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Diversification of Camphorosmeae (Amaranthaceae *s.l.*) during the Miocene-Pliocene aridification of inland Australia

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ABSTRACT

The Australian Camphorosmeae represent a monophyletic lineage that diversified to include ca. 150 spp. across 12 genera, and populate large parts of arid Australia. Tracking the origin and spread of this ancestrally salt and drought tolerant lineage provides additional evidence about the timing of the evolutionary history and phylogenetic assembly of arid habitats in Australia. Using a customized RADseq approach, sequence data for 104 species of the Australian Camphorosmeae representing all 12 genera were generated and included in phylogenetic and dating analyses. Furthermore, habitat type occurrences and preferences of species and clades were recorded. As suspected, the characters used to delimit current Australian Camphorosmeae genera do not support monophyletic groups, as phylogenetic analyses yielded 17 statistically supported clades across a large *Maireana* grade and crown radiation of *Sclerolaena*. The diversification of Australian Camphorosmeae is clearly linked to landscape changes and emerging new habitat types in arid Australia since the ancestral element likely arrived from temperate semi-arid to arid parts of continental Eurasia in the Middle Miocene. Migration was likely multidirectional and followed a west-to-east aridification. Crown group diversification was strongest during the Pliocene and likely promoted by the west-to-east expansion of Riverine Desert habitats and subsequent expansion and colonization of newly developing arid habitats. Rapid range expansion, fast habitat saturation, as well as periodic expansion, contraction and replacement of arid habitats, may have caused the rather species-poor clades of the earlier-divergent *Maireana* grade, compared to the continuously diversifying *Sclerolaena* clade.

1. Introduction

The relatively flat landscapes of inland Australia have been shaped by the process of aridification over the last 20 million years, resulting in a highly weathered and nutrient-deficient soils. The current climate is strongly influenced by the surrounding oceans and weather systems and for most of the continent, precipitation is the dominant environmental factor (Keast, 1959; Mabbutt, 1988; Smith and Morton, 1990; Suppiah et al., 2001; Bowler et al., 2006; Johnson, 2009; Morton et al., 2011; Crisp and Cook, 2013; Timbal and Drosdowsky, 2013; Song et al., 2017; Byrne et al., 2018; Mokany et al., 2022). The central arid zone biome and its semi-arid periphery, together account for 70 % of the continent and include environments such as sandy deserts, stony deserts and

steppes, ranges and coastal plains (Smith and Morton, 1990; Martin, 2006; Morton et al., 2011; Mabbutt, 1988; Byrne et al., 2018; McDonald, 2020). These regions experience major drought seasons, punctuated by unpredictable cyclonic rainfall events coupled with high evaporation rates, and in the driest regions results in an average annual precipitation below 250–350 mm. Numerous ephemeral lakes in extensive drainage systems characterise the continental interior (Martin, 2006; Morton et al., 2011).

These mosaic-like arid landscapes are home to a variety of sclerophyllous and xeromorphic vegetation types, such as (open) *Acacia* and Eucalypt shrub- and woodlands, spinifex, tussock and hummock grasslands, and chenopod shrublands (Martin, 2006; Morton et al., 2011; Crisp and Cook, 2013; Byrne et al., 2018). While this biome is a hotspot

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for reptiles and invertebrates, it hosts only 10 % of Australia's plant diversity (Barker and Greenslade, 1982; Byrne et al., 2008; Anderson, 2016; Byrne et al., 2018). The plants of the arid zone, however, are highly specialized survival artists, having evolved and adapted over millions of years to successfully cope with the harsh desert conditions. Among other winner-lineages (e.g.: Asteraceae, Fabaceae, Goodeniaceae, Malvaceae, Poaceae, Proteaceae, Rutaceae) (reviewed in Crisp et al., 2004; Byrne et al., 2008, 2018; Crisp and Cook, 2013) of the evolutionary race for persistence in this habitat are the Amaranthaceae.

Amaranthaceae *sensu lato*, including Amaranthaceae *sensu stricto* and Chenopodiaceae, represents the most diverse lineage (ca. 180 genera and 2500 species) of the Caryophyllales (Walker et al., 2018; Morales-Briones et al., 2021), with several species-rich genera (e.g. *Atriplex* L., *Maireana* Moq., *Sclerolaena* R.Br., *Ptilotus* R.Br., *Tecticornia* Hook.f., *Gomphrena* L., *Dysphania* R.Br.), and constitutes an ubiquitous component of Australia's arid-zone flora, especially in saline habitats (Wilson, 1984; Martin, 2006; Byrne et al., 2008, 2018; Morton et al., 2011; Crisp and Cook, 2013). The ca. 300 Australian chenopod species arose from at least nine different long distance dispersal events, which arrived from Late Pliocene to Late Eocene/Early Oligocene, with a clear culmination of arrival events during the Late Miocene and the Pliocene (Kadereit et al., 2003, 2005; Uotila et al., 2021; Zerdoner Calasan et al., 2022). Since the first signs of increasing and progressively expanding aridity in Australia in the Middle Miocene, the emergence of numerous arid-adapted taxa leave phylogenetic traces of continental desiccation (reviewed in Crisp et al., 2004; Byrne et al., 2008; Crisp and Cook, 2013; Byrne and Murphy, 2020). Three large Australian Chenopodiaceae groups such as the Australian Camphorosmeae, Salicornieae and *Atriplex* in particular, radiated rapidly after their arrival during this period (Shepherd et al., 2004, 2005; Kadereit et al., 2005; Cabrera et al., 2011; McDonald, 2020; Zerdoner Calasan et al., 2022). The pre-adaptation of ancestral elements to dry and saline conditions likely promoted their rapid diversification in a period of major climatic change that transformed the once warm and wet continent (Martin, 2006; Byrne et al., 2008).

Camphorosmeae are the chenopod tribe in Australia richest in genera and species with ca. 150 species in 12 genera, including *Didymanthus* Endl., *Dissocarpus* F.Muell., *Enchylaena* R.Br., *Eremophea* Paul G. Wilson, *Eriochiton* (R.H. Anderson) A.J. Scott, *Maireana*, *Malacocera* R.H. Anderson, *Neobassia* A.J. Scott, *Osteocarpum* F.Muell., *Roycea* C.A. Gardner, *Sclerolaena*, *Threlkeldia* R.Br. (Table 1; Wilson, 1984; Cabrera et al., 2011). They comprise predominantly woody perennials or small shrubs, rarely perennial herbs or annuals (Wilson, 1984; Kadereit and Freitag, 2011). Besides the endemic species, the Camphorosmeae include an additional 30–40 non-Australian species centered in the Old World desert belt from the Canary Islands to Asia, with a few species distributed in North America and South Africa (Kadereit and Freitag, 2011). The Australian Camphorosmeae were found to form a monophyletic clade, sister to the Central Asian genus *Grubovia* Freitag & G. Kadereit (Kadereit and Freitag, 2011; Kadereit et al., 2014).

The Australian Camphorosmeae grow in all floristic regions of the continent, including the tropical north and the temperate and Mediterranean south (Wilson, 1984; Cabrera et al., 2009); however, they dominate the landscape in the arid and semi-arid regions of the interior, as a component of the characteristic chenopod shrubland (Kershaw et al., 1994; Martin, 2006; Morton et al., 2011). They occur in diverse arid and non-arid habitats, such as Coast, Mesic Plains, ephemeral Riverine and Desert Lake habitats, as well as in the most extreme desert landscapes such as Sand and Stony Desert habitats (Mabbutt, 1988; McDonald, 2020; Fig. 1) with centers of diversity in the Yilgarn Plateau in Western Australia and in the Lake Eyre–Murray Basin in the Eastern Desert (Wilson, 1984; McDonald, 2020). These hardy plants grow in a wide range of soils of various, mostly nutrient-poor, substrates (e.g. sandy, loamy, clayey, calcareous, gypseous, stony) and ranging salinity from non-saline, slightly saline to saline conditions (Wilson, 1984; Harden, 1990; Walsh, 1996; Paczkowska and Chapman, 2000). Because

of their ability to survive long periods of drought and to accumulate salts and heavy metals, a number of Australian Camphorosmeae gained economic interest. Some species are valuable resources for livestock in zones of low rainfall and high soil salinity (Leigh et al., 1979; Malcolm, 2000; Norman et al., 2010; Revell et al., 2013; El Shaer and Squires, 2015; Certain et al., 2021) and are the focus of sustainable agriculture strategies to protect soils and waters from degradation and desiccation (Barrett-Lennard et al., 2003; Blache et al., 2016; Certain et al., 2021). Several species are promising candidates or already established species for the restoration and revegetation of mine waste (Brearley, 2003; Squires et al., 2012; Wu et al., 2021; Zhong et al., 2021; Valliere et al., 2022). Some species are recognised under state jurisdictions as species of conservation concern, as they or their habitats are threatened by deforestation, intensive mining of economically valuable soil resources, introduction of non-native taxa, and overgrazing by livestock (Fairfax and Fensham, 2000; Sharp et al., 2009; Mavromihalis, 2010a, 2010b; Linley et al., 2016; Fensham et al., 2018; Silcock and Fensham, 2018; Amor et al., 2020).

Taxonomy of the Australian Camphorosmeae is primarily based on characteristics of the fruiting perianth for generic delimitation with a history of frequent revision (e.g. Mueller, 1882a, 1882b; Anderson, 1923; Ulbrich, 1934; Ising, 1961, 1964; Wilson, 1975, 1984; Scott, 1978; Chinnock, 1980; Jacobs, 1988). In particular, the shape, position (tepaline vs. vertepaline) and number of fruiting perianth appendages, were used to describe, delineate and revise genera, sections and species complexes in the Australian Camphorosmeae. Apart from the two species-rich genera *Maireana* (ca. 57 species with mostly wing-like fruiting perianths, Fig. 2F) and *Sclerolaena* (ca. 65 species with mostly spine-like fruiting perianths, Fig. 2K), ten species-poor genera are currently accepted (Table 1, Fig. 2). These include species with perianth appendage modifications and positions that do not strictly match the main perianth appendage types of the major genera (Wilson, 1975, 1984). In the monotypic genus *Didymanthus* (Fig. 2A), the paired flowers are fused at their bases (unlike *Sclerolaena* or *Maireana*), the seed is erect (as in many *Sclerolaena* species) and the perianth develops five horizontal wings in fruit (as in *Maireana*). In the monotypic genus *Eriochiton* (Fig. 2E), the fruiting perianth develops two series of appendages: an inner circle of five erect wing-like tepaline appendages and an outer circle of five spinose appendages arising from wing-like appendages. Species of the genus *Dissocarpus* (4 spp.) (Fig. 2B) develop spinous appendages (as in *Sclerolaena*) but these are tepaline in position (as in *Maireana*) and the fruiting perianths are paired or aggregated into woody, ball-like infructescences. In *Eremophea* (2 spp.) (Fig. 2D), the fruiting perianths develop tepaline spines and become embedded in the woody branch axis. In *Neobassia* (2 spp.) (Fig. 2H), the fruiting perianth produces five tepaline spines that arise from the perianth base and unite into an apical cup. In *Threlkeldia* (2 spp.) (Fig. 2L), the perianth becomes succulent or dry in fruit and is without spines or wings but develops intertepaline knobs. In *Osteocarpum* (5 spp.) (Fig. 2I), the fruiting perianth develops 1–5 intertepaline, vertical wings on top of the perianth. In *Malacocera* (4 spp.) (Fig. 2G), the fruiting perianth bears 3–5 sub-cylindrical, tepaline appendages forming a Y or star-shaped configuration. In *Enchylaena* (2 spp.) (Fig. 2C), the perianth becomes succulent in fruit and, if present, develops a shallow, succulent wing-like cup at the perianth apex. Finally, in *Roycea* (3 spp.) (Fig. 2J), the five tepals do not enlarge in fruit and the fruit is surrounded by the perianth at its base.

