Coloured nectar: distribution, ecology, and evolution of an enigmatic floral trait

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ABSTRACT

While coloured nectar has been known to science at least since 1785, it has only recently received focused scientific attention. However, information about this rare floral trait is scattered and hard to find. Here, we document coloured nectar in 67 taxa worldwide, with a wide taxonomical and geographical distribution. We summarise what is currently known about coloured nectar in each of the lineages where it occurs. The most common nectar colours are in the spectrum from yellow to red, but also brown, black, green, and blue colours are found. Colour intensity of the nectar varies, sometimes even within one taxa, as does the level of contrast between flower petals and nectar. Coloured nectar has evolved independently throughout the angiosperms at least 15 times at the level of family, and is in many cases correlated with one or more of three parameters: (1) vertebrate pollination, known or hypothesised, (2) insularity – many species are from islands or insular mainland habitats, and (3) altitude – many species are found at relatively high altitudes. We discuss the evolution and speculate on possible ecological functions of coloured nectar. Apart from being a non-functional, perhaps pleiotropic, trait, we present several hypotheses on possible ecological functions of coloured nectar. Firstly, for some plant species it can be interpreted as an honest signal, leading to high pollination efficiency. Secondly, it can function as a deterrent against nectar-thieves or inefficient pollinators, thus acting as a floral filter. Thirdly, nectar colour-pigments can have anti-microbial qualities that may protect the nectar in long-lived flowers. Neither of these possibilities are mutually exclusive. Recent studies have provided experimental evidence for the first two hypotheses, and we suggest promising avenues for future research into this little-known floral trait.

Key words: floral trait, nectar properties, mutualism, pollination biology, pollinator attraction, signalling theory, honest signal, floral filter.

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I. INTRODUCTION

Ever since Sprengel's landmark publication in 1793, researchers have tried to understand how floral traits affect interactions with pollinators, and *vice versa*. One floral trait that has received much attention is nectar, the main 'currency' of many pollination interactions. Analytical research on nectar properties has focused on the composition of sugars (Percival, 1961; Baker & Baker, 1983; Baker, Baker & Hodges, 1998) and amino acids (Baker & Baker, 1973, 1986; Gottsberger, Schrauwen & Linskens, 1984). Lately, more specific ecological traits and functions of nectar have been studied; e.g. taste (Gardener & Gillman, 2002), toxicity (Ehlers & Olesen, 1997; Adler, 2000), and scent (Raguso, 2004b), including how these traits interact with the physiology and behaviour of flower-visiting animals. The general conclusions in these studies are that little is known about 'nectar ecology'. Herein we review the occurrence of a particularly enigmatic nectar

trait, colour, and speculate about its ecological functional significance and evolution.

A divine liquid in mythology, red nectar is known from antiquity. In the Illiad, Homer describes the actions of the goddess Thetis as she preserves the body of the dead warrior Patroclus: "she then dropped ambrosia and red nectar into the wounds of Patroclus, that his body might suffer no change." (Book XIX, verses 37–39). In modern science, coloured nectar has a long history as well. The first reference to coloured nectar is found in *Dissertatio de Aloe* (Hesselius, 1785), where the description of *Aloe spicata* includes the line, "*Corollae repletae sunt succo melleo purpurascente*", clearly referring to the corolla being replete with sweet, dark-red nectar. The most eloquent early description of coloured nectar is found in one of the oldest volumes of Curtis's Botanical Magazine (1795, Volume 9, Plate 301), where the description of *Melianthus minor* (= *M. comosus*) (Melianthaceae) states: "There are few flowers that do not secrete from some kind of a glandular substance, honey, or

