Notes on the origins of Australian desert vines

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ABSTRACT

Data from six Australian deserts show that 25 genera of vines are present. Fourteen genera are likely to be from rainforest stock and a further two can be found in seral stages of rainforest. Of the other genera, two are Australian endemics from areas of Mediterranean climate, three are dry-country succulents, three are widespread temperate to tropical Fabaceae, and *Convolvulus* L. is cosmopolitan. Of the 37 species represented, 10 can be found in dry or monsoon rainforest at present. As many as 59% of the species are from, or likely to be derived from, rainforest lineages. Adaptation to increasing aridity by the aseasonal wet rainforests of the Early Tertiary led to the development of seasonally dry rainforests by the mid-Tertiary. Subsequently, in the face of greater aridity, some dry rainforest lineages have produced species capable of surviving desert conditions, the most obvious adaptation being reduction in leaf area. Evolution of some of the dry-country succulent vines may be more recent, involving pre-adapted immigrant taxa.

KEY WORDS
Australia,
biogeography,
desert,
immigrant taxa,
leaf size,
rainforests,
vines.

RÉSUMÉ

Notes sur les origines des lianes du désert australien.
L'analyse comparée de six déserts australiens montre que 25 genres de lianes peuvent y être reconnus. Quatorze genres sont probablement originaires de la forêt ombrophile et deux autres participent à la succession d'associations végétales menant à celle-ci. Parmi les genres restants, deux sont endémiques australiens croissant dans les zones de climat méditerranéen, trois sont succulents de zones arides, trois sont des Fabaceae à large répartition tempérée

à tropicale, et enfin on note la présence du genre cosmopolite *Convolvulus* L. Des 37 espèces actuellement reconnues, 10 croissent dans la forêt ombrophile sèche ou de mousson. Au moins 59 % des espèces paraissent issues de lignées de la forêt humide ombrophile, sans saisons marquées, dont l'adaptation à une aridité croissante au début du Tertiaire a conduit au développement d'une forêt ombrophile sèche dès le milieu de l'ère. La poursuite de l'aridification a alors sélectionné des taxons capables de coloniser les déserts, surtout par réduction des surfaces foliaires. Certains genres de lianes succulentes semblent s'être différenciés plus récemment à partir de taxons allochtones préadaptés.

INTRODUCTION

Although it is widely recognised that both herbaceous and woody vines extend from their stronghold in the wet tropics into a range of drier habitats, including deserts (Krings 2000), much remains to be done before we fully understand all aspects of this phenomenon. Recently, I tabulated the known species of vines from six Australian deserts and compared the incidence of vines and the phylogenetic lineages represented with those from other continents (Parsons 2005). Since then, I have located published work that allows the origins of the Australian desert vine flora to be analysed. Specifically, in this paper I discuss to what extent the desert vine taxa: 1) have arisen within lineages from arid areas; 2) have arisen by selection within the rainforest taxa which once occupied the areas in question; or 3) are morphologically indistinguishable from existing rainforest taxa. The paper was conceived as a short note on desert vine origins rather than as a comprehensive treatment of the evolution of eremaean floras and its relationship to climatic changes since the Early Tertiary.

METHODS

The Australian desert vine flora considered is that specified in the earlier paper (Parsons 2005), where, with a few exceptions, I followed Hegarty & Clifford (1984) supplemented by recent Australian floras (Stanley & Ross 1986; Paczkowska & Chapman

2000) in determining what species to list as vines. This results in the inclusion of some "unarmed climbing herbs" (Hegarty & Clifford 1984) which can also be found as non-climbers, namely some species of *Boerhavia* L., *Einadia* Raf., *Lotus* L. and *Zygophyllum* L. which might not be treated as vines by some workers.

Sources and location for the data are as for Parsons (2005). The deserts involved are the Great Sandy, Little Sandy, Gibson, Great Victoria, Simpson and the Stony Deserts of South Australia (Fig. 1). I follow Liede (1996) in restricting *Sarcostemma* R.Br. to the non-campanulate Old World taxa. Following Barker & Barker (2005), I have not implemented the changes to plant family nomenclature suggested by the Angiosperm Phylogeny Group because "there is as yet no new, stable classification encompassing all genera".