That the characters delimiting Australian genera may not create natural groups has long been recognized (Anderson, 1923; Ising, 1964, 1984; Scott, 1978). In addition, species sharing very similar morphological traits, hybridization between closely allied species and between genera, as well as the evolution of homoplastic perianth traits, further complicate the taxonomy (Wilson, 1975, 1984; Cabrera et al., 2009). Cabrera et al. (2009) conducted the first molecular phylogenetic study of the Australian Camphorosmeae, using Sanger sequencing of seven molecular markers and sampling 71 species from all currently recognized

Table 1

Taxon sampling. Given are the genus (number of species sampled in this study/number of species currently recognized for each genus), epithet and authority of all species sampled, as well as the voucher information (herbarium voucher ID, collector, collection ID). In case of TERN (Terrestrial Ecosystem Research Network, University of Queensland, Brisbane) and BushBlitz (Australian Government, Department of Climate Change, Energy, the Environment and Water) samples, the voucher ID corresponds to the collection ID. Habitat types: Coast (CS), Mesic Plain & Range (MP), Riverine Desert (RL), Desert Lake (DL), Sand Desert (SD), Desert Upland (DU), Stony Desert (SP), Desert Clay Plain (CP), Shield Plain (SH), Karst Plain (KP). For description of the habitat type see [Table 2](#). The two outgroup taxa in bold.

Taxon	Authority	Voucher ID	Collector/Collection ID	Present in habitat type
<i>Didymanthus</i> (1/1)	Endl.			
<i>Didymanthus roei</i>	Endl.	MJG 028809	Hühn, P. et al. PS_PH_016	DL
<i>Dissocarpus</i> (3/4)	F.Muell.			
<i>Dissocarpus biflorus</i>	(R.Br.) F.Muell.	MJG 019199	McDonald, J.T. 1505/51	CS, RL
<i>Dissocarpus fontinalis</i>	Paul G.Wilson	MJG 019223	McDonald, J.T. 1506/9A-1	SP, RL
<i>Dissocarpus paradoxus</i>	(R.Br.) F.Muell.	NSA07586	TERN	SD, KP, RL
<i>Enchylaena</i> (2/2)	R.Br.			
<i>Enchylaena lanata</i>	Paul G.Wilson	MJG 028812	Hühn, P. et al. PS_PH_020	MP, SH, DL
<i>Enchylaena tomentosa</i>	R.Br.	NSA013625	TERN	CS, MP, DU, KP, RL, SD
<i>Eokochia</i> (1/1)	Freitag & G.Kadereit			
<i>Eokochia saxicola</i>	(Guss.) Freitag & G.Kadereit	MJG 027671	Kadereit, G. s.n.	
<i>Eremophea</i> (2/2)	Paul G.Wilson			
<i>Eremophea aggregata</i>	Paul G.Wilson	MJG 028773	Hühn, P. et al. PS_PH_033	KP
<i>Eremophea spinosa</i>	(Ewart & O.B.Davies) Paul G.Wilson	NTA016323	TERN	DU, SD
<i>Eriochiton</i> (1/1)	(R.H.Anderson) A.J.Scott			
<i>Eriochiton sclerolaenoides</i>	(F.Muell.) A.J.Scott	MJG 027696	McDonald, J.T. 1501/29 A	KP
<i>Grubovia</i> (1/3)	Freitag & G.Kadereit			
<i>Grubovia dasyphylla</i>	(Fisch.&C.A.Mey.) Freitag&G.Kadereit	MJG 011708	Miehe, G. & Miehe 96–203–02	
<i>Maireana</i> (43/57)	Moq.			
<i>Maireana amoena</i>	(Diels) Paul G.Wilson	MJG 028836	Hühn, P. et al. PK_PH_044	DL
<i>Maireana aphylla</i>	(R.Br.) Paul G.Wilson	MJG 026701	McDonald, J.T. 1411/46	RL, SP
<i>Maireana appressa</i>	(Benth.) Paul G.Wilson	MJG 026834	McDonald, J.T. 1505/110	DL
<i>Maireana atkinsiana</i>	(W.Fitzg.) Paul G.Wilson	MJG 028837	Hühn, P. et al. PK_PH_011	DL
<i>Maireana brevifolia</i>	(R.Br.) Paul G.Wilson	MJG 028772	Hühn, P. et al. PK_PH_022	MP, SH, RL, CS
<i>Maireana campanulata</i>	Paul G.Wilson	MJG 026092	McDonald, J.T. 1506/50	SP, DU
<i>Maireana cannonii</i>	(J.M.Black) Paul G.Wilson	MJG 025924	McDonald, J.T. 1508/63	DL, RL, CS
<i>Maireana carnosia</i>	(Moq.) Paul G.Wilson	WAA012606	TERN	DL
<i>Maireana ciliata</i>	(F.Muell.) Paul G.Wilson	MJG 026736	McDonald, J.T. 1409/31	SP, KP, RL
<i>Maireana convexa</i>	Paul G.Wilson	MJG 028831	Hühn, P. et al. PK_PH_014	SD, SH
<i>Maireana coronata</i>	(J.M.Black) Paul G.Wilson	NSA011389	TERN	RL, DL, SP, CP
<i>Maireana dichoptera</i>	(F.Muell.) Paul G.Wilson	QDA000652	TERN	CP, RL
<i>Maireana enchylaenoides</i>	(F.Muell.) Paul G.Wilson	MJG 028825	Hühn, P. et al. PK_PH_055	MP, RL, KP
<i>Maireana eriantha</i>	(F.Muell.) Paul G.Wilson	MJG 028825	TERN	SP
<i>Maireana erioclada</i>	(Benth.) Paul G.Wilson	VCA007109	TERN	KP, MP
<i>Maireana eriosphaera</i>	Paul G.Wilson	MJG 028761	Hühn, P. et al. PK_PH_020	DL
<i>Maireana excavata</i>	(J.M.Black) Paul G.Wilson	MJG 026124	McDonald, J.T. 1511/35	MP, RL
<i>Maireana georgei</i>	(Diels) Paul G.Wilson	MJG 027725	McDonald, J.T. 0087096	SD, DU, KP, SH, RL
<i>Maireana glomerifolia</i>	(F.Muell. & Tate) Paul G.Wilson	MJG 028838	Hühn, P. et al. PK_PH_009	SH, DL
<i>Maireana humillima</i>	(F.Muell.) Paul G.Wilson	MJG 026106	McDonald, J.T. 1511/37	MP, RL
<i>Maireana integra</i>	(Paul G.Wilson) Paul G.Wilson	NSA07271	TERN	DL, KP, DU
<i>Maireana lanosa</i>	(Lindl.) Paul G.Wilson	QDA007093	TERN	SD, DL, RL
<i>Maireana lobiflora</i>	(F.Muell. ex Benth.) Paul G.Wilson	NSA01180	TERN	RL
<i>Maireana marginata</i>	(Benth.) Paul G.Wilson	MJG 028847	Hühn, P. et al. PK_PH_004	MP, SH
<i>Maireana oppositifolia</i>	(F.Muell.) Paul G.Wilson	MJG 019212	McDonald, J.T. 1501/49	CS, DL
<i>Maireana ovata</i>	(Ising) Paul G.Wilson	NTA004902	TERN	SP, DU
<i>Maireana pentagona</i>	(R.H.Anderson) Paul G.Wilson	SAA005398	TERN	RL, MP
<i>Maireana pentatropis</i>	(Tate) Paul G.Wilson	NSA010465	TERN	KP, SD, DL
<i>Maireana planifolia</i>	(F.Muell.) Paul G.Wilson	WAA004030	TERN	SH, DU, SD
<i>Maireana platycarpa</i>	Paul G.Wilson	MJG 028826	Hühn, P. et al. PK_PH_035	DL, KP
<i>Maireana polypterygia</i>	(Diels) Paul G.Wilson	MJG 028816	Hühn, P. et al. PS_PH_027	DL
<i>Maireana pyramidata</i>	(Benth.) Paul G.Wilson	NSA013527	TERN	RL, SD, DL
<i>Maireana radiata</i>	(Paul G.Wilson) Paul G.Wilson	MJG 027694	McDonald, J.T. 1501/78	KP, SD
<i>Maireana rohrlachii</i>	(Paul G.Wilson) Paul G.Wilson	AUG000132	TERN	MP, KP
<i>Maireana schistocarpa</i>	Paul G.Wilson	NSA013425	TERN	SP, DU, SD
<i>Maireana scleroptera</i>	(J.M.Black) Paul G.Wilson	MJG 027723	McDonald, J.T. 0076456	RL
<i>Maireana sedifolia</i>	(F.Muell.) Paul G.Wilson	MJG 028820	Hühn, P. et al. PK_PH_025	KP, DU
<i>Maireana spongiocarpa</i>	(F.Muell.) Paul G.Wilson	SAA000753	TERN	SP, DU
<i>Maireana suaedifolia</i>	(Paul G.Wilson) Paul G.Wilson	MJG 026188	McDonald, J.T. 1601/93	DL
<i>Maireana tomentosa</i>	Moq.	NSA010831	TERN	DL
<i>Maireana trichoptera</i>	(J.M.Black) Paul G.Wilson	MJG 028808	Hühn, P. et al. PS_PH_015	KP, DL
<i>Maireana turbinata</i>	Paul G.Wilson	NSA013511	TERN	KP, SP
<i>Maireana villosa</i>	(Lindl.) Paul G.Wilson	MJG 028819	Hühn, P. et al. PK_PH_016	DU, SH, CP
<i>Malacocera</i> (3/4)	R.H.Anderson			
<i>Malacocera albolanata</i>	(Ising) Chinnock	MJG 029141	Hühn, P. JQG_516	RL, DL
<i>Malacocera gracilis</i>	Chinnock	MJG 029143	Hühn, P. APA_PH_043	DL
<i>Malacocera tricornis</i>	(Benth.) R.H.Anderson	NSA013825	TERN	RL
<i>Neobassia</i> (1/2)	A.J.Scott			
<i>Neobassia proceriflora</i>	(F.Muell.) A.J.Scott	NSA01615	TERN	SP, RL
<i>Osteocarpum</i> (3/5)	F.Muell.			
<i>Osteocarpum acropterum</i>	(F.Muell. & Tate) Volken	MJG 019190	McDonald, J.T. 1505/86–1	RL, DL, SP

(continued on next page)

Table 1 (continued)