nectar, to a greater or smaller amount; in those of the present genus, this liquid is particularly abundant … and is of a dark brown colour, an unusual phenomenon". Furthermore, the accompanying plate shows this detail in such quality, that it is possible to see the dark nectar through the pale green, semi-transparent sepals, much like it can be seen in the wild (Fig. 1). This species was first described only one year earlier, but the diagnosis does not mention the coloured nectar, or even the abundance of nectar (Vahl, 1794). This points to the crux of the matter in our current understanding of coloured nectar: for the majority of taxa with coloured nectar, the taxonomical description does not mention the colouration of the nectar. Another early example of this is *Jaltomata aspera* (Solanaceae) of Peru. Ruiz & Pavón (1799) described the pale cream-coloured corolla of *J. aspera*, as "violet in the centre". However, long reflected in its local name, *lágrima de la virgen*, or 'tear of the virgin', the red nectar of this plant was not described by botanists until Bitter (1921) wrote about the "copious production of a blood-red juice from glands at the bottom of the corolla between the anthers". In the case of *Melianthus* and *Aloe*, where coloured nectar has long been known, it has not been reported in mainstream ecological or botanical journals, but only in taxonomical descriptions and studies. In most other lineages, the coloured nectar is not even mentioned in the taxonomical descriptions or studies of the plants.

Given its visual impact, it is surprising that so little is known about coloured nectar. The almost complete omission of reference to nectar colour in the taxonomical literature has limited our knowledge of the geographical and taxonomical distribution of coloured nectar, and has made studies of its possible ecological function and evolution difficult. The main reason is without doubt that the original descriptions were based on herbarium material. Here, of course, the nectar has long dried out, leaving at most only discoloured marks that are difficult to interpret. Marloth (1925), for example, simply discounted the dark stains of nectar on a dry herbarium specimen of *A. spicata* as a reaction between clear nectar and the filaments or the paper used in pressing the plant – a mistake that was later pointed out by Glen & Hardy (1995). To summarise, in all taxa coloured nectar was only mentioned in the literature after investigation of living plants.

Nesocodon mauritianus (Campanulaceae) was the first species with coloured nectar for which the ecology and nectar-chemistry was studied in detail (Olesen *et al.*, 1998). The species was discovered on the island of Mauritius in 1976, but there was no mention of the blood-red colour of the nectar in the taxonomical description (Richardson, 1979). Later, after studying *N. mauritianus* plants in cultivation, Wyse Jackson (1990) was the first to mention the red nectar of this species. Olesen *et al.* (1998) also reported the presence of coloured nectar in two Mauritian *Trochetia* (Malvaceae) species, *T. blackburniana* and *T. boutoniana*, and stated that – to their knowledge – these plants, along with *N. mauritianus*, were the only ones in the world with coloured nectar. From our detailed research for this review it is now obvious that this is not true. However, information on coloured nectar is hard to find in the mainstream scientific literature, and is often known only from grey literature or observations. Our study reviews the occurrence of and knowledge on coloured nectar in flowering plants. Specifically, we aim to (1) document and investigate the geographical and taxonomical distribution of coloured nectar in flowering plants, (2) summarise the current knowledge about species with coloured nectar and the lineages in which they occur, (3) investigate possible environmental and ecological correlates of coloured nectar, and (4) discuss its possible ecological functions and its evolution.

II. METHODS

We here define coloured nectar as a floral sugary secretion that contains one or more pigments or coloured substances that are apparently produced and secreted by the plants. We include only species with nectar colours in the spectrum visible to humans. One study has documented ultraviolet-fluorescent nectar in several species (Thorp *et al.*, 1975). However, there have been no further studies of this trait, and we have not included species with known UV-fluorescent nectar in our study.

The idiosyncratic literature on coloured nectar precluded any attempt to obtain data in a standardised and methodological way. We conducted a thorough search of the literature, using library and scientific databases, web pages, scientific publications, and regional and national floras. In web-based databases and search engines we used specific queries, searching for 'nectar' in combination with each of the following words 'colour, coloured, dark, black, red, brown, yellow, orange, green, blue, purple' in English (US and UK), Spanish, Portuguese, French, German and Danish. Furthermore, we contacted many pollination biologists, plant biologists and taxonomists, attempting to cover a broad geographical and taxonomical range, and inquired about observations of coloured nectar. When coloured nectar was confirmed for a species, we also acquired information from the literature about related species, and by contacting researchers studying related species within the same lineage. We also included our personal observations on taxa with coloured nectar. We compiled a database with data on growth form, geographical

