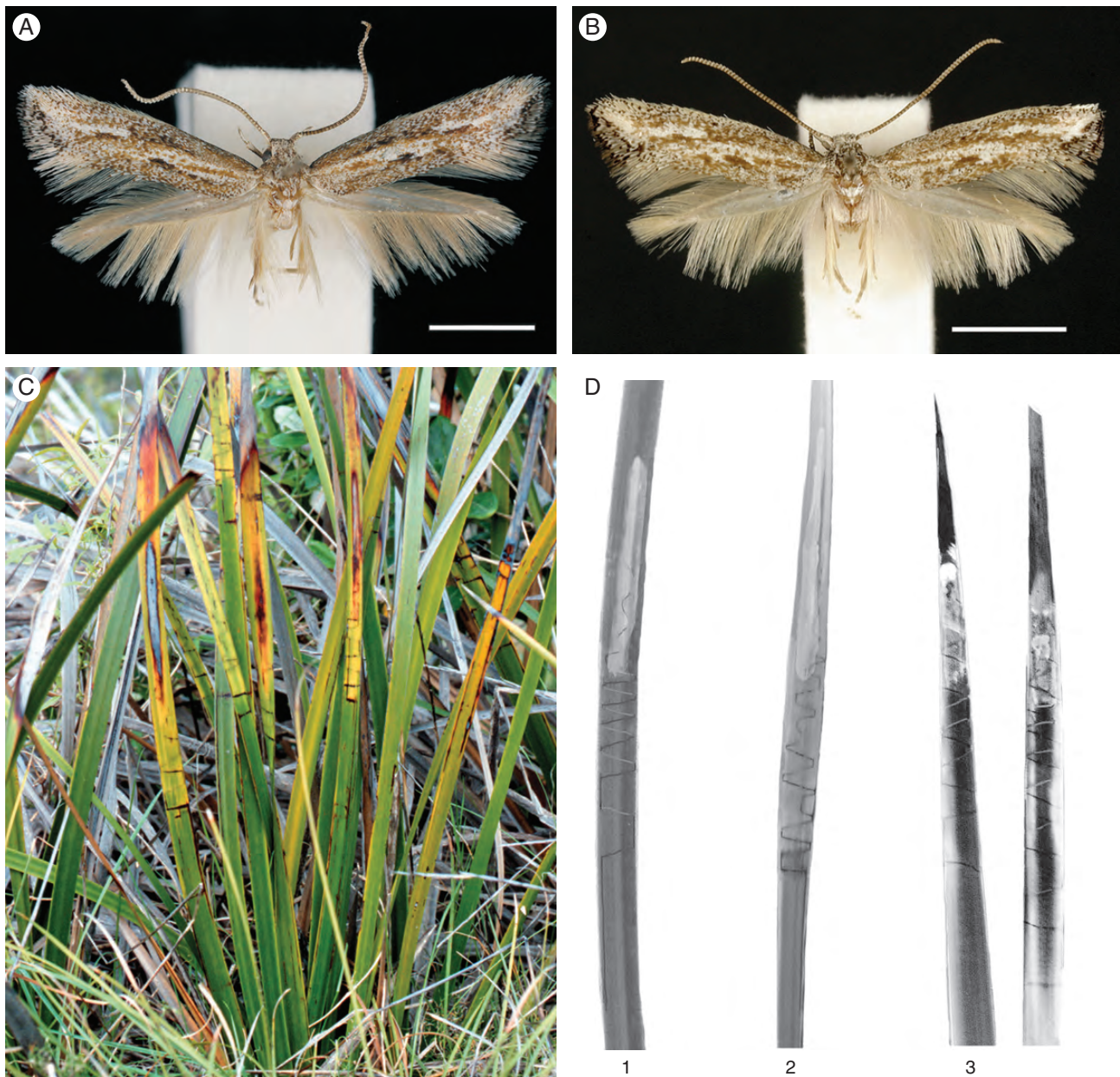


FIG. 6. Elachistine moths associated with *Lepidosperma* species. (A) *Elachista tetraquetri* (host = *L. tetraquetrum*); (B) *Elachista flavicilia* (host = *L. effusum*); (C) mines of *Elachista gladiograptia* on *L. gladiatum*; (D) (1) mines of *Elachista gladiatrix* on *L. gladiatum*; (2) *Elachista gladiograptia* on *L. gladiatum*; and (3) *Elachista spongicola* on *Machaerina arthropphylla* (photos: Lauri Kaila). Scale bars: A, B = 2 mm.

several other *Synemon* species are also known to feed on *Lepidosperma* species in Western Australia, but the exact species associations are yet to be determined (T. Edwards, pers. comm.). Larvae of *Synemon parthenoides* are known to feed on *L. carphoides* in South Australia and Victoria (Douglas, 2008). A newly recognized *Synemon* species, the Kangaroo Island sunmoth, restricted to Kangaroo Island, feeds on *L. viscidum* (Grund, 2011; A. Young pers. comm.; Fig. 7).