Taxon	Authority	Voucher ID	Collector/Collection ID	Present in habitat type
<i>Osteocarpum dipterocarpum</i>	(F.Muell.) Volkens	MJG 019226	McDonald, J.T. 1506/15	RL, DL
<i>Osteocarpum salsuginosum</i>	F.Muell.	SAS001910	TERN	DL, RL
<i>Roycea</i> (3/3)	C.A.Gardner			
<i>Roycea pycnophylloides</i>	C.A.Gardner	MJG 028821	Hühn, P. et al. PK_PH_062	DL
<i>Roycea spinescens</i>	C.A.Gardner	MJG 028762	Hühn, P. et al. PK_PH_052	DL
<i>Roycea divaricata</i>	Paul G.Wilson	MJG 028835	Hühn, P. et al. PK_PH_017	DL
<i>Sclerolaena</i> (40/65)	R.Br.			
<i>Sclerolaena alata</i>	Paul G.Wilson	MJG 028845	Hühn, P. et al. PK_PH_012	DL
<i>Sclerolaena articulata</i>	(J.M.Black) A.J.Scott	NSABHC06184	TERN	SP
<i>Sclerolaena bicornis</i>	Lindl.	MJG 026086	McDonald, J.T. 1506/34	RL, CP, CS
<i>Sclerolaena blackiana</i>	(Ising) A.J.Scott	SAA001813	TERN	SP
<i>Sclerolaena brachyptera</i>	(F.Muell.) S.W.L.Jacobs	SAS001876	TERN	SP, RL
<i>Sclerolaena brevifolia</i>	(Ising) A.J.Scott	MJG 019214	McDonald, J.T. 1501/67	KP
<i>Sclerolaena burbridgeae</i>	(Ising) A.J.Scott	MJG 028781	Hühn, P. et al. PS_PH_054	RL
<i>Sclerolaena convexula</i>	(R.H.Anderson) A.J.Scott	WAA003994	TERN	DU, SD
<i>Sclerolaena cornishiana</i>	(F.Muell.) A.J.Scott	QDA007001	TERN	SD, SH, RL
<i>Sclerolaena costata</i>	(R.H.Anderson) A.J.Scott	MJG 028802	Hühn, P. et al. PS_PH_014	DU, SD, RL
<i>Sclerolaena cuneata</i>	Paul G.Wilson	MJG 019220	McDonald, J.T. 1501/115	SP, RL, SH
<i>Sclerolaena decurrens</i>	(J.M.Black) A.J.Scott	NTA016548	TERN	SP, RL
<i>Sclerolaena densiflora</i>	(W.Fitzg.) A.J.Scott	WAA009919	TERN	SH, DU
<i>Sclerolaena deserticola</i>	Paul G.Wilson	WAA011226	TERN	DL, SH
<i>Sclerolaena diacantha</i>	(Nees) Benth.	MJG 026848	McDonald, J.T. 1501/84	
<i>Sclerolaena divaricata</i>	(R.Br.) Sm.	NSA013619	TERN	RL, SP
<i>Sclerolaena drummondii</i>	(Benth.) Domin	WAA001796	TERN	SH, MP
<i>Sclerolaena ericantha</i>	(F.Muell.) Ulbr.	QDA007895	TERN	DU, SP
<i>Sclerolaena eurotioides</i>	(F.Muell.) A.J.Scott	WAA001472	TERN	DL
<i>Sclerolaena fimbriolata</i>	(F.Muell.) A.J.Scott	MJG 026273	McDonald, J.T. 1601/30	DL
<i>Sclerolaena fusiformis</i>	Paul G.Wilson	MJG 028842	Hühn, P. et al. PK_PH_005	SH
<i>Sclerolaena glabra</i>	(F.Muell.) Domin	QDA007733	TERN	SP, RL
<i>Sclerolaena holtiana</i>	(Ising) A.J.Scott	MJG 019222	McDonald, J.T. 1506/10	SD, DL, RL, SP
<i>Sclerolaena intricata</i>	(R.H.Anderson) A.J.Scott	MJG 026936	McDonald, J.T. 1505/47	SP, RL
<i>Sclerolaena johnsonii</i>	(Ising) A.J.Scott	BS1137–183	Bush Blitz	SD
<i>Sclerolaena lanicuspis</i>	(F.Muell.) F.Muell	NSA013547	TERN	SP, RL, DU, SH, CP
<i>Sclerolaena limbata</i>	(J.M.Black) Ulbr.	MJG 025912	McDonald, J.T. 1508/86	SP, RL, DU
<i>Sclerolaena minuta</i>	(Ising) A.J.Scott	NSA01109	TERN	DU, SP, SH
<i>Sclerolaena muricata</i>	(Moq.) Domin	MJG 026111	McDonald, J.T. 1511/48	RL, CP
<i>Sclerolaena napiformis</i>	Paul G.Wilson	MJG 026161	McDonald, J.T. 1511/26	MP
<i>Sclerolaena obliquicuspis</i>	(R.H.Anderson) Ulbr	MJG 019203	McDonald, J.T. 1411/8 A	KP
<i>Sclerolaena parallelicuspis</i>	(R.H.Anderson) A.J.Scott	NSA013599	TERN	SP
<i>Sclerolaena parviflora</i>	(R.H.Anderson) A.J.Scott	BS1137–221	Bush Blitz	SD, KP
<i>Sclerolaena patenticuspis</i>	(R.H.Anderson) Ulbr	MJG 026693	McDonald, J.T. 1409/21	KP, DU, RL
<i>Sclerolaena</i> sp. Yeltacowie	ineditus	BS1097–408	Bush Blitz	na
<i>Sclerolaena stelligera</i>	(F.Muell.) S.W.L.Jacobs	MJG 026818	McDonald, J.T. 1411/31	RL
<i>Sclerolaena stylosa</i>	(Ising) A.J.Scott	MJG 028817	Hühn, P. et al. PS_PH_034	KP
<i>Sclerolaena tricuspis</i>	(F.Muell.) Ulbr.	MJG 025923	McDonald, J.T. 1605/6	RL
<i>Sclerolaena uniflora</i>	R.Br.	SAA004308	TERN	CS, KP
<i>Sclerolaena ventricosa</i>	(J.M.Black) A.J.Scott	MJG 026938	McDonald, J.T. 1505/46	SP, RL
<i>Threlkeldia</i> (2/2)	R.Br.			
<i>Threlkeldia diffusa</i>	R.Br.	MJG 026729	McDonald, J.T. 1407/28 A	CS, DL
<i>Threlkeldia inchoata</i>	(J.M.Black) J.M.Black	SAA000015	TERN	RL, SP

genera. Fifteen morphological characters were also surveyed for their systematic relevance and phylogenetic inference. Of the molecular markers tested, only the external transcribed spacer (ETS) and internal transcribed spacer (ITS) yielded sufficient sequence variation for phylogenetic inference; however, several generic boundaries and decisive relationships remained unresolved. The authors suggested that Incomplete Lineage Sorting (as a consequence of rapid radiations) and ongoing hybridization in this relatively young group resulted in a lack of phylogenetic informative sequence data. Biogeographical analyses based on the same data, inferred that the Australian Camphorosmeae arrived in southern Western Australia by long-distance dispersal at the end of the Miocene and diversified during the Pliocene (Cabrera et al., 2011). Since the ancestors of the Australian Camphorosmeae likely were already adapted to dry and saline conditions, the diversification of the lineage was presumably driven by the intensifying aridification of the Australian continent during this time. The first inland migration may have taken place as species already adapted to coastal, marshy conditions, dispersed along palaeodrainage systems to increasing hypersaline inland habitats suggesting a littoral connection, resulting in multidirectional dispersal across the continent (Cabrera et al., 2011; McDonald,

2020).

In this study, the diversification of Australian Camphorosmeae across the aridifying landscapes of Australia is re-examined using new molecular data and analyses with ecological data. Aided by a modified NGS-based methodology we aim to improve the insufficient resolution of previous phylogenies based on Sanger sequence data and to reconstruct yet unrecognized species groups as statistically supported clades. Newly surveyed habitat types for each species, and their respective age, are related to the dated phylogeny to trace the diversification of the lineage in emerging habitat types of Australia. We aim to provide further evidence to postulated hypotheses regarding migration, rapid radiation and crown-group diversification of Australian Camphorosmeae corresponding to the aridification of the Australian continent since the Miocene.

2. Material and methods

Sampling — A total of 106 species representing all 12 genera of the Australian Camphorosmeae, with two representatives of the extra-Australian Camphorosmeae (*Eokochia saxicola* (Guss.) Freitag & G.

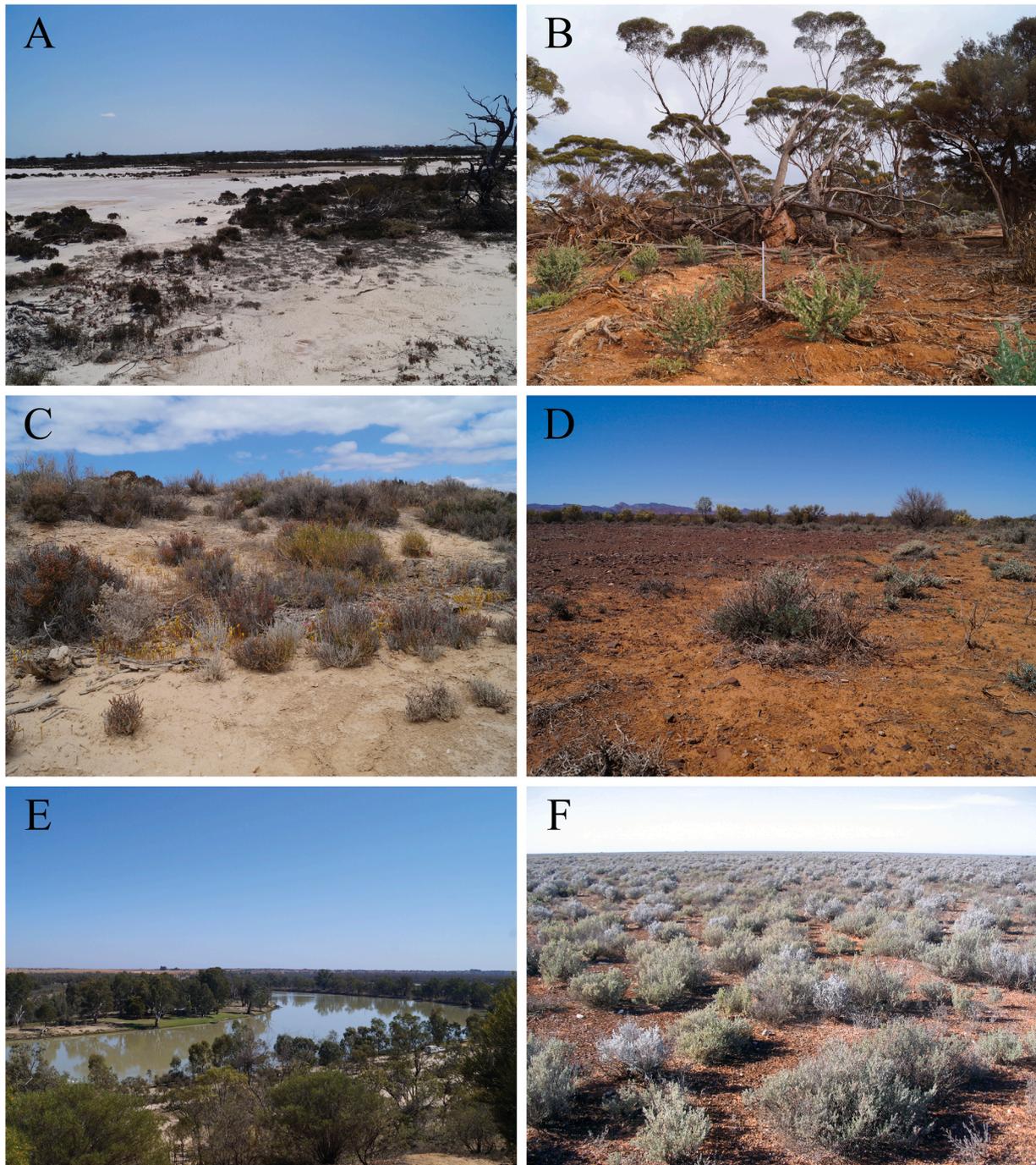


Fig. 1. A: Desert Lake habitat with mats of *Roycea pycnophylloides*, Mortlock River salt lake system, Western Australia; B: Open *Eucalyptus* Woodland vegetation with *Chenopod* understorey, Goldfields–Esperance region of Western Australia; C: Sand dune on the edge of a salt lake with low chenopodiaceous shrubs (*Tecticornia*, *Maireana*, *Atriplex*, *Malacocera*) in the Winninowie Conservation Park, South Australia; D: Stony Desert (gibber plain) habitat with *Maireana*, *Atriplex* and *Acacia* in the Flinders Ranges east of Lake Torrens, South Australia; E: Murray River with adjacent flood plains, open *Eucalyptus* and *Acacia* woodlands in the Chowilla Game Reserve, South Australia; F: Karst Plain (KP) habitat of the Nullarbor Plain with *Chenopod* shrubland (*Maireana* and *Atriplex*). Images: P. Hühn.

Kadereit from the Central Mediterranean area and *Grubovia dasyphylla* (Fisch. & C.A.Mey.) Freitag & G.Kadereit from Central Asia), were included in this study (Table 1). Supplementary Table S1 contains the sampling information of the Camphorosmeae taxa included. Leaf material was preserved in silica gel for DNA extraction.

DNA extraction and RADseq lab protocol — Lab work for DNA extraction and RADseq library preparation was carried out following Hühn et al. (2022). DNA-extraction was conducted using the DNeasy Plant Mini-Kit (QIAGEN, Venlo, Netherlands) according to the manufacturer’s protocol for “Purification of Total DNA from Plant Tissue

(Mini Protocol)”. The DNA concentration and quality were evaluated using a NanoDrop 1000 Spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA), a Qubit 3.0 Fluorometer (Thermo Fisher Scientific, Waltham, MA, USA) and gel electrophoresis. A modified RADseq approach for NGS library preparation was used (see Hühn et al., 2022). Genomic DNA (200 ng per sample) was fragmented using the restriction endonucleases (REase/s) *Bam*HI (restriction site: G’GATCC) and *Kpn*I (restriction site: GGTAC’C) in a double digest reaction. Following digestion, the fragments were ligated to sample-specific barcode adapters containing equimolar amounts of the REases motif pairs.



