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REGULAR ARTICLE

Sand-binding roots in Haemodoraceae: global survey and morphology in a phylogenetic context

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Abstract
Aims To illustrate the morphology of sand-binding roots of Haemodoraceae, to conduct a comprehensive survey of the trait, spanning different climates across four continents, and to explore evolutionary hypotheses within a molecular phylogenetic framework.
Methods Sand-binding roots in Haemodoraceae were examined, measured and photographed in the field and on herbarium specimens. Photomicrographs were taken of southwest Australian species. The presence and absence of the sand-binding trait was mapped onto previously published phylogenies and an ancestral state reconstruction was performed.
Results Sand grains were very tightly bound to the root surface by persistent root hairs in Haemodoraceae. The majority of genera and species were found to possess sand-binding roots and only 2 of the 14 genera, *Conostylis* and *Tribonanthes*, had sister taxa with and without the trait. The trait was recorded in tropical, sub-tropical and wet temperate species, but mainly in semi-arid species. Sand-binding roots were likely to have been present in the ancestor of the family and both sub-families.
Conclusions The presence of sand-binding roots is the probable ancestral condition for Haemodoraceae, associated with a high degree of phylogenetic conservatism and some secondary loss, notably in *Conostylis.* Experimental studies are needed to understand the ecological and evolutionary forces at work.

Keywords Sand-binding roots · Rhizosheath · Haemodoraceae · OCBILs · Soil nutrients · Seasonal aridity · Low phosphorus

Introduction

Sand-binding roots are perennial roots with a prominent, dense sheath of sand particles bound together by a mesh of root hairs and/or mucilaginous exudates, also including microbial components in some cases (Dodd et al. 1984; McCully 1999; Pate and Dixon 1996; Wullstein and Pratt 1981). These structures are more broadly referred to as rhizosheaths, defined in more general terms to encompass any root sheath formed from substrate particles bound to the root through modifications of the rhizosphere (Bailey and Scholes 1997). Rhizosheaths have been reported across a wide range of phylogenetically disparate plant groups of seasonally arid landscapes, including desert grasses and Restionaceae (Poales: Price 1911; Arber 1934; Buckley 1982a; Dodd et al. 1984; Meney

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and Pate 1999; Shane et al. 2009, 2010), Haemodoraceae (Commelinales: Pate and Dixon 1996) and Cactaceae (Caryophyllales: North and Nobel 1992; Huang et al. 1993).

Although known for more than 100 years (Massart 1898; Price 1911; Volkens 1887) and widely investigated in recent times, the exact functional significance of rhizosheaths remains unclear. It has been suggested that the predominant function is related to reduction of water loss and protection of the roots in dry environments such as deserts and those subject to prolonged summer drought (Dodd et al. 1984; Pate and Dixon 1996; Shane et al. 2010). In support of this hypothesis, rhizosheaths have been shown to eliminate root-soil air gaps and facilitate water uptake in moist soils and minimise water loss in drought conditions (North and Nobel 1997). However, Buckley (1982a) pointed out that it is difficult to separate and test independently the functions of the sheath and the hypodermis and cortex. He concluded that the function of the sheath may be a protective one, minimising water loss and heat stress by shielding the delicate layers underneath from damage, and that the overall function of the hypodermis and sheath together are to minimise water loss in adverse drought conditions. Robards et al. (1979) had also suggested previously that the root sheath of *Carex arenaria* provides protection for the central conducting strand in adverse conditions, without compromising water or ion uptake.

More recently, Watt et al. (1994) showed that rhizosheaths formed under conditions of low soil moisture content had a greater volume, a larger number of hairs and were more tightly bound than those formed under wet conditions. The advantage under dry conditions may result from the ability of the rhizosheath to increase the water-holding capacity of the soil, as demonstrated by Young (1995). The development of rhizosheaths has also recently been found to relate to soil texture (Bailey and Scholes 1997) and to be influenced by soil acidity (Haling et al. 2010). In the former, roots produced a larger number of epidermal hairs and more extensive rhizosheaths in sandy soils. However, since sandy soil has a lower moisture and nutrient content than other soils, the effect may be a function of these other variables and the same could also apply for soil acidity.

Low nutrient content is another possible evolutionary driver for the development of rhizosheaths, which may act to enhance nutrient uptake from impoverished soils (Nambiar 1976; Lamont 1993; Shane et al. 2009, 2010; Lambers et al. 2010) and may facilitate nitrogen fixation through microbial associations (Othman et al. 2004; Wullstein 1991). Rhizosheaths thus far documented occur predominantly in taxa from dry, nutrient poor environments such as the deeply weathered, highly infertile soils of old, climatically buffered infertile landscapes (OCBILs: Hopper 2009); ecophysiological specialisations are common in plant taxa from these regions where phosphorus is the limiting nutrient (e.g. Lambers et al. 2010). They have also been recorded in tropical epiphytic cacti (North and Nobel 1992, 1994), which occupy another extreme environment in terms of nutrient availability and moisture. Buckley (1982b) found that the sand-filled root sheaths of the desert dune grass *Zygochloa paradoxa* contain more extractable phosphorus than control soils and this could be the result of mycorrhizae or animals living in the sand of the sheath causing secondary soil phosphorus enrichment (Buckley 1982a). Good contact between roots and soil particles is essential for efficient water and nutrient uptake and rhizosheaths help to maintain this (North and Nobel 1997).

One way of distinguishing among the hypothesized benefits of sand-binding roots and their evolutionary origins is to test for biogeographic pattern within a phylogenetically constrained context. Are sand-binding roots predominantly found in sandy soils in seasonally dry environments, as present data suggest? For example, if sand-binding roots occur in both early-diverging and more recent lineages from old tropical or wet temperate environments with year-round rainfall, this would suggest against the hypothesis that drought avoidance was the major selection pressure for their origin in the species concerned, and point towards a function dealing with nutrient deficiency or other functions as more likely selective causes. This is a comparable situation to that pertaining to distinguishing sclerophylly from xeromorphy (Seddon 1974; Beadle 1966), elegantly achieved for *Banksia* by Hill (1998; Hill and Brodribb 2001) who established that sclerophyll leaves appeared in fossils of Eocene age when moist rainforest conditions prevailed across a mosaic of soils including those that were nutrient deficient (Read et al. 2009), whereas features such as sunken stomata appeared later in the Neogene, following the onset of major aridity in Australia, and were therefore likely to be xeromorphic adaptations.

A molecular phylogenetic approach enables sister clades to be resolved, and contrasts to be made for the evolution of specific attributes such as sand-binding roots. What are the correlates of habitat and life history associated with sister clades that either possess or lack sand-binding roots? To date, such an approach has yet to be explored for these intriguing structures.

In this study, we report on the global occurrence of sand-binding roots in Haemodoraceae, a small family of perennial monocots comprising some 14 genera and ca. 113 species, most common in the Southwest Australian Floristic Region (SWAFR *sensu* Hopper and Gioia 2004), but extending to other parts of Australia as well as Papua New Guinea, South Africa, the tropical Americas and the east coast of North America (Simpson 1990). Previous studies on the roots of Haemodoraceae are limited. Opitz and Schneider (2002) and Opitz et al. (2003) recorded the presence of high concentrations of phenylphenalenones functioning as phytoalexins in the tips of *Xiphidium caeruleum* roots that may afford protection from soil microorganisms and nematodes. A number of studies refer to the presence of a dimorphic root epidermis in the family (Leavitt 1904; Shishkoff 1987; Kauff et al. 2000) and Obermeyer (1971) described roots covered with a tomentum consisting of long, interlacing root hairs in *Dilatris viscosa.* However, Green (1960) was the first author to fully describe the sand-binding character of roots in Haemodoraceae. In his description of the genus *Conostylis* he documented the sheath of soil-trapping hairs, noting that older roots became glabrous and wiry. Subsequent authors did not follow up on these observations in their morphological and anatomical descriptions of Haemodoraceae (MacFarlane et al. 1987; Simpson 1990, 1998; Aerne 2007).