Larvae of several species of *Miscera* also feed on the rhizomes of *Lepidosperma* species, including *M. desmotoma*

and two undescribed species in Victoria and *M. centropis* in Western Australia (Kallies, 2004; Zborowski and Edwards, 2007; T. Edwards, pers. comm.; A. Kallies, pers. comm.). Larvae of a *Miscera* species have been observed feeding on the roots of the rare species *L. gibsonii* when grown in pots in a glasshouse in Perth, but the origin of the moths is uncertain (B. Miller, pers. comm.). The sedge moth *Glyphipterix gemmipunctella* also feeds on several *Lepidosperma* species in eastern Australia (A. Kallies, pers. comm.).

While morabine grasshoppers are polyphagous, studies by Blackith and Blackith (1966) suggest that *L. gladiatum*, a

TABLE 4. Updated nomenclature for *Lepidosperma* species with dependent species of *Elachista* (Kaila, 2011).

| <i>Elachista</i> species | Host <i>Lepidosperma</i> | Revised identification |
|---|---|--|
| <i>E. bidens</i> | <i>L. tuberculatum</i> | No change |
| <i>E. carcharota</i> | <i>L. concavum</i> and possibly also <i>L. congestum</i> | <i>L. sieberi</i> and <i>L. ?congestum</i> |
| <i>E. catagma</i> | <i>L. gladiatum</i> | No change |
| <i>E. chiloteria</i> | <i>L. tuberculatum</i> | No change |
| <i>E. crenatella</i> | <i>L. viscidum</i> | No change |
| <i>E. cylistica</i> | <i>L. sp.</i> | Probably <i>L. leptostachyum</i> , but may be <i>L. asperatum</i> , <i>L. pubisquameum</i> or <i>L. sp.</i> Darling Range Heath (K.L. Wilson 8926) |
| <i>E. cynopa</i> | <i>L. laterale</i> | This name currently includes several taxa |
| <i>E. deusta</i> | <i>L. ?elatius</i> | <i>L. effusum</i> |
| <i>E. effusi</i> | <i>L. gladiatum</i> and <i>L. effusum</i> | <i>L. gladiatum</i> and probably <i>L. persecans</i> |
| <i>E. epartica</i> | <i>L. concavum</i> and <i>L. viscidum</i> | <i>L. ?latens</i> and <i>L. aff. concavum</i> |
| <i>E. eriodes</i> | <i>L. sp. (concavum/congestum)</i> | <i>L. sp. ?several choices in this area</i> |
| <i>E. etorella</i> | <i>L. gladiatum</i> , <i>L. effusum</i> + various <i>Lepidosperma</i> | <i>L. gladiatum</i> , <i>L. ?persecans</i> , <i>L. sp.</i> Coastal Dunes (R.J. Cranfield, 9963), <i>L. sp.</i> Sand Dunes (R. L. Barrett <i>et al.</i> RLB 5034) |
| <i>E. faberella</i> | <i>L. longitudinale</i> | Eastern form |
| <i>E. flavicilia</i> | <i>L. ?elatius</i> | <i>L. effusum</i> |
| <i>E. floccella</i> | <i>L. laterale</i> | 2 species |
| <i>E. gladiatrix</i> | <i>L. gladiatum</i> | No change |
| <i>E. gladiograptia</i> | <i>L. gladiatum</i> | No change |
| <i>E. illota</i> | Two unidentified relatively small <i>Lepidosperma</i> species | <i>L. sp.</i> Sand Dunes (R. L. Barrett <i>et al.</i> RLB 5034) and <i>L. sp.</i> |
| <i>E. lachnella</i> | <i>L. longitudinale</i> | Eastern form |
| <i>E. magidina</i> | <i>L. laterale</i> and <i>L. elatius</i> | No change (<i>s.l.</i>) |
| <i>E. melanthes</i> | <i>L. semiteres</i> | No change |
| <i>E. ophelma</i> | <i>L. gladiatum</i> | No change |
| <i>E. paragauda</i> | <i>L. concavum</i> and <i>L. laterale</i> | May be <i>L. concavum</i> or <i>L. sieberi</i> . |
| <i>E. paryphoea</i> | <i>L. curtisiae</i> and <i>L. sp. nr. laterale</i> | Probably both are <i>L. spp. nov.</i> |
| <i>E. platysma</i> | <i>L. tuberculatum</i> | No change, plus <i>L. sp.</i> Jerdacuttup, <i>L. sp.</i> |
| <i>E. ruscella</i> | Several spp. | <i>L. sp.</i> Coastal Dunes (R.J. Cranfield, 9963) <i>L. sp.</i> Sand Dunes (R. L. Barrett <i>et al.</i> RLB 5034) and <i>L. sp.</i> |
| <i>E. spathacea</i> | <i>L. longitudinale</i> | Western form |
| <i>E. species A, E. melanthes</i> complex | <i>L. longitudinale</i> | Western form |
| <i>E. spongicola</i> | Presumably a <i>Lepidosperma</i> species | Probably <i>Schoenoplectus validus</i> |
| <i>E. stictifica</i> | <i>L. sp.</i> | <i>L. effusum</i> |
| <i>E. tetraquetri</i> | <i>L. tetraquetrum</i> | No change |
| <i>E. toralis</i> | <i>L. concavum</i> and <i>L. viscidum</i> | Probably = <i>L. sieberi</i> and <i>L. concavum</i> |
| <i>E. toryna</i> | <i>L. longitudinale</i> | Eastern ?and Western forms |
| <i>E. velutina</i> | <i>L. longitudinale</i> and ? <i>L. limicola</i> | Eastern form |