Geographical distribution and habitat of vine taxa were established from Hegarty & Clifford (1984), Stanley & Ross (1986) and Paczkowska & Chapman (2000) and used to assign the taxa to floristic elements. Then, the published work on rainforest in Australia and nearby areas (New Guinea, Malaysia) was searched to see which genera and species of Australian desert vines now occur in rainforest. The term "rainforest" was taken to include the deciduous to semi-evergreen rainforests of the dry tropics and sub-tropics of Australia's eastern seaboard because of their strong structural and floristic affinities to the rainforests of wetter environments (Fensham 1995). These were often called vine thickets by earlier workers but, in
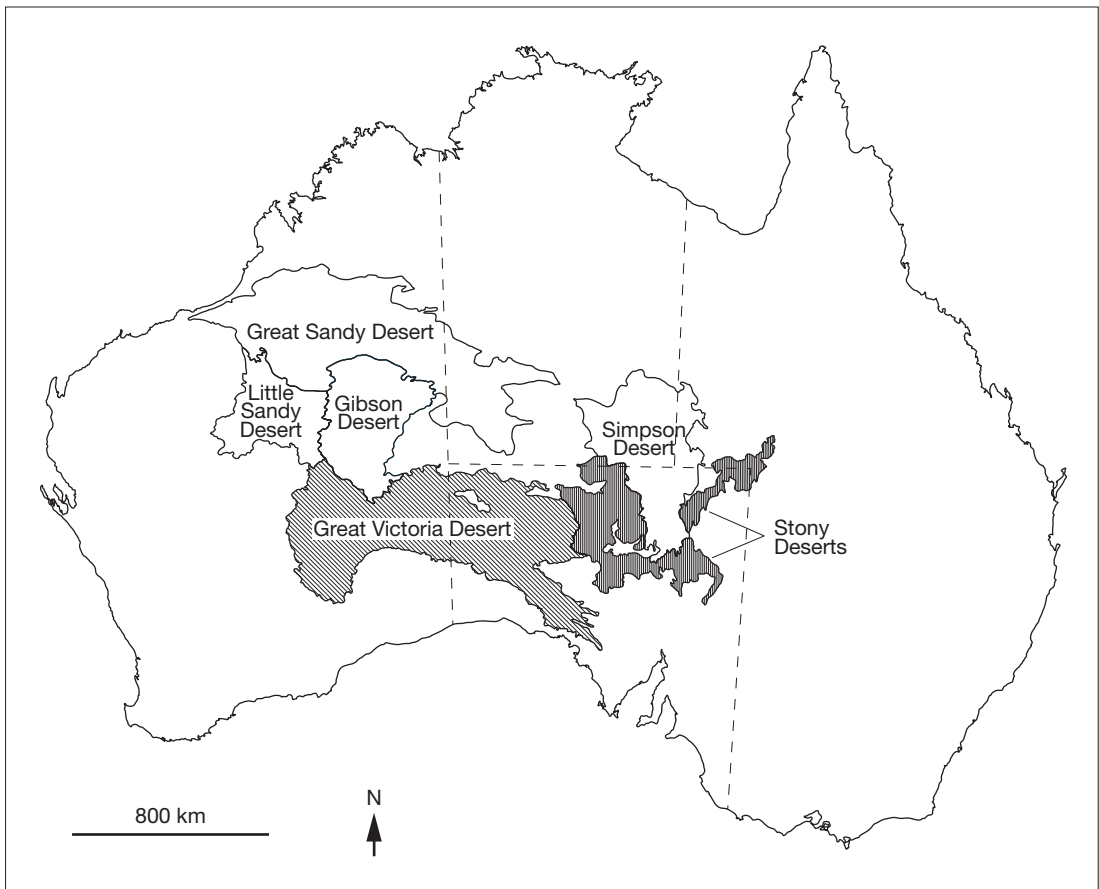
FIG. 1. — Location of the Australian deserts studied in detail. State boundaries shown as dashed lines. From Parsons (2005).