(caption on next page)

Fig. 2. A: *Maireana atkinsiana*; B: *Maireana georgei*; C: *Maireana lobiflora*; D: *Sclerolaena burbridgeae*; E: *Sclerolaena eurotioides*; F: *Sclerolaena alata*; G: *Didymanthus roei*; H: *Dissocarpus paradoxus*; I: *Enchylaena tomentosa*; J: *Eremophea aggregata*; K: *Eriochiton sclerolaenoides*; L: *Malacocera tricornis*; M: *Neobassia proceriflora*; N: *Osteocarpum dipterothecum*; O: *Roycea spinescens* (male) in flower; P: *Roycea pycnophylloides*; Q: *Threlkeldia diffusa*. Images and voucher: A: C.J. French 13178, NW Coastal Hwy 18.7 km N Woodleigh Rd, WA, 31 Aug. 2019; B: C.J. French 13186, Butchers Track 95.5 km E of NW Coastal Hwy, 2 Sep. 2019; C: P. Hühn D: C.J. French 13198, Twin Peaks–Wooleen Rd at turn-off to Twin Peaks station, 2 Sep. 2019; E: C.J. French 13208, 1.5 km N Bell & Vandeleur Rds, 4 Sep. 2019; F: C.J. French 13194, Carnarvon–Mullewa Rd 5.3 km S Butchers Track, 2 Sep. 2019; G: C.J. French 13162, Binu West Rd Causeway W of Binu Bins, WA, 30 Aug. 2019; H: K.R. Thiele 3262 (PERTH 07892381); I: P. Hühn; J: C.J. French 13181, NW Coastal Hwy 4.5 km S White Bluff Lookout, WA, 1 Sep. 2019; K: P. Hühn; L: K.R. Thiele 4532 (PERTH 08788308). M: K. Nicolson (CC-BY–), Opalton QLD 4735, Australia, <https://www.inaturalist.org/observations/38353144>; N: K.R. Thiele (PERTH 4973941); O: P. Hühn; P: P. Hühn; Q: *Cinclosoma* (CC-BY) Victoria, Australia <https://www.inaturalist.org/photos/301726584>.

Reactions were incubated for 3 hours at 37°C. Subsequently, the libraries were multiplexed, purified (NucleoSpin Gel and PCR Clean-up Mini kit by Macherey-Nagel, Düren, Germany) and quantified using a Qubit 3.0 Fluorometer. A Pippin Prep (Sage Science, Beverly, MA, USA) was used for size selection with a segregation range of 350–720 nt. The size-selected product was amplified using a low-cycle 2-step PCR protocol, followed by column-based purification and fluorometric quantification. A second size selection was performed with SPRI magnetic beads (NucleoMag NGS kit, Macherey-Nagel, Düren, Germany) using a ratio of 0.8 bead suspension to one part library. Library quality was validated using fluorometric quantification and assessment of fragment length range with a Bioanalyzer (Agilent, Santa Clara, CA, USA) electropherogram. Sequencing was done using the Illumina MiSeq v3 kit for 300 bp PE reads (San Diego, CA, USA) at the Macrogen NGS facility (Seoul, Republic of Korea). For a detailed description of the wet lab procedures see Hühn et al. (2022).

Data assembly — RADseq data assembly was carried out following Hühn et al. (2022). Raw data was demultiplexed using ipyrad v0.9.52 (Eaton and Overcast, 2020). No mismatch in the barcode sequence was allowed. Adapter trimming was done using cutadapt version 2.3 (Martin, 2011). We used FastQC (Andrews, 2010) and MultiQC (Ewels et al., 2016) for read quality validation. For *de novo* data assembly, we used ipyrad v0.9.52 (Eaton and Overcast, 2020). We used default assembly settings except for the following settings: The assembly method was set to *denovo-reference*, using three *Amaranthaceae* plastomes to remove reads of plastid origin (*Amaranthus viridis* L., NCBI accession: PRJNA720789, Ding et al., 2021; *Beta vulgaris* L., NCBI accession: PRJEB45680, De Marchis et al., 2009; *Chenopodium acuminatum* Willd., NCBI accession: PRJNA671764, Wariss and Qu, 2021). The thresholds for statistical and majority rule base calling were raised from six to ten, the datatype was defined as “pairgbs”, we selected strict adapter filtering, required a minimum locus length of 200 nt and raised the maximum number of indels per locus from eight to 24 (due to the extended sequencing range). For a detailed description of the assembly parameters and the selected thresholds see the ipyrad documentation (Eaton and Overcast, 2020; <https://ipyrad.readthedocs.io>, revision 1f88f521) and Hühn et al. (2022), respectively.

To determine suitable clustering thresholds (CTs) for in-sample-clustering (ISC) and between-sample-clustering (BSC), the customized CT selection approach by Hühn et al. (2022) was used. For ISC threshold selection, the demultiplexed samples were clustered using a CT range of 0.88–0.96. The heterozygosity and the proportion of detected paralogs were recorded for each sample individually, plotted across the CT range and evaluated with respect to a balance between both metric maxima, as suggested by Ilut et al. (2014) and McCartney-Melstad et al. (2019). Suitable thresholds for ISC were averaged to consensus values for each sample. Following ISC threshold selection, the samples were merged and clustered across all accessions for BSC threshold selection (CT range: 0.88–0.96). The assembly output statistics were evaluated with respect to the proportion of duplicates and putative paralogs detected, the proportion of missingness in the SNPs and sequence matrix, and the number of new polymorphic loci (NPL, Paris et al., 2017) between adjacent CTs. The BSC threshold was selected with respect to a minimized missingness in the data matrix within a CT-range of decreasing duplicates and paralogs detected and a maximized NPL proportion (Ilut et al., 2014; Paris et al., 2017; McCartney-Melstad et al., 2019; Hühn

et al., 2022).

Phylogenetic inference & molecular dating — Maximum likelihood (ML) phylogenies of the concatenated sequence matrices were inferred using RAxML-NG v0.9.0 (Kozlov et al., 2019) under the GTR+GAMMA model. ML tree search was initiated with 10 random and 10 parsimony trees. Statistical support was assessed using 100 Felsenstein’s bootstrapping replicates (Felsenstein, 1985) as implemented in RAxML-NG.

Divergence time estimation for the *Camphorosmeae* phylogeny was carried out using a previously published age estimate for the split of the Central Asian clade of *Grubovia dasyphylla* plus *Eokochia saxicola* from the Australian *Camphorosmeae* (i.e., 19.0 million years (Myr); 95 % HPD = 14.7–24.0 Myr) as calibration point (Kadereit and Freitag, 2011; Kadereit et al., 2014). A second calibration point was pre-defined for the divergence of the clade comprising *Maireana ciliata* (F.Muell.) Paul G. Wilson through *M. cannonii* (J.M.Black) Paul G. Wilson from the clade of *Neobassia proceriflora* (F.Muell.) A.J.Scott and *Sclerolaena*, i.e., 5.0 Myr (95 % HPD = 3.9–6.2 Myr; Cabrera et al., 2011).

The dating analysis was performed using BEAST v2.6.4 (Bouckaert et al., 2019). The topology of the *Camphorosmeae* phylogeny was fixed by setting the weight of the BEAST operators *subtree slide*, *narrow exchange*, *wide exchange* and *Wilson Balding* to zero. A lognormal relaxed clock and birth-death process were used for calculations. The ucl.d.mean parameter was defined as gamma-distributed with 0.001 and 1000 as lower and upper bounds, respectively, and the GTR+I+Γ substitution model was used. Four independent runs were performed with between 50 and 77 million generations per run, and the resulting log files were checked for convergence using Tracer v1.7.1 (Rambaut et al., 2018). Runs were combined using LogCombiner v2.6.3 (Bouckaert et al., 2019) pre-defining a burn-in of 10 %, and a maximum clade credibility (MCC) tree was constructed using TreeAnnotator v2.6.3 (Bouckaert et al., 2019) and inspected using FigTree v1.4.4 (Rambaut, 2018).

High levels of missing data can decrease the estimation accuracy of dating analyses using BEAST (Wiens and Morrill, 2011; Zheng and Wiens, 2015). To decrease the level of missing data and thus, to improve the accuracy of the BEAST analysis, the data matrix was filtered regarding a minimum locus coverage of 10 (minimum number of samples per locus).

Survey of habitat types — Australian desert landscapes have been mapped and described by Mabbutt (e.g. 1969, 1977, 1984, 1988) and have been used to describe and explain associated vegetation, desert ecology and arid geomorphic processes (Cunningham et al., 1981; Fox, 1999; Whitford, 2002; Yang and Goudie, 2007). The interaction of climate with base geology and geomorphology determines soil characteristics and impacts ecosystem processes and the nature and distribution of vegetation (Whitford, 2002). McDonald (2020) used the abundance of Australian chenopods on eight arid landscapes to describe the preferred habitat types of chenopod species. Two more habitats were added by McDonald (2020) to cover temperate to sub-tropical (Mesic Plain & Range) and coastal (Coast) species distributions in adjacent areas of the arid zone (Table 2). By mapping these land type occupations on the phylogenetic tree, clade-specific shifts and adaptations may be observed and may be put in relation to chronological diversification events. The species-specific habitat type occupations were taken from McDonald (2020; Table 1). The definitions of habitat types (Table 2) were largely adopted from McDonald (2020), who based the

Table 2

Habitat types as defined by Mabbutt (1988) and McDonald (2020). Given are the habitat types with abbreviations in parentheses and characteristic geomorphological and floristic features, as well as a geochronological explanation of their origins. Descriptions were largely adopted from McDonald (2020). The occurrences of the sampled species in the various habitat types are given in Table 1.

Habitat Type	Landforms	Vegetation/Soil/Salinity	Origin
Sand Desert (SD)	Aeolian dune fields and sandplains; discontinuous or in long, linear dunes; stable slopes under vegetation cover, with mobile sand on dune crests.	Hummock grassland, <i>Acacia</i> spp. tall shrubland or <i>Eucalyptus</i> spp. open woodland. Only saline where thin sand sheets cover older landscapes.	Formation of dune fields is associated with substantial denudation of landscapes (Twidale and Wopfner, 1990; Laity, 2008).
Desert Upland (DU)	Rocky ranges, hillslopes and tablelands of sedimentary rock (sandstone and quartzite); includes major uplands such as Flinders Ranges and the Kimberley Plateau.	Sclerophyllous woodland, <i>Acacia</i> shrubland and hummock grassland. Thin, stony soils; non-saline and non-alkaline except on limestone substrates. Saline or alkaline sections downslope.	Uplands are younger than their constituent rock types. Major uplands in place through the Neogene.
Stony Desert (SP)	Dissected tablelands and plains of pebbly pavements (gibbers); complex drainage networks due to lack of infiltration that causes high surface run-off (McKenzie et al., 2004).	Low grassy/chenopod formations (Brandle, 1998) due to extreme exposure and very dry conditions. Clayey soils, moderately to strongly saline; much varied lime and gypsum.	Maximum Australian development occurred in areas of least rainfall during global dry phase (Fujioka and Chappell, 2010).
Shield Plain (SH)	Subdued, rocky landscapes of igneous and metamorphic rocks in Western, Central and South Australia, that has sandplain mantles.	Vegetation similarly varied with sclerophyllous woodland, shrubland and grassland. Varied calcareous, deep or shallow soils with surface sand or clay; non-saline or saline.	Cratonic platform that retains past elements of peneplanation and deep-weathering.
Riverine Desert (RL)	Desert drainage systems mainly in Lake Eyre and Murray Basins. Occasional channel flows with infrequent inundation of extensive floodplains.	Vegetation open and arborescent along channels and floodplains; grassy and chenopod formations in broad flats; extensive chenopod low shrubland on dry alluvial plains. Regularly inundated features less saline than more distant plains of mild to moderate salinity. Soil type variable.	Emerged in the west in the Middle Miocene when palaeo valleys ceased to flow (Van de Graaff et al., 1977).
Desert Clay Plain (CP)	Broad, alluvial plains of heavy soil in north-east Australia.	Open <i>Astrelba</i> spp. grasslands; chenopod species in groundcovers. Strongly alkaline or mildly saline dark clays.	Tertiary lacustrine and alluvial clay deposits, exposed in the later Neogene (Edgoose, 2003).
Karst Plain (KP)	Undulating plains of pedogenic sheet calcrete across southern Australia. Bunda Plateau on the Nullarbor Plain is a flat plain of low elevation on	Prominently chenopod (<i>Atriplex</i> and <i>Maireana</i>); limestone taxa dominate shrub layers and groundcovers. Shallow, alkaline loams over thin	The Nullarbor Plain has always been arid. The atypically flat surface of the Bunda Plateau is interpreted as evidence of little rainfall since the Late Miocene uplift (

Table 2 (continued)

Habitat Type	Landforms	Vegetation/Soil/Salinity	Origin
Desert Lake (DL)	crystalline limestone. Disconnected, saline complexes in pans, flats with marginal lunettes; vast lakes of regional lowlands; highly saline lowlands of temperate plains.	calcrete; saline near the coast. Vegetation zones of different chenopod taxa across sharp salinity gradients from bare salt crust to slight salinity on margins.	Benbow et al., 1995). Desert Lake emerged from Riverine Desert landscapes, forming disconnected flats in the vast, flat Australian continent.
Mesic Plain & Range (MP)	Temperate to subtropical ranges and plains of eastern, southern and western continental margins; includes igneous peneplain, alluvial plain and fixed dunes.	Sclerophyllous vegetation dominant; chenopod taxa in very seasonal climates or on heavy soils in drier areas. Soils commonly acid-neutral trend, but alkaline in drier regions.	Present since the Early Miocene.
Coast (CS)	Beach-dune complexes; coastal lagoons and estuaries; rocky shores or cliffs; humid northern and eastern coast has more estuarine habitat than arid western and southern coasts.	Coastal shrubland, heath and saltmarsh. Marine chemistry determines saline characteristics; dominated by sodium chloride.	The arid and humid coastal contrast likely developed over the Neogene.

descriptions on Stace et al. (1968), Mabbutt (1988) and McKenzie et al. (2004).