Fig. 1. *Melianthus minor* flowers. (A) Part of an illustration in Curtis's Botanical Magazine (1795, Volume 9, Plate 301). (B) Photograph of flowers of a botanical garden plant. Note how the black nectar is clearly visible through the pale, semi-translucent sepals in both pictures. Photograph by W. Barthlott.

and taxonomical distribution and altitudinal range; on floral traits, including size, colour and morphology; and on nectar traits, including volume, concentration and sugar composition. Then we examined this database, aiming to identify any potential correlations that would help us formulate hypotheses on its possible ecological functions and evolution of coloured nectar. Furthermore, we gathered information on the different lineages with coloured nectar and their closest relatives to summarise our current knowledge within each lineage. If available, we included ecological and evolutionary information in our summary.

III. RESULTS

(1) Taxonomical and geographical distribution

In total, we were able to document the presence of coloured nectar in 68 taxa from 20 genera in 15 families (Table 1; Fig. 2). These taxa occur in tropical and subtropical regions, with a wide geographical distribution (Table 1). We found that coloured nectar occurs in at least 13 angiosperm orders, covering widely separated branches of the phylogenetic tree. Coloured nectar is found in both monocots and eudicots, but not in the magnoliids or paleoherbs (Fig. 3).

(2) Flower and nectar traits

The flowers of species with coloured nectar show large variation in nectar colours (Table 1, Fig. 2). The colours of nectar can be divided into the following broad categories (using the 'darkest' recorded nectar colour for a taxon in Table 1; relative frequency in parenthesis): yellow (15 taxa; 22.1%), amber – orange (six taxa; 8.8%), red (17 taxa; 25%), brown (14 taxa; 20.6%), green (five taxa; 7.4%), blue (two taxa; 2.9%) and black (nine taxa; 13.2%). Thus, we find that 55.9% of the taxa have nectar colours in the range from yellow to red, and most of those with darker colours (brown or black) are very dark hues of red. Only in *Schiedea* does the black colouration seem to originate from grey hues (S. G. Weller, personal communication). The green colours of the nectar in some *Banksia* species are also clearly outside the 'red' group, even though the nectar in young flowers of these species has a yellow colouration (Markey & Lamont, 1995). *Puya alpestris* and *Schwartzia brasiliensis* are the only known species with blue or blue-red nectar. The level of contrast between the flower petals and the nectar also varies (Table 1). In most species, the nectar contrasts well against the petals in the human visible spectrum, but even in plants with overall petal colours similar to the nectar colour, the nectar often still contrasts due to being present on lighter parts of the corolla (see Fig. 2, and Section IV.4).

Species with coloured nectar also vary widely in growth form and floral morphology, with plants ranging from vines and small shrubs to large trees, and having from radially symmetrical to strongly zygomorphic flowers in many different colours (Table 1; Fig. 2). However, most flowers are open and easily accessible to visitors (e.g. *Hoya*, Fig. 2B,C; *Trochetia* Fig. 2G; *Aloe* Fig. 2D,J; *Capsicum* Fig. 2P), or if more closed or tubular, the nectar can often be seen from the outside at a distance, through a pale or semi-translucent calyx or corolla (in some *Melianthus* species, Fig. 1; and in some *Jaltomata* species, Fig. 2K). For nectar traits, we have only found information for a subset of the plants with coloured nectar (Table 2). From this it is clear, however, that most produce relatively large amounts of nectar, forming visible drops in the flowers. Furthermore, most of the species for which we have information have sugars that are hexose-dominated (Table 2).

(3) Lineage descriptions

In the following we summarise and discuss our current knowledge of coloured nectar in each lineage, with an emphasis on pollination ecology if data are available.