Australia, are now usually called dry rainforests (Fensham 1995). This vegetation type (rainfall range 500 to 900 mm) shows continuous floristic variation with wetter rainforest types (Fensham 1995). Also included are the closely related "monsoon rainforests" of the Northern Territory and Western Australia (Fensham 1995).

The nature of the ancestral Australian rainforest stock and its subsequent contraction with increasing aridity are reasonably well understood from fossil and other data (Sluiter 1992; Hill *et al.* 1999 and references therein). With this as background, distribution and habitat of vine taxa can be used to assign the taxa to floristic elements and to suggest whether they arose in rainforest, as is done in Krings

(2000) and numerous other studies. The distribution of the Australian desert vine genera outside Australia is dealt with by Parsons (2005). Species nomenclature follows Stanley & Ross (1986) and Paczkowska & Chapman (2000).

RESULTS

In determining which genera are derived from rainforest stock, the most clearcut cases are genera with most extant species clearly found in relatively intact rainforest, viz. *Jasminum* L. (Oleaceae), *Porana* Burm.f. (Convolvulaceae), *Tinospora* Miers (Menispermaceae) and the asclepiads *Cynanchum* L.,

Marsdenia R.Br. and *Sarcostemma.* Most Australian species in these genera are woody (Table 1). A further asclepiad genus, *Rhyncharrhena* F.Muell. (again woody), occurs solely in areas drier than rainforest (Table 1), but is regarded as being derived from rainforest stock given that it is a segregate from the rainforest element *Pentatropis* R.Br. ex Wight & Arn. and given that all other Australian asclepiad genera have most of their species in rainforest. The hemiparasitic *Cassytha* L. (Lauraceae) includes two species found both in rainforests and deserts (Table 1) (Kenneally *et al.* 1991; Fensham 1995) and is treated here as being derived from rainforest stock as well.

It is harder to determine the origin of some of the herbaceous vine genera extending to wet tropical areas, especially the genera in the Convolvulaceae, Cucurbitaceae and Polygonaceae (*Muehlenbeckia* Meisn.) (Table 1). In general, the genera involved are shade intolerant and they tend to be more weedy than the previous group, possibly occurring as pioneer species in areas cleared of rainforest and in open areas of developing secondary rainforest as well as open, non-rainforest sites in the tropics (see Danser 1940; Van Ooststroom 1953). Here, I follow Kenneally *et al.* (1991) in treating *Boerhavia* L., *Ipomoea* L., *Merremia* Dennst. ex Endl., *Mukia* Arn., *Operculina* Silva Manso and *Rhynchosia* Lour. as occurring within rainforest (Table 1). *Bonamia* Thouars and *Muehlenbeckia*, not found in rainforest by Kenneally *et al.* (1991) or Fensham (1995) occur in seral stages of rainforest (see Danser 1940; Van Ooststroom 1953) and are categorized accordingly (Table 1). The only tabulated genus in the Convolvulaceae not listed above is *Convolvulus* L., which is primarily temperate, extending to the subtropics but rare in the tropics (Van Ooststroom 1953; Johnson 2001) and not recorded from rainforest or seral stages of it. The other genera clearly not from rainforest (mostly herbaceous) include temperate Australian endemics from areas of Mediterranean climate (*Marianthus* Hügel ex Endl., *Murchisonia*) and dry country succulents (*Calandrinia* Kunth, *Einadia* Raf., *Zygophyllum*). The Fabaceae other than *Rhynchosia* include both widespread genera (*Glycine* Willd., *Lotus*) and the mainly tropical to subtropical *Vigna* Savi.

In summary, I regard 14 genera as being from rainforest stock, two are known from seral stages of rainforest, two are from areas of Mediterranean climate, three are dry-country succulents and four are wide-ranging.

At the species level, of the 37 species of desert vines, 10 (27%) are also found in dry or monsoon rainforest or both (Kenneally *et al.* 1991). These are discussed more fully below.