3. Results

Sampling — Circa 70 % of all Australian Camphorosmeae species were sampled for this study (103 out of 147 described species; Wilson, 1984). Representatives of all genera were included (Table 1) and the morphological and ecological variation of Australian Camphorosmeae was sufficiently covered. However, some regions of Australia's arid zone are relatively under-represented. For instance, the north-west of Western Australia (including the Pilbara and Great Sandy Desert Interzone), the Central Desert spanning the north from Western Australia eastwards across the Northern Territory, and the eastern fringes of the Eastern Desert that expand into the subtropical and temperate areas of Central Queensland, Eastern Queensland and the Southeastern region. These regions harbor a number of species, the inclusion of which might alter the fine-tuned interpretation of the results presented here.

Sequencing and assembly statistics — Sequencing resulted in 33,906,603 raw reads (319,873 reads per sample) of which 88 % passed the quality filters. The selected thresholds for in-sample-clustering ranged from 0.93 to 0.95 (Supplement 3, ISCT selection). The metrics evaluated for between-sample-clustering threshold selection indicated a CT of 0.93 as most suitable for all assemblies (Supplement 3, BSCT Assembly 1–3). At this threshold, the proportion of detected duplicates decreased distinctly while the proportion of detected paralogs increased only slightly (plots: “detected duplicates” and “detected paralogs”). The plots of the new polymorphic loci showed a first strong increase at CT 93/94, which represents a CT value of 0.93 (plots: “NPL_PIS” and “NPL_VAR”). The SNPs and sequence matrix size was maximized (plots: “SNPs-“ and “Sequence matrix size”) and the proportion of missingness started to decrease (plots: “SNPs-“ and “Sequences missing”). The assembly contained 8659 loci with 316,465 variable sites, of which 72,009 sites were parsimony informative. The average sample coverage (retained loci per sample) was 560. The sequence matrix contained

93.59 % missing data. The assembly used for the BEAST analysis contained 1084 loci with 56,794 variable sites of which 16,806 sites were parsimony informative. The sequence matrix contained 84.3 % missing data. The concatenated supermatrices of both assemblies are provided as PHYLIP files in the online [supplementary material](#).

CA-ML phylogenies and dating — The CA-ML phylogeny of the entire Camphorosmeae sampling yielded 17 moderately to fully supported clades (Fig. 3; [supplementary figure S1](#)). Four accessions were resolved on individual branches. The backbone was poorly resolved for the *Maireana* grade, but fully resolved for the *Sclerolaena* clade. Collapsing branches below a bootstrap support value of 75 resulted in two polytomies for the *Maireana* grade (Fig. 3). The clades of the first polytomy contained the accessions of *Roycea*, *Eriochiton* and eleven *Maireana* species. The clades in the second polytomy comprised 32 *Maireana* species, two *Sclerolaena* species (*S. fimbriolata* and *S. stelligera*), and the accessions of *Didymanthus*, *Dissocarpus*, *Enchylaena*, *Eremophea* and *Malacocera*. The *Sclerolaena* clade contained 38 *Sclerolaena* species and the accessions of *Neobassia*, *Osteocarpum* and *Threlkeldia* (Fig. 3; [supplementary figure S1](#)).

The time calibration using BEAST suggest the Australian Camphorosmeae split from its Eurasian sister lineage during the Middle to Late Miocene ca. 12.99 Myr ago [9.96–15.97] (Fig. 3, Table 3). A first rapid diversification occurred in the Late Miocene ca. 8.34 [6.54–10.38] Myr ago (Fig. 3, Table 3, 1st polytomy). This first radiation includes clades 1–3, and *M. oppositifolia*, *M. enchylaenoides* and *M. sedifolia*. A second rapid radiation occurred ca. 7.46 [5.85–9.23] Myr ago, and comprises clades 4–11 plus the species-rich *Sclerolaena* clade (*N. proceriflora* and clades 12–17, Fig. 3, Table 3, 2nd polytomy). Crown group diversification of the first radiation started in a period of ca. 5.96–7.68 [4.22–9.67] Myr ago and was strongest during the Late Miocene (Messinian). Crown group diversification of the second radiation (excluding the *Sclerolaena* clade) was strongest during the Pliocene in a period of 4.46–6.06 [3.09–7.63] Myr ago. Crown group diversification of the *Sclerolaena* clade started ca. 6.27 Mya [4.88–7.68] Myr ago and was strongest during the Pliocene in a period of 3.54–5.32 [2.53–6.56] Myr ago (Fig. 3, Table 3). The time estimates are largely congruent with the findings of [Cabrera et al. \(2011\)](#).

Habitat preferences — By comparing the preferred habitats of the species in the two polytomies of the *Maireana* grade with those of the *Sclerolaena* clade, several habitat shifts become apparent (Fig. 3, Table 4). A general prevalence in Riverine Desert (RL) habitats (41 % of all included species) and Desert Lake (DL) habitats (33 %) is evident across the phylogeny. Stony Desert (SP) (27 %) and Karst Plain (KP) habitats (22 %) are also frequently colonized. Coastal (CS) (9 %) and Desert Clay Plain (CP) habitats (6 %) are the least frequently colonized habitats. Species of the first polytomy occur predominantly on sandy, saline soils in Desert Lake habitats (73 % of all species in the first polytomy), followed by Karst Plain and Riverine Desert habitats (both 27 %) (Fig. 3, Table 4). This ratio shifts in favor of Riverine Desert (38 %), Desert Lake (33 %), and Karst Plain habitats (27 %) for the species in the second polytomy. Other arid habitats, such as Sand Desert (SD), Desert Upland (DU) and Stony Desert landscapes become increasingly colonized. The species of the *Sclerolaena* clade occur predominantly in Riverine Desert (50 %) and Stony Desert habitats (41 %). As is the case with the *Maireana* clades of the second polytomy, other arid habitats are more frequently colonized.

4. Discussion

4.1. Diversification of Camphorosmeae in the landscapes of desiccating Miocene–Pliocene Australia

The arrival of Camphorosmeae on the Australian continent dates to the Middle and early Late Miocene (12.99 [9.96–15.97] Mya) with subsequent initial diversification (8.34 [6.54–10.38] Mya) in the Late Miocene (Figs. 3 and 4, Table 4). As suggested by [Cabrera et al. \(2011\)](#)

and [Kadereit and Freitag \(2011\)](#), the ancestors of the Australian Camphorosmeae must have arrived via long-distance dispersal, as the Australian continent had not been connected to the original Gondwana land masses since the beginning of the Cenozoic. The group probably originated in the temperate semi-arid to arid parts of continental Eurasia, where the closest relatives are distributed today. The Central Asian genus *Grubovia*, which is sister to the Australian Camphorosmeae, contains annual xerophytes that grow in summer-rainfall open steppe communities, mainly in sandy, slightly saline soils ([Zhu et al., 2003](#); [Kadereit and Freitag, 2011](#)). Species of Camphorosmeae outside Australia are either distributed in semi desert or desert habitats or in coastal habitats, suggesting a long evolutionary history of adaptation to dry and saline conditions in the tribe ([Kadereit and Freitag, 2011](#)). The species of the Eurasian genera *Bassia* All. and *Camphorosma* L., which are sister to the Australian species plus *Grubovia*, all grow in dry steppe and semi-desert communities, mainly in sandy, non-saline soils, while the closely allied Central Mediterranean genus *Eochochia* Freitag & G. Kadereit grows on coastal cliffs ([Kadereit and Freitag, 2011](#)).

The biogeographic analysis by [Cabrera et al. \(2011\)](#) showed that the most likely area of arrival and ancestral diversification is located in the south and west of the continent. This estimation coincides with the presence of chenopod pollen fossils in west and south Australia since the Late Miocene ([McDonald, 2020](#)). The group then expanded its range easterly across the interior of the continent and colonized the Eastern Desert including the Lake Eyre–Murray basin during the middle Late Miocene, which again is supported by the pollen fossil record in central Australia and the Murray Basin ([McDonald, 2020](#)). Subsequently, the peripheries of today's arid zone and finally today's tropical areas were colonized. [McDonald \(2020\)](#) investigated the migration routes along arid land types of Australian chenopods and suggested the Sandland province from north-west Western Australia through to South Australia, with its extensive network of disconnected drainage systems and river-desert and desert-lake landscapes, as a possible migration corridor through the interior of the continent. Further, Camphorosmeae migration was likely multidirectional, with steady movement of species between newly colonized areas ([Cabrera et al., 2011](#); [McDonald, 2020](#)). [Cabrera et al. \(2011\)](#) suggested that the progenitors of Australian Camphorosmeae were already adapted to arid and saline environments and thus were able to quickly colonize newly emerging arid landscapes. Successful colonization of newly emerging arid habitats may have been favored by niche pre-emption.

At the time of arrival, suitable landscapes for the colonization of the continent gradually formed as the climate became increasingly cooler and drier ([Mabbutt, 1988](#); [Martin, 2006](#); [Byrne et al., 2008](#); [Fujioka and Chappell, 2010](#); Fig. 4). Ecological adaptation may have enabled the progenitors to colonize the saline habitats of flooded basins, such as the Eucla Basin at the south coast ([Burbidge, 1960](#); [Barlow, 1994](#); [McDonald, 2020](#)). A first inland migration may have taken place by species adapted to coastal, marshy conditions, providing a littoral connection along declining palaeodrainage systems to hypersaline inland habitats ([Shmida, 1985](#); [Saintilan, 2009](#); [Cabrera et al., 2011](#); [Lomolino et al., 2010](#); [McDonald, 2020](#)). The ecologically diverse coastal habitats have inland analogues, such as inland playas of saline lake systems and inland marsh habitats surrounding lake systems and swamps. Adaption to coastal habitats is rare in Australian Camphorosmeae but present across the phylogeny (Fig. 3, 'CS' on clades 4, 6, 11, 14, 15, 17). Some Camphorosmeae species (e.g., *Disdocarpus biflorus*, *Enchylaena tomentosa*, *M. brevifolia*, *M. cannonii*, *M. oppositifolia*, *S. bicornis*, and *T. diffusa*) are found in both saltmarsh habitats (CS) and in hypersaline Desert Lake (DL) or Riverine Desert (RL) habitats ([Saintilan, 2009](#)). The low number of Camphorosmeae species found in coastal habitats today may be explained by extinction (promoted by fluctuating sea level) or progressive replacement by other more competitive taxa. Other Amaranthaceae lineages, such as *Atriplex* and *Salicornioideae*, are for example major competitors in coastal habitats ([Kadereit et al., 2005](#); [Zerdoner Calasan et al., 2022](#)) and may have displaced Camphorosmeae species from these