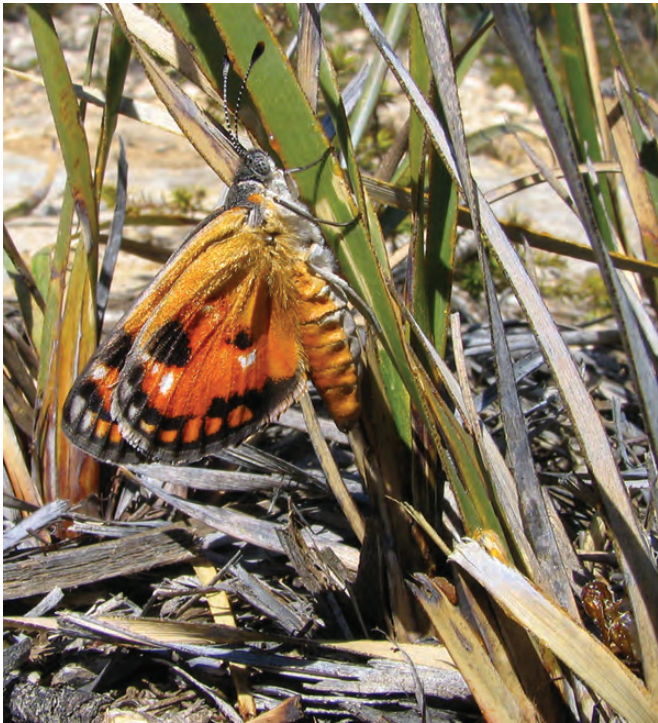


FIG. 7. The rare Kangaroo Island sun moth (*Synemon* sp.) on *Lepidosperma viscidum*, Kangaroo Island, South Australia. The larval casing can be seen in the bottom right of the image (photo: Andrew Young).

species naturally occurring in their habitat, is specifically avoided. Predation of *Lepidosperma* culms and leaves by insects has only been observed on rare occasions (R. L. Barrett, pers. obs.) and there may be some form of defence such as the flavonols identified by Harborne *et al.* (1985). The high silica concentration in the leaves and culms may also be an effective deterrent (Norton, 1967). Six grasshopper species are known to feed on *Lepidosperma* species, *Prospednura peninsularis* apparently feeding only on *L. laterale* (Rentz *et al.*, 2003; Table 5).