Sand-binding roots have been recorded in a number of species of Haemodoraceae (e.g. Green 1960; Pate and Dixon 1996) but the taxonomic coverage has previously been limited to a small number of SWAFR genera. Here we describe the morphology of sand-binding roots in the family, document the presence/absence of the trait in all genera and the majority of species of Haemodoraceae, and explore evolutionary and biogeographic questions within a molecular phylogenetic framework. The global survey, encompassing species of semiarid (Mediterranean climate), wet temperate, subtropical and tropical habitats, enables a test of the hypothesis that sand-binding roots are restricted to semi-arid to arid environments. We also explore briefly the attributes of sister clades with and without sand-binding roots, especially in the genus *Conostylis*, investigate the presence of the trait in ancestral taxa and suggest avenues for further research.

Methods

Sand-binding root morphology

Hand-cut sections were made of fresh mature roots from the base of three species (*Haemodorum paniculatum*, *Conostylis aculeata* subsp. *cygnorum* and *Anigozanthos manglesii* subsp. *manglesii*) collected in the dry season (March) from *Banksia—Eucalyptus gomphocephala* woodland on the Swan Coastal Plain, Perth, Western Australia. Some sections of mature sheathed roots were stained with toluidine blue, 0.05% (w/v) (pH 4.4) (O'Brien and McCully 1981) to increase contrast between sand grains and root hairs. Photomicrographs were recorded digitally using a Nikon D700 or using the camera fitted with an eyepiece attachment (Martin Microscopes, Easley, SC, USA) on a Wild M400 dissecting microscope (Zurich, Switzerland). Post image processing used Photoshop CS5 software (San Jose, CA, USA).

Global survey of sand-binding roots in Haemodoraceae

Herbarium specimens of Haemodoraceae in the extensive collections of the Western Australian Herbarium (PERTH), the Royal Botanic Gardens, Kew (K), and the Compton Herbarium at Kirstenbosch Botanic Garden (NBG), as well as in several other herbaria, were systematically examined for the presence of sand-binding roots. Specimens from the closely-related Pontederiaceae, Philydraceae and Commelinaceae were also examined. The trait was categorised as present, absent or rare for between 1 and 30 specimens per taxon primarily for specimens in PERTH, K and NBG, and if present an estimate of root plus sheath diameter was taken. Note that the presence of sand-binding roots may be underestimated on herbarium specimens since pulling plants out of the ground is the standard collecting technique, and it often shears away the sheath in the process. We found sand-binding roots to be rare in herbarium specimens of *Blancoa*, for example, but they were abundantly evident in specimens dug up in the field (Fig. 2h). To supplement these herbarium data, therefore, the same characteristics were noted for specimens dug up and examined in the field by SDH, MS and RJS, with photographic evidence taken after vigorously shaking surplus sand away when the specimen was obtained from dry soil.

Phylogenetic trait mapping

The distribution of sand-binding roots was mapped onto phylograms modified from those in Hopper et al. (2006, 2009). Parsimony and maximum likelihood ancestral state reconstruction were performed in Mesquite version 2.73 (Maddison and Maddison 2010) using the BEAST tree from Hopper et al. (2009) and the Markov k-state 1 parameter model. The trait was treated as binary and categorised as either present (including the taxa where sand-binding roots were present but rare) or absent. Biogeographic and habitat data were assembled from herbarium and literature records combined with extensive field data acquired over four decades of research on all but one genus of Haemodoraceae (the elusive *Pyrrorhiza*, endemic to the high equatorial tepui Cerro de la Neblina on the Venezuelan-Brazilian border—Simpson 1990).

Results

Morphology of the sandsheath

The morphology of freshly collected mature regions of sand-binding roots of three southwest Australian species is illustrated in Fig. 1a–f. The diameter of sand-binding roots including the sand sheath was found to vary greatly within the family, from 1 to 2 mm in the majority of taxa (Fig. 1e), up to a maximum in *Haemodorum* (Fig. 1a), i.e. 7 mm in *H. spicatum* and c. 6 mm in *H. paniculatum* (Fig. 1b). Sand grains were very tightly bound to the roots of all species (Fig. 1c), and not easily removed by washing or vigorous scrapping. There were extremely dense numbers of roots hairs made more visible after toluidine blue staining (Fig. 1f). Sandsheaths can be gently pulled off to reveal the root stele underneath, which in perennial plants with evergreen shoots are still alive and functional in vascular axial transport (Fig. 1d).

Global survey and trait evolution of sand-binding roots in Haemodoraceae

Observed occurrences of sand-binding roots in Haemodoraceae were documented for the majority of Haemodoraceae taxa, with the source of the observation and an estimate of root diameter noted (Appendix I). A generic summary of the data obtained from examination of herbarium specimens is presented in Table 1 and images of the roots of all genera, with the exception of *Pyrrorhiza*, are shown in Figs. 1, 2 and 3. The character state of sand-binding roots in taxa of Haemodoraceae was also mapped onto previously published phylogenies of Haemodoraceae (Hopper et al. 2009) in Fig. 4 and *Conostylis* (Hopper et al. 2006) in Fig. 5. Sand-binding roots were absent from all genera of Pontederiaceae and Philydraceae, and from *Spatholirion* in Commelinaceae. However, the trait was present in many other genera across Commelinaceae including *Weldenia, Thyrsanthemum, Aneilema, Commelina* and *Gibasis* and was particularly pronounced in *Tradescantia*, which had root plus sheath diameters of up to 5 mm. Parsimony ancestral state reconstruction showed that presence and absence of the sand-binding trait are equally likely to be the ancestral state for the family and for Haemodoroideae but the presence of sand-binding roots was conclusively shown to be the plesiomorphic state for Conostylidiodeae, with two secondary losses. Maximum Likelihood reconstruction supported the plesiomorphy of the sand-binding trait for Conostylidoideae but also gave a higher probability that sand-binding is the probable ancestral root state for Haemodoroideae and for Haemodoraceae (Fig. 4).

In the family as a whole, sand-binding roots were present in the majority of genera and species. They were present in species of the tropics such as *Xiphidium caeruleum* and the tropical clade of *Haemodorum* (Fig. 4), as well as in taxa from semi-arid and wet temperate Australia and South Africa. Sand-binding roots were absent in a few species of *Conostylis* and *Tribonanthes* within the subfamily Conostylidoideae and in *Lachnanthes, Barberetta*,