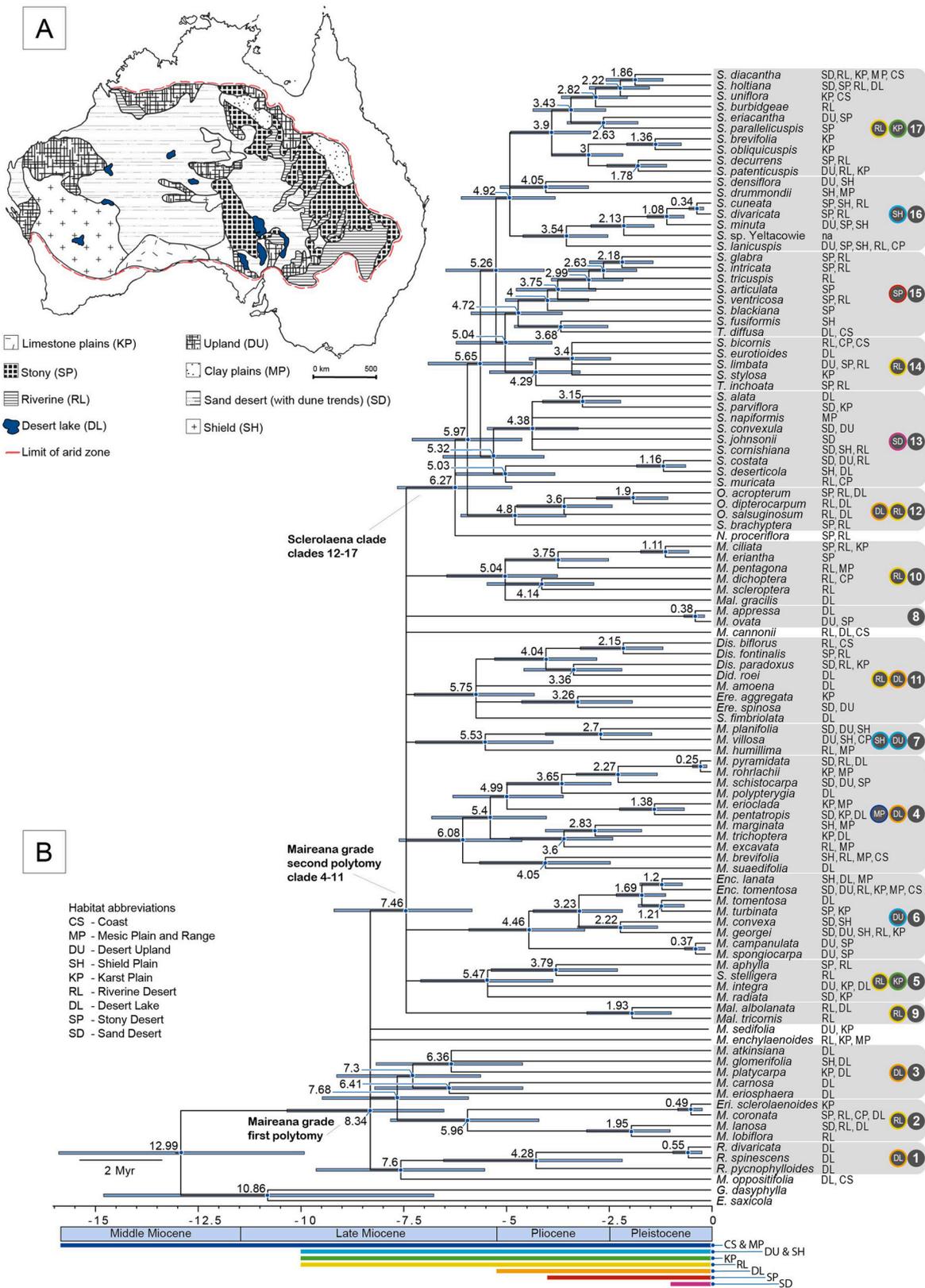


Fig. 3. A. Map of Australian Desert Landscapes (habitat types) adapted from Mabutt (1988, Fig. 1). B. Chronogram with species habitat occurrence. Shown is the collapsed topology. Given are the node age estimates and 95% confidence intervals (blue bars). Timeline 16 Million years ago to present. Timeline of landscape (habitat) history based on McDonald (2020). The occupied habitat types (defined in Table 2) are given for each species. The habitat occupations were taken from McDonald (2020); see also Table 1. Missing information was classified as "na" (not applicable). Each supported clade is shaded in grey and numbered, with the most frequently colonized 67 habitats color-coded with respect to the habitat timeline, which is also given below the time scale. Confidence intervals of the clade are shown in Table 3.

Table 3

Results of the BEAST divergence time analysis. Given are the node age estimates and 95 % confidence intervals (HPD) for the outgroup split, the two polytomies plus the *Sclerolaena* clade, and the crown group estimates for the clades.

	estimated age (Mya)	95 % HPD (Mya)
outgroup split	12.99	9.96–15.97
1st polytomy (stem age)	8.34	6.54–10.38
clade 1	7.60	5.54–9.67
clade 2	5.96	4.22–7.85
clade 3	7.30	5.64–9.16
clade 2+3	7.68	5.94–9.52
<i>M. enchylaenoides</i>	8.34	6.54–10.38
<i>M. sedifolia</i>	8.34	6.54–10.38
2nd polytomy (stem age)	7.46	5.85–9.23
<i>M. cannonii</i>	7.46	5.85–9.23
clade 4	6.08	4.63–7.63
clade 5	5.47	3.87–7.11
clade 6	4.46	3.09–5.92
clade 7	5.53	3.87–7.23
clade 8	0.38	0.16–0.68
clade 9	1.93	0.97–3.03
clade 10	5.04	3.76–6.47
clade 11	5.75	4.33–7.26
<i>Sclerolaena</i> clade	6.27	4.88–7.68
<i>N. proceriflora</i>	6.27	4.88–7.68
clade 12	4.80	3.55–6.12
clade 13	5.32	4.09–6.56
clade 14	4.29	3.25–5.42
clade 15	4.72	3.64–5.87
clade 16	3.54	2.53–4.6
clade 17	3.90	2.95–4.9

habitats. Hence, the habitation hypothesis by means of a littoral connection appears plausible.

A **first rapid radiation** of the Australian Camphorosmeae occurred during the Late Miocene, ca. 8.34 [6.54–10.38] Mya (Figs. 3, 4, Table 3). Crown group diversification of clades 1–3 started in the Late Miocene, ca. 7.6–7.68 [5.94–9.67] Mya (Fig. 3, Table 3, clades 1–3). The species of the first rapid radiation are currently distributed mainly in western and south Australia and have clear preference for sandy, saline soils and Desert Lake habitats (73 % of all species in the first polytomy), followed by Karst Plain and Riverine Desert habitats (both 27 %) (Fig. 3, Table 4). The rapid radiation and beginning crown group diversification of the first polytomy likely have been driven by the progressive expansion of drier climates and drier and increasingly saline landscapes during this period (Fig. 4). This supports the assumption proposed by Byrne et al. (2008) that the "Hill Gap" was an early period of diversification of arid zone taxa. The multidirectional expansion into the arid zone (from south-west easterly across the interior and then south-east and towards

the arid-zone periphery) (Cabrera et al., 2011; McDonald, 2020) may have taken place by species adapted to various habitats (shifting habitat preferences; Table 4), and relatively quick, as there are no major geological barriers. The species of the first polytomy (including clades 1–3 in Fig. 3, and *M. oppositifolia*, *M. sedifolia* and *M. enchylaenoides*) have soil and habitat preferences that support three west to east migration scenarios.

The first migration scenario may have occurred from south-west to north-west and then to the easterly interior and was probably favored by adaptation to ephemeral river and lake habitats. Clades 1 and 3 have their distribution center in Western Australia (with *M. carnosus* also occurring in the eastern arid-zone) and are predominantly adapted to Desert Lake habitats. The species of clade 2 are predominantly adapted to Riverine Lake habitats (Fig. 3) and their distributions range from Western Australia to the Eastern Desert and the Lake Eyre-Murray Center. Riverine Lake habitats were present in Western Australia since the Miocene and progressively expanded with ongoing cessation of the palaeodrainage system. Progenitors of the first migration scenario may have migrated northwards along increasingly saline desert river systems and diversified into vacant habitats that progressively turned into Desert Lake habitats. Easterly inland migration was likely promoted by the west-to-east gradient of declining precipitation and increasing aridity that resulted in an easterly expansion of Riverine Desert habitats throughout the continent's interior (Kershaw et al., 1994; Martin, 2006). This easterly expansion started in the upper Late Miocene and increased during the early Pliocene. As suggested by McDonald (2020), the Sandland provinces may have been the main migration corridor from the western to the eastern deserts. Today, the Riverine Desert and Desert Lake habitats of the Sandland provinces are disconnected by extensive sand plains and dune field formations of the Great Sandy, Gibson and Victoria Desert that formed in central Australia during the Pleistocene (Fujioka and Chappell, 2010). Assuming vicariance, this dissected landscape is also reflected in the disjunct distributions of *M. carnosus*, *M. lobiflora* and *M. lanosa*.

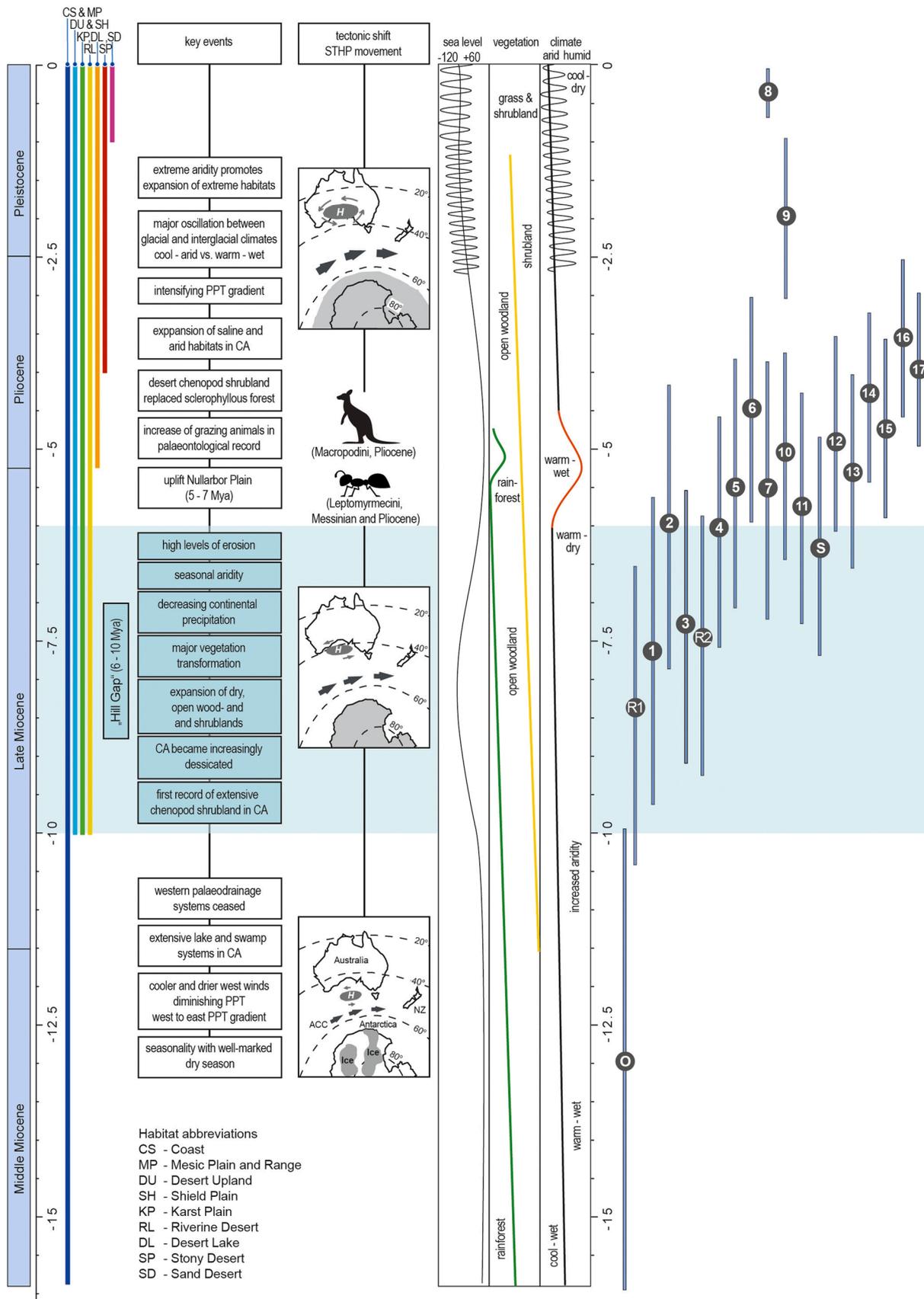
For the second and third scenario, the origin of the Nullarbor Plain may be of importance. Prior to the uplift of the Nullarbor Plain in the upper Late Miocene (Fig. 4), the coastline was along the southern portion of the Sandland South province (Webb and James, 2006; McDonald, 2020). With the retreating sea, the coastline slowly moved to its today's southern margin and exposed the Nullarbor Limestone to weathering. The surface slopes gently towards the sea and is traversed by old river courses. The plain terminates abruptly in a cliff line that extends ca. 900 km, with coastal plains in the center and in the west.