A further 11 species are from genera found in rainforest. Adding *Rhyncharrhena linearis* to these (see above) gives 22 species or 59% from, or likely to be derived from, rainforest stock. Thirteen species (35%) are clearly not derived from rainforest stock, leaving the species of *Bonamia* and *Muehlenbeckia* as cases where the genus is known from seral stages of rainforest.

DISCUSSION

After the wet climates and widespread rainforest of the Early Tertiary, it is thought that increasing dryness later in the Tertiary led to rainforest simplification and contraction and the evolution of dry rainforest types (Sluiter 1992). Since then, the marked climatic fluctuations of the Pleistocene have occurred. During the glacial periods, the central Australian desert was considerably larger and more stressful to plants than at present, much of it becoming virtually unvegetated and with much of the desert flora retreating to refugia, especially outwards towards the present-day coast (Crisp *et al.* 2001). Then, on climatic amelioration in the interglacials and after the Last Glacial, surviving plant taxa would have re-expanded their ranges from the refugia (Crisp *et al.* 2001). Similar contractions and re-expansions will apply both to dry rainforest and wetter rainforest types (Fensham 1995).

Desert vine lifeforms encompass a range from annuals to woody perennials, even within the single genus *Ipomoea* (Table 1). A number of the herbaceous perennials die back to ground level in dry periods (e.g., *Cynanchum floribundum*, *Ipomoea muelleri*) but comprehensive data on biology and phenology are lacking in most cases. While it is known that the Asclepiadaceae and the *Jasminum*

TABLE 1. — Species list of vines found in six Australian deserts, showing growth form and which taxa are recorded from rainforest. Data from Danser (1940), Van Ooststroom (1953), Kenneally *et al.* (1991), Fensham (1995) and Parsons (2005). Abbreviations for growth forms: **A**, annual; **H**, herbaceous perennial; **P**, hemi-parasitic; **W**, woody. "Seral" indicates that the genus can be found in seral stages of rainforest.

Species	Growth form	Occurrence of genus in rainforest	Occurrence of species in rainforest
Asclepiadaceae			
Cynanchum carnosum (R.Br.) Schltr.	W	yes	yes
C. floribundum R.Br.	W	yes	no
Marsdenia australis (R.Br.) Druce	W	yes	no
Rhyncharrhena linearis (Decne.) K.L.Wilson	W	no	no
Sarcostemma viminale (L.) R.Br.	W	yes	yes
Chenopodiaceae			
Einadia nutans (R.Br.) A.J.Scott	H	no	no
Convolvulaceae			
Bonamia media (R.Br.) Hallier f.	H	seral	no
Convolvulus eyreanus R.W.Johnson	H	no	no
C. remotus R.Br.	H	no	no
Ipomoea coptica (L.) Roth	A	yes	no
I. costata Benth.	W	yes	no
I. muelleri Benth.	H	yes	no
I. racemigera F.Muell. & Tate	A	yes	no
Merremia davenportii (F.Muell.) Hallier f.	H	yes	no
Operculina aequisepala (Domin) R.W.Johnson	H	yes	yes
Porana commixta Staples	W	yes	no
Cucurbitaceae			
Mukia maderaspatana (L.) M.Roem.	H	yes	yes
M. micrantha (F.Muell.) F.Muell.	H	yes	no
Fabaceae			
Glycine canescens F.J.Herm.	H	no	no
G. rubiginosa Tindale & B.E.Pfeil	H	no	no
G. tomentella Hayata	H	no	no
Lotus cruentus Court	H	no	no
Rhynchosia minima (L.) DC.	H	yes	yes
Vigna lanceolata Benth.	H	no	no
Lauraceae			
Cassytha capillaris Meisn.	P	yes	yes
C. filiformis L.	P	yes	yes
C. melantha R.Br.	P	yes	no
Lomandraceae			
Murchisonia volubilis Brittan	H	no	no
Menispermaceae			
Tinospora smilacina Benth.	W	yes	yes
Nyctaginaceae			
Boerhavia dominii Meikle & Hewson	H	yes	yes
Oleaceae			
Jasminum calcarium F.Muell.	W	yes	no
Jasminum didymum G.Forst.	W	yes	yes
Pittosporaceae			
Marianthus bicolor (Putt.) F.Muell.	W	no	no
Polygonaceae			
Muehlenbeckia coccoloboides J.M.Black	W	seral	no
Portulacaceae			
Calandrinia volubilis Benth.	A	no	no
Zygophyllaceae			
Zygophyllum angustifolium H.Eichler	H	no	no
Z. eremaeum (Diels) Ostenf.	H	no	no
Total number of vines: 37			