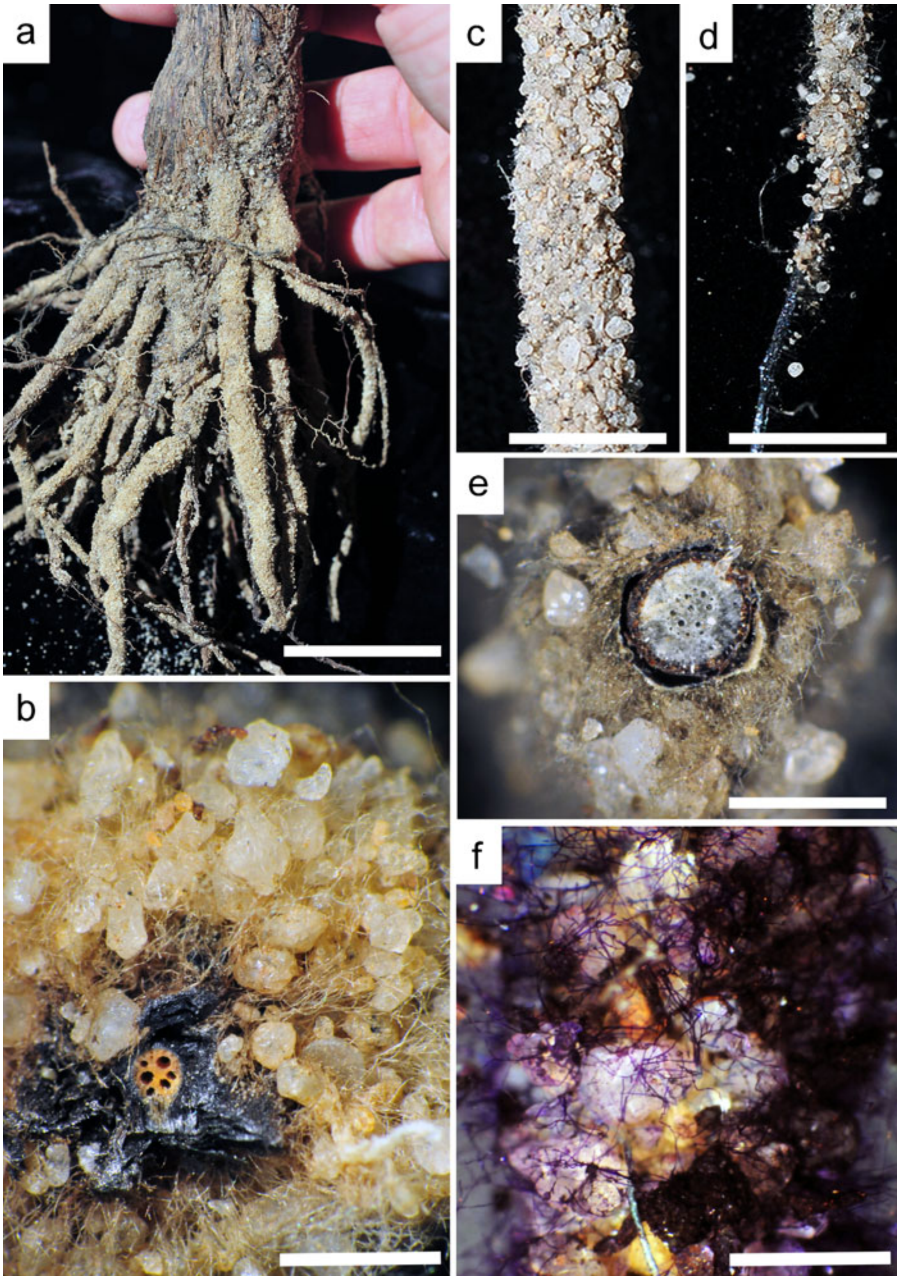


Fig. 1 Mature sand-binding root morphology of Haemodoraceae collected in the field. (**a, b**) *Haemodorum paniculatum*, (**c, e**) *Conostylis aculeata* subsp. *cygnorum*, (**d, f**) *Anigozanthos manglesii* subsp. *manglesii*. **a** *Haemodorum*, known to make thickest sand sheaths, showing numerous sand-binding roots beneath the dormant bulb, **b** Transverse view of root encased by several layers of sand grains and long, persistent root hairs, **c** Higher magnification of sand grains firmly bound to underlying root, **d** Sand sheath stripped off showing underlying stele, **e** Transverse view of root encased by a few layers of sand grains and persistent root hairs characteristic of the genus, **f** Abundant root hairs (blue) clearly visible against white sand grains after staining with toluidine blue. Scale bars, a=25 mm, b=2 mm, c=4.5 mm, d=5 mm, e=1.5 mm, f=1 mm. Photos and photomicrographs by MW Shane

Schiekia and *Wachendorfia* in subfamily Haemodoroideae (Table 1 and Fig. 4). However, an intermediate condition occurred in a small number of specimens of all three *Schiekia* subspecies and in *Wachendorfia paniculata* and *W. multiflora*. In these two genera, sparse lateral root hairs trapped some sand but this did not form a robust sheath (see Appendix 1). In Fig. 3d the image of *Schiekia* shows that sand is adhering to some roots but not to others and closer examination of this specimen did not reveal a significant sheath. However, there was an intermediate form of sand-binding as described above. The sand-binding condition was also variable within some species, particularly in *Anigozanthos*, with some specimens displaying the characteristic sheaths and others with no visible root hairs. Variability between different roots of the same specimen was also noted for a number of species in this genus. However, during

Table 1 The occurrence of sand-binding rhizosheaths in herbarium specimens of Haemodoraceae

Genus	# spp with SB roots conspicuous	# spp with SB roots rare	# spp with SB roots absent	% spp with SB roots	# spp sampled
Anigozanthos	11	1	0	100	12
Barberetta	0	0	1	0	1
Blancoa	0	1	0	100	1
Conostylis	30	8	9	81	47
Dilatris	4	0	0	100	4
Haemodorum	21	2	0	100	23
Lachnanthes	0	0	1	0	1
Macropidia	1	0	0	100	1
Phlebocarya	3	0	0	100	3
Pyrrorhiza	1	0	0	100	1
Schiekia	0	0	1[a]	0	1
Tribonanthes	0	3	3	50	6
Wachendorfia	0	0	5[a]	0	5
Xiphidium	2	0	0	100	2
Haemodoraceae	72	14	19	80	107

For each taxon, 1–30 specimens having roots were inspected at PERTH by SDH & MWS, at K by RJS and at NBG by SDH

[a] Intermediate form of sand-binding observed in some specimens with sand particles trapped in sparse root hairs but not forming a continuous robust sheath

field examination of roots it was noted that in *Anigozanthos humilis* the sand-binding characteristic was only present on young roots (unpublished data).

Only two of the 14 genera of Haemodoraceae displayed variability among clades with regard to the presence or absence of sand-binding roots: *Conostylis* and *Tribonanthes*. Within *Conostylis*, an endemic SWAFR genus and the largest in the family, 80% of species examined possessed sand-binding roots. Of those species that lacked sand-binding roots, the majority are found in *Conostylis* subgen. *Pendula*, particularly *C.* sect *Catospora* (see Fig. 5, Appendix I and Hopper et al. 2006). Along with occurrences in *C.* sect. *Divaricata*, *C.* subgen. *Androstemma*, *C.* subgen. *Greenia* and *C.* subgen. *Brachycaulon*, the taxa lacking sand-binding roots occur almost exclusively in one of the two major clades of *Conostylis* (Hopper et al. 2006; Clade A in Fig. 5). The one exception is *Conostylis hiemalis* (*C.* sect. *Appendicula*), which is the only member of the second major clade of *Conostylis* (Clade B in Fig. 5) to lack the trait. *C.* subgen. *Conostylis* is the only subgenus and clade to have sand-binding roots expressed in all taxa, although they were recorded as rare in *C. festucacea* subsp. *filifolia*.

Discussion

This study has extended the geographical scope of previous work documenting sand-binding roots to cover species on four continents and in a variety of climates: wet temperate, semiarid (Mediterranean climate), subtropical and tropical. The general morphology of sand-binding roots in Haemodoraceae appears similar to that documented in detail for other families such as Restionaceae (Shane et al. 2009, 2010) but further investigation is needed to assess the involvement of mucilage and/or bacteria.

Root plus sheath diameter in Haemodoraceae was found to be largest in *Haemodorum* species of southwest Australia (up to 7 mm), in agreement with Pate and Dixon (1996), who recorded root diameters of up to 10 mm in *Haemodorum spicatum*. Pate and Dixon (1996) reported the occurrence of sand-binding roots in four genera of SWAFR Haemodoraceae but with lower proportions of species than documented here. For example, they reported the trait in only one of twelve SWAFR *Haemodorum* species examined, whereas our systematic study of herbarium and field specimens has confirmed the presence of conspicuous sand-binding roots in 22