(a) *Asparagales – Asphodelaceae* – Aloe

Aloe is a large genus with some 365–400 species, native to Africa, the Arabian Peninsula and Madagascar (Mabberley, 1997; Viljoen, van Wyk & van Heerden, 1998). Growth forms vary from dwarf rosettes to trees of more than 15 m in height. Most *Aloe* species have large inflorescences with long, slender, pendulous and tubular flowers (van Wyk & Smith, 1996). However, one small section, *Anguialoe*, comprises four species with very dense racemes or spikes that carry short, sessile and campanulate flowers (Reynolds, 1940; Glen & Hardy, 1995). Coloured nectar is found in all four species currently recognised within *Anguialoe*, albeit at varying levels of colour intensity (Fig. 2D, J; Table 1). Contrary to most other lineages where coloured nectar occurs, it has been known for a long time in *Aloe*. Hesselius' (1785) treatment of the genus contains the first scientific reference to coloured nectar that we have been able to find (see Section I), and it has been mentioned regularly in the scientific literature since then. For example, Pole Evans (1925) describes the flowers of *A. sessiliflora* (= *A. spicata*), stating that they "contain drops of very dark nectar", and Groenewald (1938), in his description of *A. dolomitica* (= *A. vryheidensis*), makes a note of the dark brown nectar in the flowers. Dyer (1931) mentions the flowers of *A. sessiliflora* being "filled with a reddish nectar", and later he states that the nectar of *A. vryheidensis* "appears almost black in colour" (Dyer, 1941). In the original circumscription of *Anguialoe*, Reynolds (1940) even used the flowers' "copious supply of dark nectar" as a defining trait for the section. However, clear rather than coloured nectar has been noted in the wild for *A. alooides* (B.-E. van Wyk, personal communication), but in a greenhouse in the National Botanical Garden of Belgium, a plant produced red nectar in 2002 (B. Loison, personal communication). Lastly, the dark nectar is also mentioned in some of the more popular accounts of *Aloe* species (e.g. Court, 1981; van Wyk & Smith, 1996). For *Aloe* section *Anguialoe* in general, Reynolds (1940) remarked that the nectar seems to be of a lighter colour in young flowers, while it is darker in the oldest flowers. Nicolson & Nepi (2005) mention the same for the nectar in *A. castanea* flowers. This colour change is due to oxidation of phenolic compounds that impart the dark brown colour to the nectar (H. F. Glen, personal communication; S. D. Johnson, A. Hargreaves & M. Brown, unpublished data). A recent study has shown that *Aloe*

Table 1. Plant taxa with coloured nectar; their geographical and altitudinal distribution, growth form, flower morphology, nectar colour and observed flower visitors ('nd' = no data available)