The katydid *Chlorodectes loquax* is associated with a *Lepidosperma* sp. in coastal New South Wales (possibly *L. concavum*) (Rentz, 1985). Seven of the 11 species of the katydid genus *Kawanaphila* (*K. gidya*, *K. goolwa*, *K. iyouta*, *K. mirla*, *K. nartee*, *K. ungarunya* and *K. yarraga*) are usually found in association with a variety of *Lepidosperma* species (including *L. carphoides* and *L. tenue*). The *Lepidosperma* species provide a protective habitat during the day with the katydids feeding on the pollen of a variety of plant species by night (Rentz, 1993, 2010). *Kawanaphila* species are possible dispersal agents for pollen due to hairs on their bodies effectively holding pollen (Rentz, 1993).

Many plant species have seeds that are distributed by ants. The activity of ants in native vegetation is very important and can be a key factor in the success of ecosystem function of restored communities (Grimbacher and Hughes, 2002). Berg (1975) appears to have been the first to observe myrmecochory in *Lepidosperma*, after recording a decorator ant [*Monomorium* (*Chelaner*) sp. cf. *rothsteini*] collecting the nutlets of a *Lepidosperma* species. Siddiqi *et al.* (1976)

TABLE 5. Grasshoppers known to feed on *Lepidosperma* species (Rentz *et al.*, 2003, and references therein)

| Grasshopper species | <i>Lepidosperma</i> food species |
|---|---|
| Western coastal pyrgomorph – <i>Monistria latevittata</i> | <i>L. gladiatum</i> |
| Western flag-face – <i>Prospednura eyrei</i> | <i>L. tuberculatum</i> |
| Eastern flag-face – <i>Prospednura peninsularis</i> | <i>L. laterale</i> |
| Variable psedna – <i>Psedna nana</i> | <i>L. sp.</i> [probably <i>L. longitudinale</i>] |
| Common psedna – <i>Psedna pedestris</i> | <i>L. longitudinale</i> |
| Musgrave's psedna – <i>Psedna musgravei</i> | <i>L. spp.</i> |

recorded ants dispersing the nutlets of *L. laterale*. Drake (1981) found that the ant *Aphaenogaster longiceps* collected significant numbers of *L. laterale* nutlets on North Stradbroke Island, Queensland, and noted the hypogynous scales to function as an elaiosome type. Rice and Westoby (1981) found that *L. elatius* is a myrmecochore and suggested that *L. filiforme*, *L. flexuosum*, *L. laterale*, *L. lineare*, *L. urophorum* and *L. viscidum* (= *L. concavum*) may also be myrmecochores. Ants from the genera *Iridomyrmex* and *Phedole* were observed to remove seeds of *L. laterale* in cafeteria experiments conducted in natural habitats on Bribie Island, south-eastern Queensland (Barton, 1994). French and Westoby (1996) recorded myrmecochory in *L. flexuosum*, *L. laterale* and *L. urophorum* in fire-prone sites in the Sydney region. Barton (1994) determined the presence of lipids in the hypogynous scales, confirming their role as an elaiosome.

In December 2009, in the Bald Knob State Forest, northern New South Wales, the author observed that ants (an *Iridomyrmex* sp.) rapidly collected ten nutlets of *L. laterale* (s.l.) that were picked ripe from the plant and dropped on bare ground in the vicinity of an ant nest. The whole nut was collected (the ants gripping the relatively large nutlets by the hypogynous scales) and taken into the nest (Fig. 8). No discarded nutlets or hypogynous scales were observed around the entrance to the nest.

A number of ants (*Chelaner*, *Iridomyrmex*, *Myrmecorhynchus*, *Prolasius*, *Solenopsis* and *Strumigenys* species) are most common in tall open forests, often with *L. elatius* dominant in the understorey in sites at Wilsons Promontory in Victoria (Andersen, 1986). The golden spiny ant (*Polyrhachis ammon*) regularly builds its nests in tussocks of *L. laterale* in woodland in New South Wales (Gibb and Hochuli, 2003). Other unidentified ants have been observed preferentially nesting in *Lepidosperma* tussocks in Western Australia (R. L. Barrett, pers. obs.).

While there are some records of native bees collecting pollen (Houston, 2000), *Lepidosperma* species are all considered to be wind pollinated, as are most Cyperaceae (Goetghebeur, 1998). There are some exceptions (Friedman, 2011), and more observations would be beneficial as it is likely that bees collecting pollen do occasionally cause pollination. The implications of wind pollination for speciation in monocotyledons have been widely discussed (see Barrett *et al.*, 2000; Friedman and Barrett, 2009a, b; and references therein).