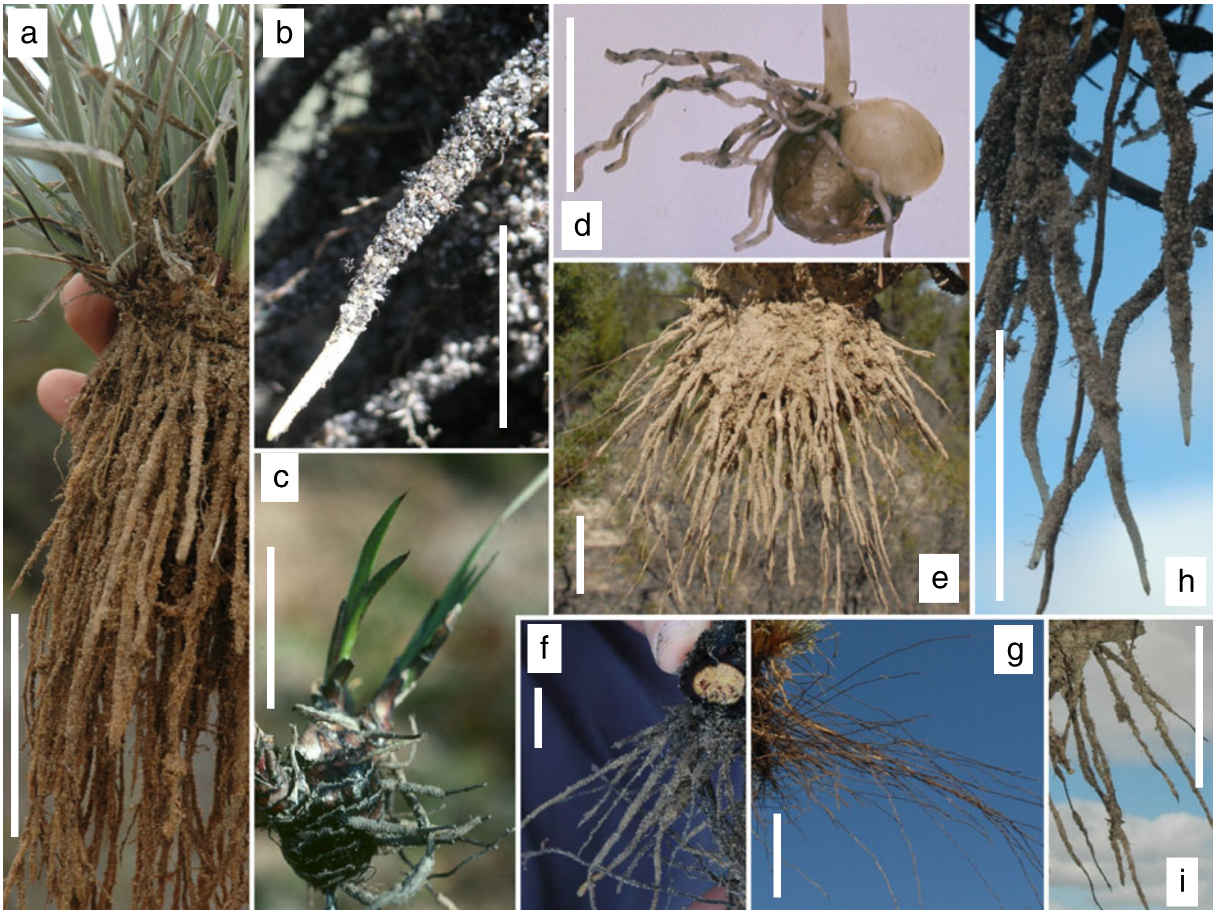


Fig. 2 Roots of Conostylidoideae **a** *Conostylis candicans*, **b** *Conostylis serrulata*, **c** *Anigozanthos flavidus*, **d** *Tribonanthes australis*, **e** *Conostylis glabra*, **f** *Macropidia fuliginosa*, **g** *Conostylis teretifolia*, **h** *Blancoa canescens*, **i** *Phlebocarya pilosissima*. Scale bars: a, c, e, h, i=5 cm; b, d, f, g=2 cm All photos by S.D. Hopper except d by K.W. Dixon

species of *Haemodorum*, including all SWAFR species except *H. brevisepalum*.

The sand-binding root trait was variable in Haemodoraceae but phylogenetic conservatism has occurred within genera. Sand-binding roots were present in all genera except *Lachnanthes, Barberetta*, *Schiekia* and *Wachendorfia*, although the latter two displayed an intermediate condition in some specimens, where sparse hairs trapped sand but did not form a robust, continuous sheath. As previously mentioned, of the 14 genera of Haemodoraceae, only *Conostylis* and *Tribonanthes* displayed variability in presence or absence of the trait and phylogenetic clustering of taxa without sand-binding roots was apparent. In the family as a whole, sand-binding roots were present in the majority of species (80% of those examined) and ancestral state reconstruction supported this as a plesiomorphic character for Conostylidoideae, with two secondary losses. Although the parsimony analysis gave equal weight to presence and absence of the trait as an ancestral character for Haemodoroideae and Haemodoraceae, the maximum likelihood method estimated a higher likelihood of the presence of sand-binding roots in the ancestor of the family and those of both subfamilies. It is therefore reasonable to conclude that sand-binding roots represent the ancestral state for Haemodoraceae, particularly as the reduction in the expression of sand-binding roots in some species is consistent with a scenario of secondary loss of the trait in the family.

Secondary loss has occurred in certain clades in semi-arid southwest Australia, notably in *Conostylis*, and reduction in the trait has occurred in other Conostylidoideae genera such as *Tribonanthes* and

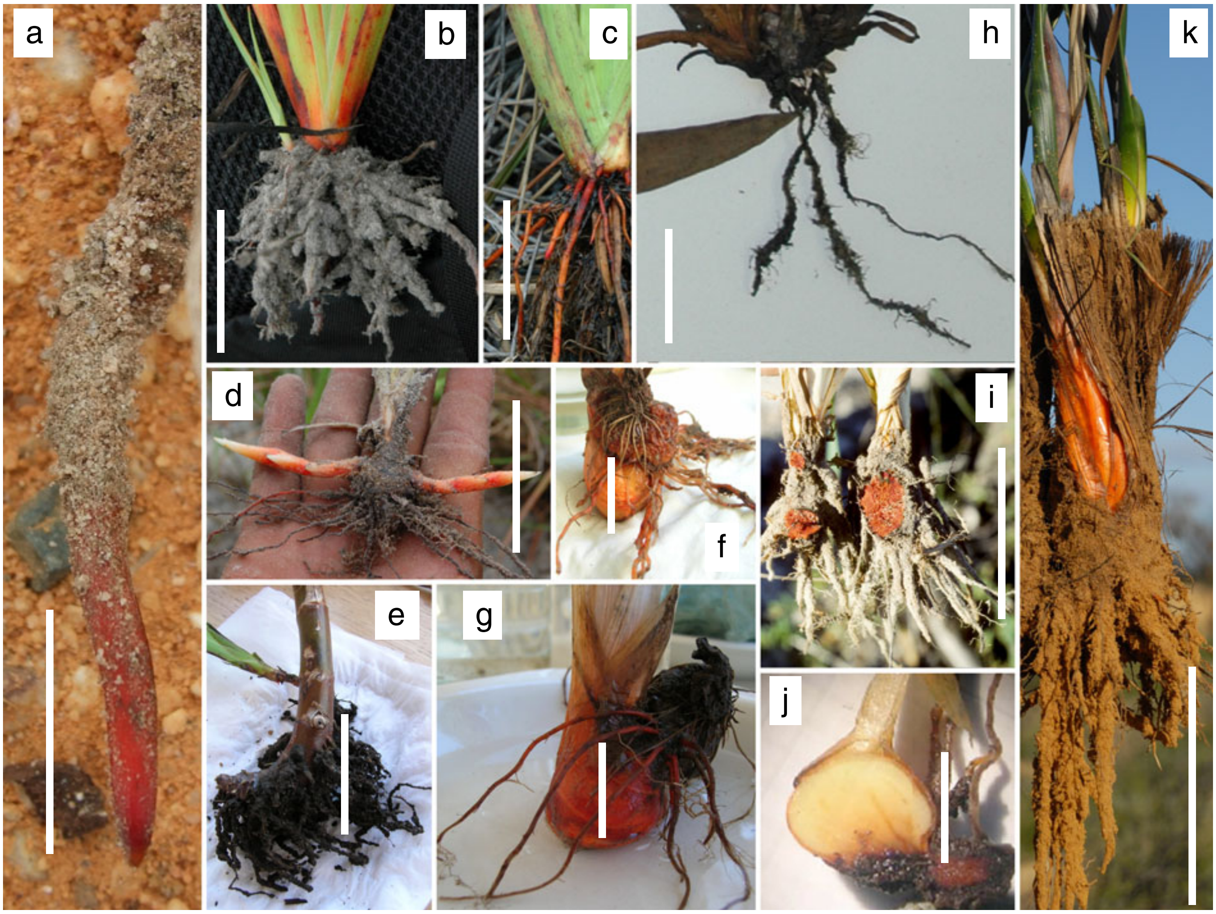


Fig. 3 Roots of Haemodoroideae **a**, **b** *Xiphidium xanthorrhizon* (Cuba), **c** *Lachnanthes caroliniana* (Cuba), **d** *Schiekia orinocensis* subspecies *orinocensis* (Guyana), **e** *Xiphidium caeruleum* (Brazil), **f** *Wachendorfia paniculata* (Republic of South Africa), **g** *Wachendorfia multiflora* (Republic of South Africa), **h** *Dilatris viscosa* (Herbarium specimen collected in Republic of South Africa), **i** *Haemodorum coccineum* (Queensland, Australia), **j** *Barberetta aurea* (Republic of South Africa), **k** *Haemodorum discolor* (SWAFR). Scale bars: a, e, f, g, h, j= 2 cm; b, c,d, i, k=5 cm. Photos by R.J. Smith (a,b,c,d), E. Hickman (e,f,g, j), S.D. Hopper (h, i, k)