Order	Family	Species	Distribution	Altitude (masl)	Growth form	Flower form	Flower size (mm)[1]	Flower colour[2]	Nectar colour[2]	Flower visitors[3]
Asparagales	Asphodelaceae	*Aloe alooides*	South Africa	1450–2000	shrub	campanulate	9	yellow	clear – red	B, I
		A. castanea	South Africa	1400–1700	shrub	campanulate	18–19	orange – red	yellow – brown	B, I
		A. vryheidensis	South Africa	1300–1550	shrub	campanulate	14	yellow	dark red – brown	B, I
		A. spicata	South Africa, Zimbabwe	700–1000	shrub	campanulate	18–20	yellow	dark red – brown	B, I
	Hemerocallidaceae	*Phormium tenax*	New Zealand	0–1000	shrub	tubular	26 × 7–9	orange – red	clear – yellow	B, L
Asterales	Campanulaceae	*Nesocodon mauritianus*	Mauritius	5–600	subshrub	campanulate	50 × 30	blue	orange – red	B?, L?, B†
Caryophyllales	Caryophyllaceae	*Schiedea lychnoides*	Kaua'i	1090–1320	vine	campanulate	5, 9–12[4]	white[5]	black	u, B?
		S. obovata	O'ahu	550–800	shrub	campanulate	7–8.4[4]	white[5]	black	u, B?
		S. trinerve	O'ahu	900–1230	subshrub	ball-shaped	6–8[4]	white[5]	black	u, B?
		S. viscosa	Kaua'i	820–1150	vine	campanulate	5, 6.5–9[4]	white[5]	black	u, B?
Ericales	Marcgraviaceae	*Schwartzia brasiliensis*	Brazil	0-800	vine	urceolate[6]	10–12 × 8–10[6]	dark purple-brown[6]	blue	B, I
Fabales	Fabaceae	*Calliandra calothyrsus*	S Mexico to C Panama	0–1800	tree	brush-type	6–8, 40–60[7]	green and red[8]	yellow	M, I, B
		Erythrina caffra	South Africa	nd	tree	zygomorphic	42–70 × 27–40	red	clear – pale brown	B
		E. humeana	Southern Africa[9]	nd	shrub	zygomorphic	35–50 × 14–21	red	amber	B
		E. zeyheri	South Africa	1700–1750	subshrub	zygomorphic	24–44 × 14–22	red	pale yellow	B
Gentianales	Apocynaceae	*Hoya diversifolia*	Asia[10]	lowland	vine	rotate	13 (diameter)	cream – pale pink[11]	amber – brown	u
		H. excavata	Malaysia	nd	vine	rotate	13 (diameter)	pink[11]	brown	u
		H. kerrii	Asia[10]	390	vine	rotate	9–13 (diameter)	white – cream[11]	amber – brown	u
		H. meliflua	Philippines	lowland	vine	rotate	15 (diameter)	pink – purple[11]	dark red	u
		H. obovata	Asia[10]	nd	vine	rotate	15 (diameter)	cream – pink[11]	brown	u
Geraniales	Melianthaceae	*Melianthus comosus*	South Africa, Namibia	400–2000	shrub	zygomorphic	15–32 × 10^{12}	green – pale pink[13]	black	B, I
		M. dregeanus	South Africa	600–1800	shrub	zygomorphic	15–20 × 10^{12}	red[13]	brown	B
		M. elongatus	South Africa	0–300	shrub	zygomorphic	15–22 × 8[12]	green[13]	black	B
		M. gariepinus	South Africa, Namibia	400–2000	shrub	zygomorphic	15–22 × 7–10[12]	green[13]	brown	B
		M. insignis	South Africa	900–1800	shrub	zygomorphic	15–40 × 10^{12}	red[13]	brown	B
		M. major	South Africa	300–900	shrub	zygomorphic	15–35 × 10–12[12]	dark red – brown[13]	brown	B
		M. pectinatus	South Africa	0–900	shrub	zygomorphic	10–17 × 5–10[12]	green[13]	black	B
		M. villosus	South Africa	1600–2000	shrub	zygomorphic	15–35 × 10–12[12]	purple – brown[13]	black	B, I
Lamiales	Bignoniaceae	*Deplanchea tetraphylla*	New Guinea, Australia	0–1000	tree	zygomorphic	25 × 25 × 10^{14}	yellow	amber – dark brown	B, M
		Fernandoa magnifica	Eastern Africa[15]	0–500	tree	broadly campanulate	50–110	yellow – red	dark brown – black	B?, M?

Table 1 (*cont.*)