Three native bee species have been recorded collecting pollen from *L. ?gladiatum*: *Amegilla pulchra* (Apidae),



FIG. 8. *Iridomyrmex* sp. collecting mature nutlets of *Lepidosperma laterale* (s.l.) in the Bald Knob State Forest, northern New South Wales. Nutlets were gripped by the white hypogynous scales, an elaiosome type recognized by Berg (1975).

Megachile macularis (Megachilidae) and *Stenotritus* sp. SM7 (Stenotritidae) (Houston, 2000). Given that the majority of *Lepidosperma* species rapidly flower *en masse* following season-breaking rains in late autumn in south-west Western Australia and in the Mediterranean climate parts of South Australia and south-west Victoria, at a time when relatively few native plants are flowering, this may well be a critical source of pollen for these and other bee species at this time of year. As *Lepidosperma* flowers are protogynous, these pollen-collecting bees are unlikely to cause pollination of *Lepidosperma* species. The introduced European Honey Bee (*Apis mellifera*, Apidae) has also been noted to collect pollen from *Lepidosperma* species (Paton, 1996) and collection of pollen of *L. gladiatum* has been observed in Perth suburbs (M. Wallace, pers. comm.).

The collembola species *Xenylla* cf. *obscura* has been found living in *Lepidosperma* tussocks in South Australia (da Gama, 1979). A scale insect *Paraonidiella cladii* (as *Chrysomphalus*) is known to feed on *Lepidosperma* species (Fernald, 1903). Other scale insects have been observed, but not formally identified (Fig. 9). Slater (1975, 1976) recorded *L. squamatum* (s.l.) (as *L. angustatum*) as a host plant for both nymphs and adults of the sap-sucking bug *Ontiscus obscurus* (Lygaeidae), which feeds on the nutlets of this species.

Snail associations

Regan *et al.* (2001) and Taylor *et al.* (2003) have recorded *L. elatius* as a component of the habitat of a rare land snail (*Tasmaphena lamproides*) in north-eastern Tasmania. The introduced common garden snail (*Helix aspersa*) is commonly found on *L. gladiatum* on the Swan Coastal Plain in Western Australia (R. L. Barrett, pers. obs.).

Arachnid associations

While sampling *Lepidosperma* specimens, a large number of unidentified spider species have been found foraging, or building webs in the tussock bases (R. L. Barrett, pers. obs.). One is most likely from the ground-dwelling spider genus *Miturga*



FIG. 9. Scale insect on the rare Kalbarri sword sedge (*Lepidosperma rupestre*), Kalbarri Gorge, Western Australia.

(Miturgidae) which commonly builds silken retreats in protected sites such as in sedge tussocks or at the base of shrubs (M. Rix, pers. comm.; Fig. 10). *Lepidosperma australe* is a habitat species for the rare red katipo spider (*Latrodectus katipo*) in New Zealand (Patrick, 2002). In Western Australia, five short-range endemic spiders, the synotaxid *Calcarsynotaxus benrobertsi*, the archaeids (assassin spiders) *Zephyrarchaea barrettiae*, *Z. melindae* and *Z. robinsi* and the malkarid *Perissopmeros darwini*, are all found under or near the shaded leaves of *Lepidosperma* species (mainly *L. sp.* Bluff Knoll Robust (G.J. Keighery 12595) and possibly *L. persecans*; Rix *et al.*, 2009; Rix and Harvey, 2012a; S. Barrett, pers. comm.). These spider species are only known from a few peaks and gullies in the Stirling Range National Park (Rix *et al.*, 2009; Rix and Harvey, 2012b). Similarly, Main's assassin spider *Zephyrarchaea mainae* is restricted to litter lodged in the



FIG. 10. Silken retreat from a juvenile ground-dwelling spider in the genus *Miturga* (Miturgidae) built in the base of a large *Lepidosperma* tussock, Mount Lesueur, Western Australia.

crown of Restionaceae species, *L. gladiatum* and *L. effusum*, which grow under long-unburnt stands of weeping peppermint (*Agonis flexuosa* (Willd.) Sweet; Rix and Harvey, 2009, 2012a). This habitat also supports a range of smaller spiders on which the assassin spiders feed (Rix and Harvey, 2009). Assassin spiders represent a relictual lineage with similar fossil relatives dating back to the Jurassic (150 Mya) (Platnick, 1991; Rix and Harvey, 2012a, b).