Anigozanthos. In Haemodoroideae, phylogenetic conservatism was particularly pronounced, with absence of sand-binding roots in the sister genera *Barberetta* and *Wachendorfia* and the presence of sand-binding roots in the sister clades of *Haemodorum* and *Dilatris*. The most closely related families to Haemodoraceae are Pontederiaceae then Philydraceae (Hopper et al. 2009), and although they were not found to possess sand-binding roots, they are aquatic or semi-aquatic plants and could easily have lost the trait on transition to this habitat. Commelinaceae is the next most closely related plant family and although not present in *Spatholirion* (used here as an outgroup in the phylogeny), sand-binding roots were found in many genera across the family.

The question therefore remains whether poor nutrient availability, drought/heat stress, or a combination of these and other factors, was responsible for the development of the sand-binding root adaptation and conversely whether the alleviation of one of these pressures has led to its secondary loss. Lamont (1993) highlighted the presence of large numbers of long dense root hairs in cluster-rooted species growing in nutrient-impoverished soils of Australia and advocated a probable function primarily for nutrient acquisition. The same may hold true for the parallel structures in Haemodoraceae as we will now discuss, but other functions are possible and may even be complementary, and careful experimentation is needed to explore the various hypotheses.

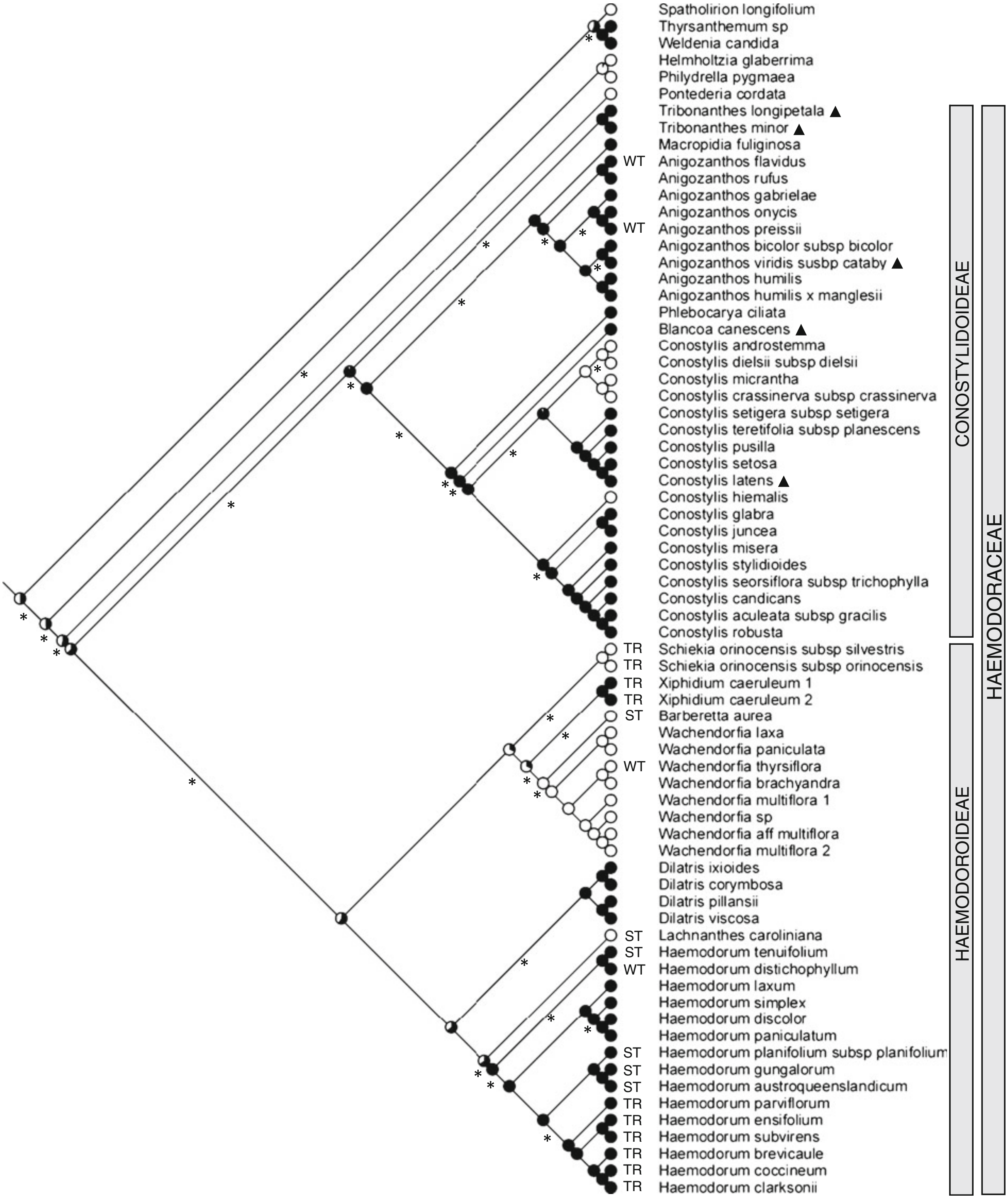
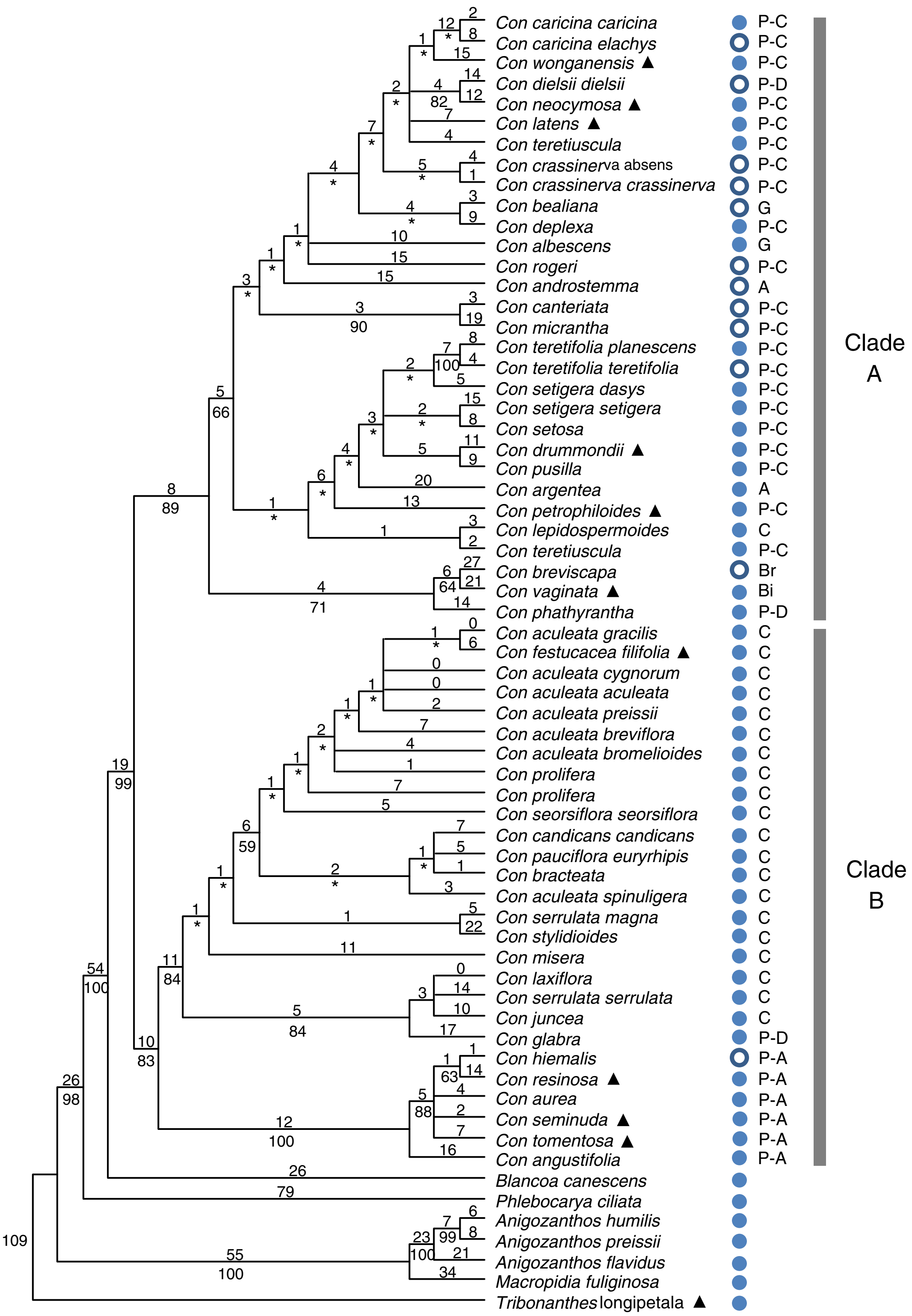