Order	Family	Species	Distribution	Altitude (masl)	Growth form	Flower form	Flower size (mm)[1]	Flower colour[2]	Nectar colour[2]	Flower visitors[3]
	Lamiaceae	*Leucosceptrum canum*	Himalaya to China[16]	610–2600	shrub – small tree	campanulate	8–10 × 6	white – cream	dark brown	B, I
Malvales	Malvaceae	*Dombeya a.* ssp. *acutangula*	La Réunion	0–1200	shrub – small tree	broadly campanulate	20–30 (diameter)	white – cream	yellow	B, I†
		D. a. ssp. *palmata*	La Réunion	nd	shrub – small tree	broadly campanulate	20–25 (diameter)	white – cream	yellow	B, I, I†
		D. a. ssp. *rosea*	Mauritius	200–600	shrub – small tree	broadly campanulate	20–25 (diameter)	pink	yellow	B, I, I†
		D. cacuminum	Madagascar	montane forests	tree	campanulate	40	red	yellow	M, B?
		D. elegans	La Réunion	800–1800	shrub – small tree	campanulate	10–14	pink	yellow	B
		D. kefaensis	Ethiopia	2200	shrub	campanulate	13–17	white – pale pink	red	u
		Trochetia blackburniana	Mauritius	300–700	shrub – small tree	campanulate	15–25 × 18–25	pale pink – red	clear – amber	B, L, I†
		T. boutoniana	Mauritius	400–600	shrub – small tree	campanulate	45–50 × 45–50	pink – red	orange – red	B, L, I†
		T. granulata	La Réunion	1200–1600	shrub	campanulate	36–41 × 29–32	white	yellow	B, I†
		T. parviflora	Mauritius	300–600	shrub	crateriform rotate	8–11 × 18–21	white – pale pink	clear – yellow	u, I?
		T. triflora	Mauritius	500–700	shrub – tree	broadly campanulate	25–40 × 50–70	white	yellow	B, I†, M?
		T. uniflora	Mauritius	400–700	shrub	campanulate	25–30 × 19–28	pink – red	orange – red	B, I†
Myrtales	Combretaceae	*Lumnitzera littorea*	Guam[17]	lowland, coastal	shrub – tree	campanulate	8–10 × 8–10[18]	red	orange	B, I
Poales	Bromeliaceae	*Puya alpestris*	Chile	1000[19]	shrub	tubular-campanulate	50	blue	pale pink – blue	B, I
Proteales	Proteaceae	*Banksia grossa*	SW Australia	nd	shrub	zygomorphic	34–45	brown	yellow – green	I, M, B?
		B. incana	SW Australia	nd	shrub	zygomorphic	21–23	yellow	yellow – green	I, M, B?
		B. leptophylla	SW Australia	nd	shrub	zygomorphic	35–45	yellow – brown	yellow – green	I, M, B
		B. nutans	SW Australia	nd	shrub	zygomorphic	22–33	purple – brown	yellow	I, M, B?
		B. sphaerocarpa	SW Australia	nd	shrub	zygomorphic	24–39	brown	yellow – green	I, M, B?
		B. telmatiaea	SW Australia	nd	shrub	zygomorphic	22–25	orange – pale brown	yellow – green	I, M, B?
		Grevillea robusta	E Australia	0–1120	tree	zygomorphic	23	yellow – red	pale yellow – red	B, M?, I†
Solanales	Solanaceae	*Capsicum baccatum*	South America[20]	500–1500	vine – shrub	rotate	3.5–7[21]	white – cream	clear – yellow	u
		C. pubescens	Bolivia[22]	1200–2000	vine – shrub	rotate	nd	purple, white	clear – yellow	I

C. eximium	Bolivia, Argentina	1500–3000	vine	rotate	20–25 (diameter)	purple, white	clear – yellow	u
Jaltomata aspera	Peru	0–500 /1600–2550[23]	subshrub	crateriform rotate	49 (diameter)	pale yellow-green	red	u, B?
J. biflora	Peru	2700–3200	shrub	urceolate	13 × 14	pale green	clear – orange	u. B?
J. contumacencis	Peru	2840	shrub	campanulate-tubular	10 × 25–28	pale green	clear – orange	u, B?
J. herrerae	Peru, Bolivia	3000–3800	shrub	campanulate	15–20 × 35–45	pale green	red	u, B?
J. leviae	Peru	2530–3000	vining shrub	urceolate-tubular	12 × 18–19	red, blue – purple[24]	red	u, B?
J. paneroi	Peru	3200–3550	shrub	campanulate	5–10 × 23–25	pale green	red	u, B?
J. umbellata	Peru	0–500	shrub	tubular, rotate limb	9–11 × 14–23	cream – pale green	red	u, B?
J. ventricosa	Peru	2500–3200	shrub	urceolate	8–10 × 12–14	white – pale yellow	orange – red	u, B?
J. weberbaueri	Peru	3300–3700	subshrub	broadly campanulate	40–45 × 55–60	pale green – violet	red	u, B?, I?
J. sp. '642'[25]	Peru	2630–2650	shrub	urceolate	7–9 × 14	pale green	red	u, B?
J. sp. '647'[25]	Peru	3400–3530	shrub	broadly campanulate	19–27 × 32–36	pale green – purple	clear – orange	u, B?
J. sp. '669'[25]	Peru	2840	shrub	campanulate-tubular	10 × 25–28	pale green	red	u, B?
J. sp. '711'[25]	Peru	1420–1870	shrub	campanulate	10 × 28	green	orange – red	u, B?