Freshwater organisms

Freshwater pools in creeks and rivers provide habitat for a wide range of organisms. In summer months, numerous animals, including fish, lampreys and freshwater crayfish, require shade provided by fringing vegetation during the day. Sedges such as *Lepidosperma* play an important role in many riparian areas (Pen, 1999). Three species of freshwater crayfish, the Dunsborough burrowing crayfish (*Engaewa reducta*), the Margaret River burrowing crayfish (*Engaewa pseudoreducta*) and the Walpole burrowing crayfish (*Engaewa walpolea*), are found in southern Western Australia and all are considered to be federally endangered (Department of Environment and Conservation, 2008). These species occur in small swamps and creeklines that are dominated by dense vegetation (including several *Lepidosperma* species) that provides cover for their fragile burrows in the banks of pools (Burnham *et al.*, 2007). In north-eastern Tasmania, the endangered Scottsdale burrowing crayfish (*Engaewa spinicaudatus*) is found in creek and swamp habitats where *L. elatius* is a common part of the vegetation cover and *L. filiforme* is also occasionally present (Wapstra *et al.*, 2006). Traylor *et al.* (1996) have identified 192 aquatic invertebrate, fish and amphibian species in south-western Australian ecosystems, many of which are likely to be reliant on the condition

and species composition of wetland vegetation where *Lepidosperma* species are often prominent. Specific associations with wetland vegetation patterns and individual plant species are yet to be studied for the majority of these animal species.

Macroinvertebrates

Dense riparian vegetation, including *L. tetraquetrum*, which can form monospecific stands along creeklines, is highly beneficial to the health of macroinvertebrate communities in these ecosystems (Armstrong *et al.*, 2005).

Microbial activity

The combination of living stands and dead litter of *L. longitudinale* supports microbial activity, which captures excess phosphorus from agricultural systems and incorporates it into the wetland sediments (Chambers, 1988; Chambers *et al.*, 1993). Sedge communities bounding wetlands, waterways and estuaries act as an important nutrient trap (Pen, 1999; Brearley, 2005). *Lepidosperma longitudinale* often dominates wetlands with impeded drainage (Benson, 1981; Brearley, 2005). While little is known of specificity (or even taxonomy), amoebae have been found associated with the rhizosphere of *L. semiteres* (Foster, 1988).

Fungal associations

While smuts are considered detrimental to the host plant, reducing seed production through infection of the inflorescence, Savile (1979) and Lutz *et al.* (2012) have highlighted the value of rust and smut fungi in providing an independent assessment of evolutionary trends in the Cyperaceae. Two smut species were described from *Lepidosperma* species by McAlpine (1910) as *Tolyposporium lepidospermae* and *T. rodwayi*, both now included in *Moreaua*. Websdane *et al.* (1994) recorded smuts on five *Lepidosperma* species from Western Australia, assigning them to the genus *Tolyposporium*. Vánky and Shivas (2008) have now recorded five smut fungi on 15 *Lepidosperma* species (Table 6), including the monotypic genus *Heterotolyposporium* which is only known from *L. ensiforme* in Tasmania (Vánky and Shivas, 2008; Lutz *et al.*, 2012). Additional records have recently been made from a broad range of *Lepidosperma* species from south-western and south-eastern Australia but the fungal species are yet to be identified (R. L. Barrett, M. D. Barrett, J. J. Bruhl and K. L. Wilson, pers. obs.; Fig. 11).

McAlpine (1902) described the ascomycete *Metasphaeria lepidospermae* from a *Lepidosperma* species in Victoria near Werribee as having a significant impact on the species, actually killing hundreds of plants. The ascomycete *Nemacyclus gilvus* was named from dead leaves of *L. laterale* (Rodway, 1918; Dennis, 1958).

The septorioid fungus *Clypeopycnis lepidospermatis* (teleomorph *Mycosphaerella lepidospermatis*) occurs on *L. gladiatum* (Priest, 2006). The generic placement of this fungus is in doubt and it possibly represents a Cyperaceae-specific genus currently only known from *L. gladiatum* (Priest, 2006).