Fig. 4 Maximum likelihood ancestral state reconstruction mapped onto a molecular phylogeny of Haemodoraceae (from Hopper et al. 2009: *trnL*, *trnL-F* intergenic spacer and partial *matK* gene). All Haemodoraceae taxa are from semi-arid Mediterranean-climate habitats except where indicated by TR (Tropical), ST (Subtropical) or WT (Wet temperate). Open circles on ends of branches indicate absence and closed circles indicate presence of sand-binding roots. Circles positioned on nodes reflect the relative probability of sand-binding root presence/absence at that node. Triangles indicate taxa where sand-binding roots were rare in herbarium specimens examined. Bayesian posterior probabilities >0.90 are denoted by asterisks beneath branches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Con teretiuscula ● P-C
Con crassinerva absens ○ P-C
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Con deplexa ● P-C
Con albescens ● G
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Con petrophiloides ▲ ● P-C
Con lepidospermoides ● C
Con teretiuscula ● P-C
Con breviscapa ○ Br
Con vaginata ▲ ● Bi
Con phathyrantha ● P-D
Clade A
Con aculeata gracilis ● C
Con festucacea filifolia ▲ ● C
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Con seorsiflora seorsiflora ● C
Con candicans candicans ● C
Con pauciflora euryrhipis ● C
Con bracteata ● C
Con aculeata spinuligera ● C
Con serrulata magna ● C
Con stylidioides ● C
Con misera ● C
Con laxiflora ● C
Con serrulata serrulata ● C
Con juncea ● C
Con glabra ● P-D
Con hiemalis ○ P-A
Con resinosa ▲ ● P-A
Con aurea ● P-A
Con seminuda ▲ ● P-A
Con tomentosa ▲ ● P-A
Con angustifolia ● P-A
Clade B
Blancoa canescens ●
Phlebocarya ciliata ●
Anigozanthos humilis ●
Anigozanthos preissii ●
Anigozanthos flavidus ●
Macropidia fuliginosa ●
Tribonanthes longipetala ▲ ●

◀ **Fig. 5** Character states of sand-binding roots mapped onto a combined *ITS* and *matK* molecular phylogeny of *Conostylis* (from Hopper et al. 2006; number of changes shown above the line, bootstrap values below). Nodes marked by an asterisk collapsed in the consensus tree. Open circles on ends of branches indicate absence and closed circles indicate presence of sand-binding roots. Triangles indicate taxa where sand-binding roots were rare in herbarium specimens examined. Subgenera and sections (from Hopper et al. 1987) indicated as follows: P-C = *Conostylis* subgen. *Pendula* sect. *Catospora*; P-D = *C.* subgen. *Pendula* sect. *Divaricata*; P-A. = *C.* subgen. *Pendula* sect. *Appendicula*; G = *C.* subgen. *Androstemma*; Br = *C.* subgen. *Brachycaulon*; Bi = *C.* subgen. *Bicolorata*; C = *C.* subgen. *Conostylis*

Within the genus *Conostylis, C.* subgenus *Conostylis* was the only major clade with ubiquitous expression of sand-binding roots and occurs predominantly in the northern kwongan of the SWAFR (Hopper and Gioia 2004; Hopper et al. 2006), which has less summer rainfall than the southern kwongan and extremely low levels of available phosphorus. The prolonged summer heat and lack of moisture, and/or subtle differences in the nutrient status of the substrate, may have provided strong selective pressure for the retention of sand-binding roots in this subgenus and in its sister clade. The only species of *Conostylis* subgenus *Conostylis* that lacked sand-binding roots was *C. hiemalis*; this species tends to occur in winter-wet depressions in the sand-plain and would therefore have greater access to water than other members of the clade, less need for protection against desiccation and less need for the reduction of the root-soil gap for efficient nutrient uptake. In a very small number of specimens, some sand-binding root structures were observed but the majority of specimens had bare roots. The species may therefore have undergone reduction/loss of the ancestral sand-binding trait, as a result of a shift to a slightly wetter microhabitat with more organic matter and nutrients, or may show differential expression of the trait under different environmental conditions.

In *Tribonanthes*, three of the five species examined had sand-binding roots: *T. australis*, *T. longipetala* and *T. minor*. However, only a few specimens within these taxa exhibited the characteristic and it is possible that the ancestor of the genus was sand-binding but that the trait has been lost in three of the species and has undergone reduction in the remaining three, as we have postulated for *C. hiemalis*. All *Tribonanthes* species occur in seasonally wet habitats, in soils with a marginally higher proportion of organic matter than those occupied by other members of the subfamily and the selective pressure for retention of the sand-binding trait may therefore be reduced. Variability in this characteristic within some species, particularly in the genus *Anigozanthos* also suggests that the trait has undergone a reduction from an ancestral state and that it may be variably expressed within species and between roots within individuals.

The documentation of sand-binding roots in tropical species such as *Xiphidium caeruleum* and in the tropical clade of *Haemodorum*, as well as in wet temperate species such as *Haemodorum distichophyllum* and *Anigozanthos flavidus*, provides some evidence to suggest that selection for drought avoidance may not be the primary driver in the evolution of sand-binding roots in Haemodoraceae. Selection for improved nutrient uptake is an alternative hypothesis and in the ancient soils occupied by Haemodoraceae the limiting nutrient is likely to be phosphorus, which is depleted in the soils of old landscapes through leaching and erosion over long periods (Lambers et al. 2008) The question remains open as to whether or not some of these species release organic acids as part of their strategy to mine the mineral bound soil P fraction, which is typically an order or two of magnitude greater than the available P fraction (McArthur 1991).

A closer look at phylogenetic and biogeographical patterns in the data provides an opportunity for the comparison of distantly related taxa occupying the same habitat and of sister taxa occupying different habitats. Species of the South African genus *Wachendorfia*, such as *W. paniculata*, occur in seasonally dry, sandy environments comparable to those of *Haemodorum*, *Anigozanthos*, *Macropidia* and *Phlebocarya* in the SWAFR but the genus does not exhibit the full sand-binding trait. While the climates are similar in these two regions, differences in soil nutrient status may occur (Lambers et al. 2010), with the soils of the South African Cape being marginally richer in phosphorus than those of the ancient deep sand-plains of the SWAFR. However, this is speculative as in any landscape mosaics of microclimate and soils occur and the hypothesis would need detailed investigation to verify. This is one avenue of future study that may provide further illumination on the topic.