taxa in Table 1 are evergreen and that *Tinospora* is often leafless (R. J. Fensham pers. comm.), data on deciduousness are lacking for the other taxa.

For the 27% of species occurring both in deserts and in rainforests at present (Table 1), adaptation to desert conditions has been without any noticeable change in morphology in many cases. Conversely, in the case of *Jasminum didymum*, the non-rainforest populations are of the subspecies *lineare* (R.Br.) P.S.Green, while the rainforest populations have wider leaves and are classified as subsp. *didymum* and *racemosum* (F.Muell.) P.S.Green (Stanley & Ross 1986).

A similar case is the vine *Pandorea pandorana* (Andrews) Steenis (Bignoniaceae) which is common in wet forests of eastern Australia. Although not found in deserts, disjunct stands occur in very dry, rocky ranges in central Australia and elsewhere (Paczkowska & Chapman 2000). The dry country stands have narrower leaves than the others and are sometimes recognised at the species level as *P. doratoxylon* (J.M.Black) J.M.Black. The orthodox view is that the morphological differences within *Jasminum didymum* and *Pandorea* Endl. (Spach) have a genotypic component and are not merely phenotypic. Work is desirable to check this.

Of the 10 species found both in deserts and rainforest, five are widely spread across the six deserts sampled while the desert occurrences of the others are confined to the Great Sandy Desert (plus the Little Sandy in one case; Parsons 2005). For the latter five, namely *Cassytha capillaris*, *C. filiformis*, *Cynanchum carnosum*, *Operculina aequisepala* and *Tinospora smilacina*, this may reflect greater proximity of the Great Sandy Desert to wetter country carrying rainforests (to the north – Kenneally *et al.* 1991) than is the case for the other deserts.

For eight rainforest genera, adaptation to aridity has involved morphological changes recognised at species level. One such genus, *Marsdenia*, is used by Sluiter (1992) as an example of Tertiary rainforest stock which became a key component of the dry rainforests which evolved in the Late Tertiary and in turn gave rise to extant arid zone relatives not known in rainforests. In this case, Sluiter (1992) places the semi-arid to desert *Marsdenia australis*

(Table 1) in a "generic pairing" with the rainforest species *Marsdenia rostrata* R.Br. He invokes a similar general background for the evolution of the dry country populations of the vines *Jasminum*, *Pandorea* and *Sarcostemma* as well as for the evolution of the asclepiad vine genus *Rhyncharrhena* and, possibly, the dry country species of *Ipomoea* and *Porana*.

Sluiter (1992) also applies the scenario used for *Marsdenia* (above) to a range of tree and shrub species found in dry rainforest which have congeneric species in semi-arid to arid areas, including species of *Alectryon* Gaertn., *Beyeria* Miq. and *Pittosporum* Banks ex Gaertn. Gell & Bickford (1996) provide analogous species pairs in the tree genera *Capparis* L. and *Codonocarpus* A.Cunn. ex Endl. and point out that a common feature of the arid zone taxa is reduced leaf area compared to their rainforest partners, for example in *Alectryon*, *Beyeria*, *Marsdenia* and *Pittosporum*. The same reduced leaf area in arid zone taxa occurs in many Convolvulaceae, such as *Bonamia*, *Ipomoea*, *Merremia*, *Porana* and *Wilsonia* R.Br. (Staples 1987) and is noted above for arid zone populations of *Jasminum* and *Pandorea*. The decline in leaf area with decreasing rainfall also occurs in other growth forms and has recently been quantified for Mexican vines and related to temperature and water loss regulation (Molina-Freaner *et al.* 2004 and references therein).