The second migration scenario along southern coastlines may have taken place by species adapted to coastal and marshy conditions.

Table 4

Habitat preferences. Comparison of species occurrence in defined habitats, given in percentages. Given are the percentages for all included species, for the species of the *Sclerolaena* clade, for the species of the second polytomy (excluding the *Sclerolaena* clade) and for the species of the first polytomy (Fig. 3). The four highest values in bold. Habitat abbreviations: SD = Sand Desert, DU = Desert Upland, SP = Stony Desert, SH = Shield Plain, RL = Riverine Desert, CP = Desert Clay Plain, KP = Karst Plain, DL = Desert Lake, MP = Mesic Plain and Range, CS = Coast.

	SD	DU	SP	SH	RL	CP	KP	DL	MP	CS
all species										
count	18	19	28	16	43	6	23	34	12	9
%, n=104	17.3	18.3	26.9	15.4	41.4	5.8	22.1	32.7	11.5	8.7
<i>Sclerolaena</i> clade										
count	7	8	18	8	22	3	7	8	3	4
%, n=44	15.9	18.2	40.9	18.2	50.0	6.8	15.9	18.2	6.8	9.1
<i>Maireana</i> grade 2nd Polyto										
count	10	10	9	7	17	2	12	15	8	4
%, n=45	22.2	22.2	20.0	15.6	37.8	4.4	26.7	33.3	17.8	8.9
<i>Maireana</i> grade 1st polyto										
count	1	1	1	1	4	1	4	11	1	1
%, n=15	6.7	6.7	6.7	6.7	26.7	6.7	26.7	73.3	6.7	6.7



(caption on next page)

Fig. 4. Overview of climatic, tectonic, landscape, and biotic changes in Australia since the Middle Miocene with respect to the diversification of the Australian Camphorosmeae. Given from left to the right: Timeline 16 Million years ago to present. Timeline of landscape (habitat) history based on McDonald (2020) and Table 2. Key climatic, geological and biotic events of Australia's aridification. Tectonic shift of the Australian plate and movement of the Sub-Tropical High Pressure system, according to Bowler (1982) and Fujioka and Chappell (2010). Changes in sea level based on Martin (2006) and Byrne et al. (2008). Changes in vegetation composition based on Martin (2006) and Fujioka and Chappell (2010). Climatic changes based on Byrne et al. (2008) and Fujioka and Chappell (2010). Diversification events of the Australian Camphorosmeae taken from Table 4 and Fig. 3. The encircled clade numbers are shaded in grey: O: outgroup split, R1: rapid radiation of the first polytomy (clades 1–3), R2: rapid radiation of the second polytomy (clades 4–11), S: diversification of the *Sclerolaena* clade (clades 12–17). Aridification of Australia became evident at the end of the Middle Miocene: cooler and drier west winds resulted in a diminishing west to east precipitation (PPT) gradient, and the western palaeodrainage systems ceased. The Late Miocene was characterized by major environmental changes leading to the development of more arid conditions and an early expansion of the arid zone in central Australia (CA). This period is known as the "Hill Gap". The Pliocene was a period of intensifying aridity throughout the continent in which characteristic arid-zone habitats greatly expanded. The beginning of the Pleistocene represents the onset of major oscillations between glacial and interglacial climates, resulting in fluctuating temperatures and sea levels. Along with these major climatic oscillations, extreme aridity promoted the expansion of extreme arid habitats such as Stony and Sand Desert habitats. Initial diversification of the Australian Camphorosmeae coincides with an early expansion of arid climates and landscapes during the "Hill Gap". Crown group diversification increases with increasing aridification of the arid interior at the end of the Late Miocene and in particular during the Pliocene. Diversification of the *Sclerolaena* clade during this period also coincides with the occurrence and diversification of large herbivores, such as kangaroos (Macropodini) and wombats (Archer et al., 1994; Couzens and Prideaux, 2018), and with rapid radiations of arid-adapted ants (Leptomyrmecini) and termites (Ward et al., 2010; Heimburger et al., 2022). Image sources: Timeline of landscape (habitat) history in Australia since the Middle Miocene based on McDonald (2020), Fig. 3.1. Tectonic shift and movement of the Sub-Tropical High Pressure system taken from Fujioka and Chappell (2010), Fig. 2, who based their illustration on Bowler (1982). Cartoon Kangaroo vector by Ery Prihananto, free vector graphic available at < <https://www.uidownload.com/>>, < <https://www.uidownload.com/en/vector-jgslh>>. Cartoon ant vector by Brian Goff, Published under the "free licence" by Vecteezy: < https://support.vecteezy.com/en_us/new-vecteezy-licensing-ByHivesvt>, < <https://de.vecteezy.com/vektorkunst/546797-cartoon-ant-insektenwanze>>. Changes in sea level based on Martin (2006): Fig. 3) and Byrne et al. (2008): Fig. 1). Changes in vegetation composition based on Martin (2006) and Fujioka and Chappell (2010): Fig. 5). Changes in climate based on Byrne et al. (2008): Fig. 1) and Fujioka and Chappell (2010): Fig. 5).

Maireana oppositifolia is found in Coastal and Desert Lake habitats (Fig. 3) and is distributed along the south coast from Western Australia to South Australia, spreads into the southern Yilgarn Plateau in Western Australia and across Eyre Peninsular northwards up to Lake Torrens in South Australia. Noticeably, this species occurs only along the coast at the Nullarbor, avoids the limestone plain, but can be found at the north-eastern and north-western margins, which reflect the coastline prior to the uplift of the Nullarbor Plain at the end of the Late Miocene (Webb and James, 2006). The habitat preferences of this species to both saline coastal habitats and saline desert lake habitats, represents an ecological niche in which progenitors could migrate along the coastline and progressively colonize inland habitats.

The third migration scenario may have taken place by species adapting to calcareous Karst Plain habitats. *Maireana sedifolia* and *Eriochiton sclerolaenoides* prefer calcareous soils of Karst Plain habitats. Both species have a southern distribution from the Western Desert areas across the Nullarbor Plain. The emergence of *M. sedifolia* (ca. 7–8 Mya) coincides roughly with the uplift of the Nullarbor Plain at the end of the Late Miocene (Figs. 3 and 4). *Eriochiton sclerolaenoides* emerged much later during the Pleistocene. It appears plausible that the uplift of the Nullarbor Plain and spread of limestone across the interior favored ecological adaptation to these calcareous soils and provided a southern migration path across this newly elevated plain.

A **second rapid radiation** event of the Australian Camphorosmeae occurred ca. 7.46 [5.85–9.23] Mya (Figs. 3, 4; Table 3). Crown group diversification of the *Maireana* clades (clades 4–11) started in the Late Miocene and early Pliocene (Figs. 3, 4; Table 3) with diversification continuing throughout the Pliocene, and only clades 8 and 9 diversifying during the Pleistocene. *Maireana* species from the second polytomy are widespread across the continent. Compared to the species of the first polytomy, the preferred habitat types shift in favor of Riverine Desert (38%), Desert Lake (33%), and Karst Plain habitats (27%), and other arid habitats, such as Sand Desert, Desert Upland and Stony Desert landscapes, are becoming increasingly colonized (Table 4). In addition, the occupied soils become less saline. The high degree of diversification during this period was probably driven by the intensifying aridification and consequent major expansion of interior arid habitats, in particular in central and eastern areas of the arid-zone that became increasingly saline and arid (Fig. 4).

The relatively species-poor clades of the *Maireana* grade (compared to the species-rich *Sclerolaena* clade) and longer branches of these clades indicate either lower speciation or higher extinction rates (Crisp et al., 2004). There are several plausible scenarios for this pattern. First, the

short return to a warm and humid climate at the beginning of the Pliocene (Fig. 4) with accompanying expansion of rainforest communities in suitable river slopes may have contributed to increased extinction rates in *Maireana* lineages that were adapted to Desert Lake and Riverine Desert habitats. Second, colonized habitats may have been quickly saturated due to rapid radiations of other arid-adapted taxa (Fig. 4) and ecological adaptation and expansion to new, vacant habitats was slow. Third, a rapid multidirectional colonization and constant migration between habitats may have resulted in increased gene flow, which in turn decreased divergence among populations and thus reduced speciation of these lineages (Hamrick and Godt, 1996, 1997; Räsänen and Hendry, 2008; Kisel and Barraclough, 2010). Fourth, during the extremely arid periods of glacial maxima in the Pleistocene, the central Australian desert was much larger in extent (desert dunes covered up to 85% of the continent during peak aridity) and much more hostile to plant growth (Jones and Bowler, 1980; Crisp et al., 2001; Bowler et al., 2006; Byrne et al., 2008; Andersen, 2016). This may have led to the contraction of species distributions and extinction events of narrowly endemic species. Fifth, the emergence of large herbivores in the early Pliocene may have favored extinction events (Fig. 4). However, these herbivores prefer grasses as a primary food source (Couzens and Prideaux, 2018) and feed on the sodium rich *Maireana* species (Revell et al., 2013) mainly during drought periods or in the presence of fresh water (Wilson, 1984). Whether this herbivory pressure led to increased extinction rates is doubtful, but grazing animals may have had an effect on perianth trait evolution and thus on dispersal syndromes and dispersal speed.

The **diversification of the *Sclerolaena* clade** (including *N. proceriflora* and clades 12–17) started in the Late Miocene, ca. 6.27 [4.88–7.68] Mya with continuous speciation throughout the Pliocene and Pleistocene (Figs. 3, 4; Table 3). Diversification coincides with an increase in chenopod pollen fossils in central Australia and the Murray Basin at the end of the Late Miocene and early Pliocene (McDonald, 2020). The species of the *Sclerolaena* clade are also widespread across the continent but have their center of diversity in the Lake Eyre–Murray basin of the Eastern Desert. The species of the *Sclerolaena* clade have a clear preference for Riverine Desert (50%) and Stony Desert habitats (41%) (Table 4). As is the case with the *Maireana* clades of the second polytomy, other arid habitats such as the Desert Upland, Sand Desert and Shield Plains, are more frequently colonized. Diversification was likely favored by the increasing aridity across Australia's interior and expansion of Stony Desert habitats (Fig. 4). The species-richness and continuous cladogenesis of this clade may be explained at least partly by

the appearance of spiny perianths.

Sclerolaena species of clades 13 and 15 are predominantly found in Sandy Desert habitats and Stony Desert habitats, respectively (Fig. 3). The crown group diversification of clade 15 fits the formation of stony pavements in the eastern arid zone, across the Great Artesian Basin and the Lake Eyre Basin in the Pliocene (Fujioka and Chappell, 2010). The Riverine Desert landscapes may again have taken an important role as a migration corridor. Four species (*S. glabra*, *S. intricata*, *S. tricuspis*, *S. articulata*) are sympatric across a large area in the Eastern Desert. *Sclerolaena glabra* has a disjunct distribution with occurrences in Riverine Desert habitats in north-western Australia and a main distribution in Riverine Desert and Stony Desert habitats in the eastern desert. The two range parts are separated by Sand Desert formations of the Great Sandy Desert, Gibson Desert and Great Victoria Desert. *Sclerolaena intricata* is distributed across the Riverine Desert and Stony Desert habitats of the Great Artesian Basin and the Lake Eyre Basin. *Sclerolaena tricuspis* is sympatric with *S. intricata* but found only in Riverine Desert habitats, avoiding the Stony Desert gibber plains of the Eastern Desert. *Sclerolaena articulata* is distributed only across the Stony Desert landscapes of the Eastern Desert, avoiding Riverine Desert habitats. The prevailing Stony Desert habitat preference suggests a directed adaptation to these habitats with emergence during the middle Pliocene. The persistence of Riverine Desert habitat preferences indicates a possible migration corridor between western and eastern ranges prior to or along the formation of Stony Desert and Sand Desert landscapes. However, the migration may have also been bidirectional in time and space. For instance, from easterly Stony Deserts to westerly Riverine Desert habitats, after the emergence of pebbly pavements and prior to the formation of Sand Deserts.