At the infra-generic level, within the genus *Conostylis*, there is also no consistent pattern in the general moisture content of the habitats of sand-binding and non sand-binding species (Hopper et al. 1987, 2006). There is however, some indication that there may be a correlation with differences in soil type. For example, *Conostylis caricina* and its sister species *C. wonganensis*, in contrast with the majority of sand-binding species, occur on marginally richer clay-loam or lateritic sands, rather than deep sand. *C. caricina* subpsecies *elachys* has lost the sand-binding trait completely and *C. caricina* subspecies *elachys* and *C. wonganensis* have both undergone a reduction in the extent of the root specialisation, which was recorded as rare in herbarium specimens. Sand-binding roots are also rare in *C. latens*, which occurs on sand and sandy loam over gravel.

Other species of *Conostylis* where sand-binding roots were recorded as absent include *C. crassinerva*, *C.rogeri* and *C. androstemma*, which occur on sand over laterite or lateritic gravel, *C. bealiana*, which occurs on sandy loam and gravel, and *C. dielsii* subsp *dielsii*, a species of yellow sand. There is therefore a suggestion that the majority of the *Conostylis* taxa without sand-binding roots, or with reduced expression of the trait, occur on substrates that have a lower sand content and may be marginally richer in nutrients, although rigorous investigation would be required to verify this. Bailey and Scholes (1997) also found a correlation between the proportion of sand in the soil and the extent of the rhizosheath. However, since sandy soils generally have less moisture and a lower nutrient content than clay and loam soils the individual effects of the variables cannot be determined. Further studies investigating the link between soil type, texture, particle size, moisture levels and detailed nutrient content are essential to understanding the origin and functional significance of sand-binding roots in Haemodoraceae and other taxonomic groups.

Distinguishing between the functional hypotheses for sand-binding roots and between the selective pressures which were responsible for their appearance in this lineage of Haemodoraceae is therefore not possible from the data presented here. Despite the suggestion that nutrient limitation may be important, it is possible that sand-binding roots evolved initially in response to water stress and were subsequently lost in tropical/subtropical taxa such as *Schiekia* and *Lachnanthes* when the ancestral lineages spread into these habitats. We also must consider the possibility that rhizosheaths have multiple functions, providing an adaptive solution to a number of inter-related selective pressures.

It is clear that further experimental studies are needed to understand the ecological and evolutionary forces at work leading to the secondary loss of sand-binding roots in some clades of Haemodoraceae and those that were operating at the time of the origin of the trait. The testing of the various hypotheses relating to the adaptive significance of sand-binding roots can be best achieved through detailed experimental study of the subtle differences in the habitats and edaphic microhabitats of sister species and clades that differ in their expression of the trait. Based on the molecular framework provided in this study, sister species and sister clades of *Conostylis* would provide the best study system and may help to elucidate the evolutionary drivers for the origin of the sand-binding adaptation and its secondary loss.

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Appendix I

Table 2 Detailed documentation of the occurrence of sand-binding roots in recognised taxa of Haemodoraceae from herbarium and field evidence

Status of sand-binding roots	Root + sheath diam., mm	Taxon	Additional comments
		Haemodoraceae	
+	1–2	*Anigozanthos bicolor* subsp. *bicolor* Endl.	Recorded from PERTH specimens. Variable in K specimens
+	1–2	*Anigozanthos bicolor* subsp. *decrescens* Hopper	
+	1–2	*Anigozanthos bicolor* subsp. *exstans* Hopper	
+	1–2	*Anigozanthos bicolor* subsp. *minor* (Benth.) Hopper	
+	2–4	*Anigozanthos flavidus* DC.	
+	1–3	*Anigozanthos gabrielae* Domin	Recorded from PERTH specimens. Variable in K specimens
+	1–2	*Anigozanthos humilis* subsp. *chrysanthus* Hopper	Recorded from PERTH specimens. Variable in K specimens
+	1–2	*Anigozanthos humilis* subsp. *grandis* Hopper ms.	Recorded from PERTH specimens. Variable in K specimens
+	1–2	*Anigozanthos humilis* Lindl. subsp. *humilis*	Recorded from PERTH specimens. Variable in K specimens
+	1–2	*Anigozanthos kalbarriensis* Hopper	Recorded from PERTH specimens. Variable in K specimens
+	1–3	*Anigozanthos manglesii* D.Don subsp. *manglesii*	Recorded from PERTH specimens. Variable in K specimens
+	1–3	*Anigozanthos manglesii* subsp. *quadrans* Hopper	
+	1–2	*Anigozanthos onycis* A.S.George	
+	1–3	*Anigozanthos preissii* Endl.	
+	1–3	*Anigozanthos pulcherrimus* Hook.	
+	1–3	*Anigozanthos rufus* Labill.	
±	1–2	*Anigozanthos viridis* subsp. *metallica* Hopper ms	Recorded from PERTH specimens. Very few seen
±	1–2	*Anigozanthos viridis* subsp. *terraspectans* Hopper	Recorded from PERTH specimens. Very few seen
±	1–2	*Anigozanthos viridis* Endl. subsp. *viridis*	Recorded from PERTH specimens. Very few seen
0		*Barberetta aurea* Harv.	
± ++	1–2	*Blancoa canescens* Lindl.	Very few seen in herbarium specimens but significant in the field.
+	2–3	*Conostylis aculeata* R.Br. subsp. *aculeata*	
+	1–2	*Conostylis aculeata* subsp. *breviflora* Hopper	
+	2–3	*Conostylis aculeata* subsp. *bromelioides* (Endl.) J.W.Green	
+	1–2	*Conostylis aculeata* subsp. *cygnorum* Hopper	
+	2–3	*Conostylis aculeata* subsp. *echinissima* Hopper	
+	1–2	*Conostylis aculeata* subsp. *gracilis* Hopper	
+	1–2	*Conostylis aculeata* subsp. *preissii* (Endl.) J.W.Green	Recorded from PERTH specimens. Some specimens with none.
+	1–2	*Conostylis aculeata* subsp. *rhipidion* J.W.Green	
+	1–2	*Conostylis aculeata* subsp. *septentrionora* Hopper	
+	1–2	*Conostylis aculeata* subsp. *spinuligera* (F.Muell. ex Benth.) Hopper	
+	1	*Conostylis albescens* Hopper	Recorded from PERTH specimens. None on K specimens
0		*Conostylis androstemma* F.Muell.	
+	1–2	*Conostylis angustifolia* Hopper	
+	1–2	*Conostylis argentea* (J.W.Green) Hopper	Recorded from PERTH specimens. None on K specimens

Table 2 (continued)