TABLE 6. Fungal smuts infecting *Lepidosperma* species

| Smut species | <i>Lepidosperma</i> hosts | References |
|---|---|--|
| <i>Heterotolypodium lepidospermatis</i> | <i>L. ensiforme</i> | Ványky, 1997a, 1998; Lutz <i>et al.</i> , 2012 |
| <i>Moreaua gigaglomerulosa</i> <i>M. lepidospermatis</i> | <i>L. neesii</i> <i>L. lineare</i> (as <i>L. gunnii</i>), <i>L. sieberi</i> (as <i>L. angustatum</i>), <i>L. semiteres</i> and <i>L. sieberi</i> (as <i>L. concavum</i>) | Ványky and Shivas, 2008 Ványky and Shivas, 2008 |
| <i>M. megaglomerulosa</i> | <i>L. filiforme</i> , <i>L. laterale</i> , <i>L. longitudinale</i> , <i>L. neesii</i> and <i>L. sieberi</i> (as <i>L. concavum</i>) | Ványky, 1997b |
| <i>M. rodwayi</i> | <i>L. effusum</i> , <i>L. flexuosum</i> , <i>L. gladiatum</i> , <i>L. laterale</i> , <i>L. lineare</i> (as <i>L. gunnii</i>), <i>L. neesii</i> , <i>L. quadrangulatum</i> , <i>L. sieberi</i> (as <i>L. squamatum</i>), <i>L. viscidum</i> and <i>L. species</i> (indet.) | Ványky and Shivas, 2008 |
| <i>Moreaua rodwayi</i> (as <i>Tolyposporium</i>) | <i>Lepidosperma laterale</i> in New Zealand | McKenzie, 1990 |

FIG. 11. Fungal smut-infected spikelets of *Lepidosperma costale* at Wubin Rocks, Western Australia.

Cooke (1891) described *Anthostomella lepidosperma* from a *Lepidosperma* species in Victoria. *Anthostomella lepidosperma* is now considered to be a synonym of *A. leptospora* (Lu *et al.*, 1999). *Coniosporium pterospermum* (= *Arthrinium pterospermum*) has been recorded from *Lepidosperma* in Victoria (McAlpine, 1895). Hennings (1901) described the Sordariomycete fungus *Pestalotia lepidospermatis* from *L. angustatum* in Western Australia. McAlpine and Tepper (1895) described a new stone-maker fungus (*Laccocephalum basilapiloides* = *Polyporus basilapiloides*) from the mallee of South Australia, noting that it was regularly found among tussocks of *L. viscidum* (s.l.).

Mycorrhizal and microbial associations

Generally, Cyperaceae are considered to be non-mycorrhizal (e.g. Powell, 1975). *Lepidosperma squamatum* (s.l., as *L. angustatum*) has been recorded as being ‘usually uninfected’ by mycorrhizal fungi (Lamont, 1984). More recently, Meneý *et al.* (1993) have recorded seasonal infection by arbuscular mycorrhizal fungi (*Acaulospora* sp. and *Glomus* sp.) in *L. gracile* (probably = *L. leptostachyum*). Some authors consider it unlikely that these records represent a true mycorrhizal relationship, although this is difficult to prove conclusively (Brundrett, 2009). Brundrett (2002) suggests that the presence of non-mycorrhizal nutrient acquisition through the presence of dauciform roots may have facilitated the success of the Cyperaceae. This is a common strategy in soils with very low available phosphorus (Lambers *et al.*, 2008). It may be that a mycorrhizal relationship is only present under specific circumstances. In studies of the normally non-mycorrhizal genus *Hakea*, Boulet and Lambers (2005) found in *H. verrucosa*, a species with cluster roots similar in function to the dauciform roots found in *Lepidosperma*, that arbuscules were present in roots in ultramafic soils with high nickel and low phosphorus concentrations. It may be that *Lepidosperma* species (and other Cyperaceae) are mycorrhizal under certain environmental conditions, which disadvantage the carboxylate-releasing strategy of dauciform roots. Perrier *et al.* (2006) and Lagrange *et al.* (2011) have confirmed that arbuscular mycorrhizas are regularly found in the roots of the metallophytic species *L. perteres* in the metal-rich ultramafic soils of New Caledonia. Muthukumar *et al.* (2004) concludes that many Cyperaceae should be considered to be mycorrhizal, although often only under particular environmental conditions, with the specific benefits of these relationships still remaining unknown.