The species of clade 13 are predominantly found in Sand Desert habitats that emerged during the late Pleistocene, ca. 1 Mya (Fig. 3) (Fujioka and Chappell, 2010); however, the crown age of this clade (ca. 5.32 Mya, Table 4) considerably predates the formation of sand plain and dunefield landscapes. This drastic difference between the diversification of this clade and the emergence of the preferred habitat might be explained by two scenarios. Firstly, the discrepancy may be due to dating methods that yield high uncertainties for desert dune formation prior to the late Pleistocene (Fujioka and Chappell, 2010). Alternatively, taken together, the species of this clade have a large west-east inland range and colonize not only sandy desert landscapes but also arid habitats less characterized by sand dune formations and sandy plains, such as Riverine Desert habitats. These landscapes emerged earlier than Sand Deserts, during the Late Miocene and Pliocene. Thus, these species could originally have been adapted to Riverine Desert habitats and are only found in sand-dominated landscapes as a consequence of the formation of sandy habitats in north to central Australia during the last 1 Million years (e.g., Great Sandy Desert, Gibson Desert, Simpson Desert). Assuming vicariance, this second scenario is further supported by the disjunct distribution ranges of *Sclerolaena costata* and *S. deserticola*. The lineage of these two species emerged ca. 5 Mya and diversified ca. 1.2 Mya (Fig. 3, clade 13), slightly prior to the formation of sand deserts. As indicated by the preferred habitats (Sand Desert, Desert Upland, Riverine Desert, Desert Lake and Shield Plain) and their chronological emergence, the distribution ranges may have ranged continuously from the western to the eastern extant along ephemeral river and lake systems in the middle Pleistocene and were only separated by sand deserts formations during the late Pleistocene.

There seems to be a slowdown in speciation in Australian Camphorosmeae during the Pleistocene (Fig. 3). A similar observations has been made in other arid-adapted taxa (Crisp et al., 2004; Byrne et al., 2008, 2018; Crisp and Cook, 2013; Byrne and Murphy, 2020). Several scenarios to explain this pattern are being discussed. Repeated cycles of localized habitat contraction and expansion, along with climate oscillation and extreme drought, may have resulted in “species diversity maintenance” (Chesson, 2000; Byrne et al., 2008). The extreme climatic fluctuations did not lead to a higher speciation rate, but to a finer scale

phylogeographic structuring and speciation by hybridization and polyploidy (Byrne et al., 2008). Alternatively, the extreme climatic fluctuations may have led to stabilizing species diversity (Chesson, 2000). For example, if the density of species lowers due to harming environmental conditions during extreme drought periods, species numbers tend to recover during more favorable periods. However, species of similar ecology in the same spatial region mutually limit resource availability, hence, cause interspecific competition. Extreme climatic fluctuations and strongly limited resources impair speciation and result in maintained or stable species richness over long timescales. The expansion of the central Australian desert during the extremely arid periods of glacial maxima in the Pleistocene may have led to the contraction of species distributions and extinction of narrowly endemic species (Jones and Bowler, 1980; Crisp et al., 2001; Bowler et al., 2006; Byrne et al., 2008; Andersen, 2016). It should be noted, in contrast to the extreme climatic oscillations that are usually described for this period, a study by Herando-Moraira et al. (2022) found that the climate in Australia during the Pleistocene was relatively stable with low climatic fluctuations. Thus, if the climate was more stable than previously postulated, this may have contributed to higher species richness of arid-adapted taxa (García-Palacios et al., 2018; Herrando-Moraira et al., 2022).

Frequent shifts in distribution during the Pleistocene may have resulted in admixture between species (or clades) that were previously separate, complicating the recent phylogenetic history of the Australian Camphorosmeae. Intraspecific relationships were not investigated in this study and are to be tested in future studies. In particular, the effects of hybridization on species richness and morphological variation are worthy of future investigation. The strong expansion of extreme arid habitats during glacial maxima may have resulted in increased extinction rates of lineages that may have been endemic to once larger ranges. Other clades may have benefited from the formation and expansion of extremely arid habitats (Sandy and Stony Deserts) and diversified. Without further molecular analysis, however, explanations for the apparent speciation slowdown in Australian Camphorosmeae during the Pleistocene remain highly speculative.

Other Australian xeric and halophytic plant lineages showed comparable patterns of diversification

The rapid radiations and subsequent diversification of crown groups in the Australian Camphorosmeae reflects the continuous aridification of the Australian continent since the Miocene. The intensifying aridification during the Pliocene likely favored crown group diversification by migration into and adaptation to newly emerging habitats. This diversification trend found in Australian Camphorosmeae is in line with other xeric and halophytic taxa that occupied the arid zone with the beginning of Australian aridification (Crisp et al., 2004; Byrne et al., 2008, 2018; Crisp and Cook, 2013; Byrne and Murphy, 2020). In addition, a growing number of studies has shown that lineage diversification is probably promoted by frequent biome shifts (e.g. Toon et al., 2015; Cardillo et al., 2017; Renner et al., 2020).

Molecular phylogenetic studies by Shepherd et al. (2004, 2005) showed the endemic Australian Salicornioideae, which include some of the most salt-tolerant land plants (English and Colmer, 2013), to have rapidly radiated during the Late Miocene and Pliocene as Australian aridity intensified. Diversification of this halophytic group was likely driven by adaptation to saline inland lake systems. Salt tolerance, likely a high selfing rate as in other Salicornioideae (Kadereit et al., 2007, 2012) and small, easily dispersed seeds promoted the rapid diversification across newly emerging arid habitats spreading across the continent.

Australian *Atriplex* experienced a rapid radiation during the Late Miocene, followed by intensifying diversification during the Pliocene (Kadereit et al., 2010; McDonald, 2020). A wide and rapid range expansion was likely promoted by dispersal along drainage axes of Riverine Desert habitats that connected coast and inland habitats (McDonald, 2020). Diversification was likely driven by several migration events and subsequent adaptation to varied inland habitats (e.g.

Karst Plain, Stony Desert). The formation of Karst Plain habitats and Stony Desert habitats coincides with the emergence of species and clades adapted to these habitats. Further, tolerance of coastal habitats likely enabled pre-adapted *Atriplex* progenitors to colonize arid inland regions via migration along littoral connections.

Diverse *Eucalyptus* L'Her (Myrtaceae) clades have adapted to a drying environment starting with the onset of Australian aridity during the Miocene (Thornhill et al., 2019). The lineages radiated and diversified over the emerging semi-arid landscapes dominated by open woodlands in the recent past, as evident by a steady increase in diversification rates during the Pliocene and a significant increase during the Pleistocene. Today *Eucalyptus* inhabit every biome across the continent.

The Australian spinifex grasses (Triodiinae Benth., Poaceae), diversified rapidly during the Middle Miocene, coincident with global cooling and aridification when drier habitats expanded in Australia (Toon et al., 2015). Niche shifts into savannah habitats (open woodland with grassy understorey) were concurrent with the expansion of woodlands, shrublands and grasslands during the Late Miocene and Pliocene and Biome shifts correlated with changes in leaf anatomy from amphistomatous to epistomatous leaves. The authors suggested additional trait shifts such as drought tolerance and a quick growth response to rainfall were further adaptive traits allowing these taxa to migrate into highly seasonal savannah habitats. Diversification was relatively constant during the Pliocene and slowed towards the present, likely due to a progressive saturation of niches.

Phylogenetic and biogeographic studies of *Hakea* Schrad. & J.C. Wendl. (Cardillo et al., 2017) and *Acacia* Mill. (Renner et al., 2020) revealed the role of biome shifts during diversification on a continental scale. In *Hakea*, species distribution expanded with a transition to more open, drought and fire-prone habitats, promoted by aridification during the Miocene. While diversification appeared to be driven by frequent biome shifts between semi-arid and arid biomes during the Pliocene. In *Acacia*, changing climate profiles during the Miocene and Pliocene may have affected diversification processes and promote radiation across the lineage, and glacial–interglacial cycles during the Pleistocene may have stimulated more recent speciation.

Extended sampling and new data analyses improve the resolution of phylogenetic relationships among Australian Camphorosmeae

This study sequenced two thirds of the 150 species of Australian Camphorosmeae using a modified RADseq protocol and assembly workflow tailored to the yielded sequence data (Hühn et al., 2022). This RADseq approach has been successfully applied in a number of taxonomically challenging plant groups from various angiosperm families (Hühn et al., 2022, 2023; Messerschmid et al., 2023). However, in contrast to the other studies, this study showed a RADseq-inherent limitation: The relatively large divergence of the Australian Camphorosmeae (ca. 10–16 million years) considerably increases the proportion of missing data (almost 94 % in Assembly 1; 84 % in the more rigorous Assembly 2 used for dating). A high proportion of missing data is generally unproblematic in RADseq analyses (e.g. Huang and Knowles, 2016; Eaton et al., 2017; Tripp et al., 2017; Graham et al., 2020), but it does limit the applicable methods for phylogenetic inference (e.g. Chou et al., 2015; Xu and Yang, 2016; Molloy and Warnow, 2018; Hühn et al., 2022). Still, the methodology used here has confirmed the previously assumed biological processes that led to the observable phylogenetic signal. Further, it yielded 17 statistically supported clades (Fig. 3), several of yet unrecognized species groups. Many of these clades may only be characterized by combinations of multiple morphological traits among which the fruit morphological traits remain the most important diagnostic features (Wilson, 1975; Cabrera et al., 2009; McDonald, 2020; Hühn, 2023). The further increase and improvement of sampling could have a positive effect on data assembly and phylogenetic inference in future studies (e.g. Huang and Knowles, 2016; Eaton et al., 2017). In a subsequent publication, we plan to propose a revised classification of the Australian Camphorosmeae including a detailed survey of generative and vegetative traits and their systematic relevance.

While further work is planned, this study has shown that the Australian Camphorosmeae radiated concurrently with the development of arid habitats starting in the Late Miocene as shown in previous studies (Cabrera et al., 2009, 2011) and other various arid-zone taxa that evolved in response to the continent's intensifying aridity (Crisp et al., 2004; Byrne et al., 2008, 2018; Crisp and Cook, 2013; Byrne and Murphy, 2020). The arrival of the Camphorosmeae dates to a period of major climatic, landscape and biotic transition. Establishment and inland migration may have been favored by pre-adaptation as progenitors adapted to coastal, marshy conditions may have migrated along Riverine Desert landscapes that developed as a consequence of ceasing palaeodrainage systems in south and western Australia. Despite the lack of phylogenetic resolution, a shift in habitat preferences is evident between the two rapid *Maireana* radiations and the crown *Sclerolaena* clade. Originating from Riverine Desert habitats, progressively forming arid landscapes may have favored rapid range expansion across the continent and diversification into newly emerging arid habitats. Migration was probably multidirectional and likely followed a west-east aridification trend of the continent. Crown group diversification was strongest during the Pliocene and likely promoted by the west-to-east expansion of Riverine Desert habitats and subsequent expansion and colonization of newly developing arid habitats. However, the diversification pattern is not uniform across the phylogeny. While some clades appear to be quite conservative with respect to their habitat, several clades show a diversification of colonized habitats. Rapid range expansion, fast habitat saturation, as well as periodic expansion, contraction and replacement of arid habitats may have caused the rather species-poor clades of the *Maireana* grade compared to the continuously diversifying *Sclerolaena* clade.

CRedit authorship contribution statement

John McDonald: Writing – review & editing, Resources, Investigation. **Kelly A. Shepherd:** Writing – review & editing, Supervision, Resources, Investigation. **Gudrun Kadereit:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Philipp Hühn:** Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ppees.2024.125811.

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