Status of sand-binding roots	Root + sheath diam., mm	Taxon	Additional comments
+	1–2	*Conostylis aurea* Lindl.	
0		*Conostylis bealiana* F.Muell.	
+	2–3	*Conostylis bracteata* Endl.	
0		*Conostylis breviscapa* R.Br.	Beard 2271 sand but no root hairs, on a sheath
+	1–2	*Conostylis candicans* subsp. *calcicola* Hopper	
+	2–3	*Conostylis candicans* Endl. subsp. *candicans*.	
+	2	*Conostylis candicans* subsp. *flavifolia* Hopper	
+	2	*Conostylis candicans* subsp. *procumbens* Hopper	
0		*Conostylis canteriata* Hopper	
±	1–2	*Conostylis caricina* Lindl. subsp. *caricina*	Recorded from PERTH specimens. Very few seen
0		*Conostylis caricina* subsp. *elachys* Hopper	Usually bare. Very small amount seen in rare PERTH specimens.
0		*Conostylis crassinerva* subsp. *absens* Hopper	
0		*Conostylis crassinerva* J.W.Green subsp. *crassinerva*	
+	1–2	*Conostylis deplexa* J.W.Green	
0		*Conostylis dielsii* W.Fitzg. subsp. *dielsii*.	
0		*Conostylis dielsii* subsp. *teres* Hopper	
±	1–2	*Conostylis drummondii* Benth.	
±	1–2	*Conostylis festucacea* Endl. subsp. *festucacea*	
±	2–3	*Conostylis festucacea* subsp. *filifolia* (F.Muell.) Hopper	
++		*Conostylis glabra* Hopper ms	
0		*Conostylis hiemalis* Hopper	Rare, very small amount in PERTH specimens, usually bare
±	1–2	*Conostylis juncea* Endl.	Recorded from PERTH specimens. Enlarged near rhizome, sand grains bound, very short hairs
±	1–2	*Conostylis latens* Hopper	Recorded from PERTH specimens. None on K specimens
+	1–2	*Conostylis laxiflora* Benth.	
+	2	*Conostylis lepidospermoides* Hopper	
+	1–3	*Conostylis magna* Hopper ms	
0		*Conostylis micrantha* Hopper	
+	1–2	*Conostylis misera* Endl.	
±	1–2	*Conostylis neocymosa* Hopper	Fine, but present in half the PERTH specimens—none on K specimen
+	1–2	*Conostylis pauciflora* subsp. *euryrhipis* Hopper	
+	1–2	*Conostylis pauciflora* Hopper subsp. *pauciflora*	
±	1–2	*Conostylis petrophiloides* F.Muell.	Recorded from PERTH specimens. None on K specimens
+	1–2	*Conostylis phathyrantha* Diels & E.Pritz.	Recorded from PERTH specimens. Scarce, short hairs
+	2	*Conostylis prolifera* Benth.	
+	1–2	*Conostylis pusilla* Endl.	
±	1	*Conostylis resinosa* Hopper	Recorded from PERTH specimens. Short sparse hairs on ca. half the specimens, with sand.
+	1–4	*Conostylis robusta* Diels & E.Pritz.	
0		*Conostylis rogeri* Hopper	
±	1–2	*Conostylis seminuda* Hopper	Recorded from PERTH specimens. Rare in K specimens
		Conostylis seorsiflora subsp. *longissima* Hopper	
+	2	*Conostylis seorsiflora* F.Muell. subsp. *seorsiflora*	

Table 2 (continued)

Status of sand-binding roots	Root + sheath diam., mm	Taxon	Additional comments
		Conostylis seorsiflora subsp. *trichophylla* Hopper	
+	2–3	*Conostylis serrulata* R.Br.	
+	1–2	*Conostylis setigera* subsp. *dasys* Hopper	
+	1–2	*Conostylis setigera* R.Br. subsp. *setigera*	
+	1–2	*Conostylis setosa* Lindl.	
+	1–3	*Conostylis stylidioides* F.Muell.	
+	1–2	*Conostylis teretifolia* subsp. *planescens* Hopper	
0		*Conostylis teretifolia* J.W.Green subsp. *teretifolia*.	
+	1–2	*Conostylis teretiuscula* F.Muell.	
±	1	*Conostylis tomentosa* Hopper	
±	1	*Conostylis vaginata* Endl.	Recorded from PERTH specimens. One specimen only with a few sparse hairs out of 20 specimens with roots.
±	1	*Conostylis villosa* Benth.	Recorded from PERTH specimens. Short sparse hairs on ca. one tenth of specimens.
±	1	*Conostylis wonganensis* Hopper	Recorded from PERTH specimens. Short sparse hairs on ca. one tenth of specimens
+ ++	2–3	*Dilatris corymbosa* P.J.Bergius	
+ ++	2–4	*Dilatris ixioides* Lam.	
+ ++	1–3	*Dilatris pillansii* W.F.Barker	
+ ++	2–4	*Dilatris viscosa* L.f.	
+	1–3	*Haemodorum austroqueenslandicum* Domin	
+ ++	1–2	*Haemodorum brevicaule* F.Muell.	
±	1–2	*Haemodorum brevisepalum* Benth.	
++		*Haemodorum clarksonii* Hopper ms.	
+ ++	2–5	*Haemodorum coccineum* R.Br.	
+	1–2	*Haemodorum corymbosum* Vahl	
+ ++	2–5	*Haemodorum discolor* T.D.Macfarl.	
+	2–3	*Haemodorum distichophyllum* Hook.	
++		*Haemodorum ensifolium* F.Muell.	
		Haemodorum flaviflorum W.Fitzg.	
		Haemodorum gracile T.D.Macfarl.	
++		*Haemodorum gungalorum* Hopper ms	
+	2–6	*Haemodorum laxum* R.Br., Prodr.	
+ ++	1–2	*Haemodorum leptostachyum* Benth.	
+ ++	3–5	*Haemodorum loratum* T.D.Macfarl.	
+ ++	2–6	*Haemodorum paniculatum* Lindl.	
++		*Haemodorum parviflorum* Benth.	
+	2–4	*Haemodorum planifolium* R.Br.	
+ ++	2–4	*Haemodorum simplex* Lindl.	
+ ++	2–6	*Haemodorum simulans* F.Muell.	
+ ++	2–4	*Haemodorum sparsiflorum* F.Muell.	
+ ++	3–7	*Haemodorum spicatum* R.Br.	
+ ++	2–3	*Haemodorum subvirens* F.Muell.	
+	2–3	*Haemodorum tenuifolium* A.Cunn. ex Benth.	
+ ++	3–4	*Haemodorum venosum* T.D.Macfarl.	
0		*Lachnanthes caroliniana* (Lam.) Dandy	
+	1–4	*Macropidia fuliginosa* (Hook.) Druce	
+	2–3	*Phlebocarya ciliata* R.Br.	
+	1–2	*Phlebocarya filifolia* (F.Muell.) Benth.	

Table 2 (continued)

Status of sand-binding roots	Root + sheath diam., mm	Taxon	Additional comments
+ ++	1–3	*Phlebocarya pilosissima* (F.Muell.) Benth. subsp. *pilosissima*.	
+	1–2	*Phlebocarya pilosissima* subsp. *teretifolia* T.D.Macfarl.	
±±		*Pyrrorhiza neblinae* Maguire & Wurdack	
0		*Schiekia orinocensis* (Kunth) Meisn. subsp. *orinocensis*.	
		Schiekia orinocensis subsp. *savannarum* Maguire & Wurdack	
0		*Schiekia orinocensis* subsp. *silvestris* Maas & Stoel	
			Note: All *Schiekia* subspecies had roots with an intermediate sand-binding form on a small number of K specimens. Root hairs were sparse and trapped a small amount of sand but this did not form a robust continuous sheath around the roots.
±	1–2	*Tribonanthes australis* Endl.	Recorded from PERTH specimens. Few specimens with roots, and, of those, very few with sand-binding roots.
0		*Tribonanthes brachypetala* Lindl.	
±	1–2	*Tribonanthes longipetala* Lindl.	Recorded from PERTH specimens. Few specimens with roots, and, of those, a few with sand-binding roots e.g. R Helms 19 July 1897 Midland Jn
±		*Tribonanthes minor* M.Lyons & Keighery	
0		*Tribonanthes purpurea* T.D.Macfarl.& Hopper	
0		*Tribonanthes violacea* Endl.	
0		*Wachendorfia brachyandra* W.F.Barker	
0		*Wachendorfia laxa* Hopper ms	
0		*Wachendorfia multiflora* (Klatt) J.C.Manning & Goldblatt	
0		*Wachendorfia paniculata* Burm.	
0		*Wachendorfia thyrsiflora* Burm.	
			Note: *Wachendorfia brachyandra, W. multiflora* and *W. paniculata* had roots with an intermediate sand-binding form on a small number of K specimens. Root hairs were sparse and trapped a small amount of sand but this did not form a robust continuous sheath around the roots.
+ ++	1–3	*Xiphidium caeruleum* Aubl.	Recorded from K specimens. Not present in all.
+ ++	5	*Xiphidium xanthorrhizon* C.Wright ex Griseb.	
0		Pontederiaceae	Absent from all specimens
0		Philydraceae	Absent from all specimens
+	1–5 mm	Commelinaceae	Present in many genera including *Weldenia, Thyrsanthemum, Aneilema, Commelina, Gibasis* and *Tradescantia*

+ = sand-binding roots present, mm = diameter; ± = sand-binding roots rare; 0 = sand-binding roots absent

[Data from 1–30 specimens with roots, per taxon, inspected by SDH & MWS at PERTH and at K by RS]

++ = sand-binding roots confirmed in the field by SDH or RJS, with photographic evidence

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