Early studies of plant species influence on microbial presence in the rhizosphere in sandy heath in Victoria by Thrower (1954) found a large number of microorganisms associated with the root zone of *L. sieberi* (as *L. concavum*): two Oomycetes, seven Zygomycetes, seven Sordariomycetes, two Saccharomycetes, 29 Eurotiomycetes, one Leotiomycete, two Dothideomycetes and one Actinobacteria. The exact nature and ecological implications of the relationship between the plant and rhizosphere mycota remain to be demonstrated. The Sordariomycete fungus *Coniella duckerae*

(Yip, 1987) was described from the rhizosphere of *L. sieberi* (as. *L. concavum*).

Pathogenic infection

While it appears that some level of infection can occur (Phillips and Weste, 1984), all Australian *Lepidosperma* species are considered to be resistant to *Phytophthora cinnamomi*, possibly due to their ability to produce new roots beyond the infection zone relatively quickly (Phillips and Weste, 1984; Weste *et al.*, 2002). Several species appear to benefit from reduced competition following the death of susceptible taxa in infected areas (Weste, 1981; Podger *et al.*, 1990; Duncan and Keane, 1996; Shearer and Dillon, 1996; Kirkpatrick and Harris, 1999; Cahill *et al.*, 2008; Dunstan *et al.*, 2008; Mordecai, 2011). Weste and Kennedy (1997), Weste *et al.* (2002) and Weste (2003) recorded a significant long-term increase in the density of *L. semiteres* in the Grampians, Victoria, in sites affected by *P. cinnamomi*. Weste (1981) recorded *L. sieberi* (as *L. concavum*) becoming dominant following the death of susceptible species due to *P. cinnamomi* infection near Melbourne, Victoria. Podger *et al.* (1990) isolated *P. cinnamomi* from the roots of *L. sieberi* (as *L. concavum*), but they did not observe any level of pathogenicity. Shearer *et al.* (2007) caution that *Lepidosperma* species may still be at risk from associated habitat change, noting some decline in *L. angustatum* in southern Western Australia without any signs of direct infection by *P. cinnamomi*. Changes in plant community structure due to the invasion of *P. cinnamomi* may have significant effects on animals reliant on plant cover for protection and resistant species such as *Lepidosperma* become even more important in these situations (Wilson *et al.*, 1994).

Shearer *et al.* (1998) found that *Lepidosperma* species are also resistant to the pathogenic fungus *Armillaria luteobubalina* in coastal areas of Western Australia.

Hosts for hemiparasitic plants

Lepidosperma species have been recorded as natural host plants for *Olox phyllanthi* (*L. gladiatum*, Pate *et al.*, 1990), *Santalum spicatum* (Fox, 1997) and *Nuytsia floribunda* (R. L. Barrett, pers. obs.), although no particular detrimental impact on the sedges has been observed.

CONCLUSIONS

While specific observations of *Lepidosperma* ecology are still poorly represented in the literature, most observations being incidental, it is clear that as a genus, sword sedges have an important place in the ecology of many ecosystems. From the scattered records that have been located, it is difficult to determine the full extent of the ecological importance of *Lepidosperma* species. There are few publications focusing specifically on *Lepidosperma* and it is likely that the records presented here represent only a small fraction of the real ecological interactions present across the range of the genus. There remains virtually nothing known of various galls, insects that feed on the plants or nematodes that may be associated with *Lepidosperma* species.

Many of the ecological association records come from rare animal species whose life histories have been studied in detail to aid their conservation. It is likely that a much larger number of more common species also have direct associations with *Lepidosperma* species that are yet to be recorded in the literature. The genus *Lepidosperma*, as a major component of many ecosystems in Australia, New Zealand and New Caledonia, is an ideal subject for additional studies on ecological interactions with other organisms that may be dependent on them. Most of the studies to date have been very limited in their assessment of habitat details and the nature and extent of the associations between species. Many opportunities therefore remain to further our understanding of ecological associations with *Lepidosperma* species. Investigation of the potential for co-speciation of *Lepidosperma* and *Elachista* species is likely to provide insights into the evolution of both genera. It is expected that many additional associations will be identified in the future once more attention is paid to the ecology of *Lepidosperma*.

The extensive nature of the ecological associations documented here for *Lepidosperma* suggest that similar reviews for sedge genera worldwide would greatly enhance our understanding of sedge ecology. Sedges clearly play a critical role in many ecosystems and their relative importance is often overlooked.

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