The desert vine flora clearly has multiple origins in time and space. In addition to taxa derived from rainforest elements, there is a group of species derived from areas of Mediterranean climate and a group of dry country succulents as well as some widespread taxa hard to categorise.

The rainforest lineages will have their origins in the Cretaceous and will have begun adapting to aridity no later than the late Oligocene-early Miocene (Hopper & Gioia 2004). A very similar scenario applies to vine-rich, southern African vegetation in 250-800 mm mean annual rainfall called subtropical thicket. Like Australian dry rainforests, this carries the vines *Cynanchum* L., *Jasminum* and *Sarcostemma* and trees like *Capparis* and *Ehretia* P.Browne (Cowling *et al.* 2005). This is regarded as part of a global tropical thicket formation that was once widespread

in the Eocene (Cowling *et al.* 2005). Similarly, the present vegetation of western Andalusia includes old plant lineages (e.g., *Jasminum*, *Olea* L.) from pre-Pliocene tropical-like climates (Herrera 1992). These are regarded as formerly tropical "ecological phantoms", being "evolutionarily unrelated to present ecological conditions" (Herrera 1992). Analogous lineages from California and Chile are discussed by Cowling *et al.* (2005).

The Australian desert vine genera clearly derived from areas of Mediterranean climate are the endemics *Marianthus* and *Murchisonia*. This relates to the way predominantly southwestern Australian taxa have "spawned widespread congeners out into Australia's deserts" (Hopper & Gioia 2004), especially during a period of rapid radiation during the aridity increase during the late Oligocene to mid-Miocene (Crisp *et al.* 2004). However, in both the present cases, it is the same species which extends from areas of Mediterranean climate into the desert (in these cases the Great Victoria Desert [Parsons 2005]).

Of the dry country succulent vines (*Calandrinia*, *Einadia*, *Zygophyllum*), *Einadia* is from the Chenopodiaceae. For this family, most lineages arrived in Australia by long distance dispersal during the late Miocene and Pliocene and then diversified rapidly in arid areas (Kadereit *et al.* 2005). Unlike the rainforest and Mediterranean climate groups, Crisp *et al.* (2004) treat the Australian chenopods as a case of "rapid radiation of pre-adapted immigrant taxa". It is not known if the same applies to *Calandrinia* and *Zygophyllum*.

Excluding the two cases from seral stages of rainforest, the remaining genera of non-rainforest origin comprise *Convolvulus* and three genera from family Fabaceae (Table 1). All are widespread and cannot readily be categorised further.

In future, biogeographers should note that the data of Noy-Meir (1970) used by Shmida & Burgess (1988) to compare Australian deserts with those of other continents are from non-desert areas significantly wetter than those treated here. Also, the correct title of Noy-Meir's Ph.D. thesis is "Component analysis of semi-arid vegetation in southeastern Australia", *contra* Shmida & Burgess (1988).

CONCLUSIONS

Floristic simplification of the aseasonal wet rainforests of the Early Tertiary in the face of increasing aridity along with evolutionary changes in their constituent taxa, initially led to the development of seasonally dry rainforests by the mid-Tertiary. In some rainforest lineages, subsequent greater aridity has produced species capable of surviving desert conditions. Some species have come to occupy desert areas with no discernable change in morphology from their rainforest populations. Others, like *Jasminum didymum*, have differentiated at the subspecies level through reductions in leaf size and other changes. Still others have differentiated at species level, like *Marsdenia australis* or even at generic level, like *Rhyncharrhena*.

The species of desert vines either found in extant rainforests or derived from rainforest taxa have present day ranges disjunct from existing rainforest. The presence of populations of taxa with rainforest affinities scattered through much of semi-arid Australia can be related to the repeated advance and retreat of dry rainforest types and other plant communities during climatic fluctuations from the Tertiary to the present.

There are also contributions to the desert vine flora from the Mediterranean-climate areas to the south and, possibly more recently, from succulent dry-country lineages which may include pre-adapted immigrant taxa.

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