[1] Perianth length, or perianth length × diameter, or as noted.

[2] A dash between two colours indicates an approximate continuous range.

[3] Hypothesised flower visitors from the literature or from personal communications are indicated with a '?', non-native flower-visitors are indicated with a '†'. Flower visitor codes: u = unknown, B = birds, I = insects, L = lizards, M = mammals.

[4] Sepal length (Wagner *et al.*, 2005).

[5] White is the colour of the petaloid sepals.

[6] Refers to the cup-shaped nectary; the flowers are red-brown, rotate and 6–8 mm in diameter.

[7] First set of numbers refers to corolla length, second set to length of staminal filaments.

[8] The small petals are green, while the numerous long staminal filaments are red.

[9] South Africa, Mozambique and Zimbabwe.

[10] Asian distributions: *H. kerrii* is found in China, Cambodia, Laos, S. Vietnam, S. Thailand and Java; *H. obovata* in India, Indonesia, Thailand and Fiji; and *H. diversifolia* in Cambodia, Laos, Myanmar, S. Vietnam, Malaysia, Singapore, Thailand and Indonesia.

[11] Colour refers to corolla; the prominent central corona is pink – purple in all species (see Fig. 2B,C).

[12] Size of outer sepals.

[13] Colour refers to the large sepals; the small petals are red or orange, but are mostly hidden inside the sepals (however, see main text on *Melianthus*).

[14] Length, height and diameter of corolla, respectively.

[15] Malawi, Mozambique, Zimbabwe, Kenya, Tanzania.

[16] Bhutan, China, India, Laos, Myanmar, Nepal, Vietnam.

[17] Guam is the only place where coloured nectar has been observed in this species. The total distribution is very wide; ranging from East Africa to Australia and the Western Pacific, but nothing is known about nectar colour in these regions.

[18] Diameter × depth of flower cup, including the part formed by the calyx.

[19] Average altitude for coastal hill and Andean.

[20] Distribution of the wild progenitor: Bolivia, Argentina, Peru, Paraguay, Brazil.

[21] Length of corolla lobe.

[22] Most likely origin of wild progenitor.

[23] Lower range is from the coastal Lomas habitat, higher range from the Andes Mountains.

[24] Tube is red, limb is blue – purple.

[25] Numbers refer to accessions by Mione, Leiva and Yacher.

vryheidensis, one of the species with dark brown nectar, is effectively pollinated by a variety of non-specialised nectarivorous birds, including white-eyes, bulbuls and rock thrushes (Johnson, Hargreaves & Brown, 2006; Fig. 2R). Earlier anecdotal records indicate that pollination by these occasional nectarivores also occurs in other members of *Aloe* section *Anguialoe* (Skead, 1967; Cheke & Mann, 2001). The experiments conducted by Johnson *et al.* (2006) showed that artificial

Fig. 3. Taxonomical distribution of coloured nectar in the angiosperms at the level of order. Arrows indicate the presence of one or more taxa with coloured nectar in the respective orders (see Table 1 for details). Figure modified from Stevens (2001 onwards).

flowers with darkened nectar receive more probes by black-capped bulbuls than do artificial control flowers with clear nectar. However, the main reason why specialised nectar-ivores such as sunbirds do not visit *A. vryheidensis* is that they find the phenolics in the nectar highly distasteful. Upon probing the flowers and sampling the nectar, these birds would rapidly retract their beaks, shaking their heads vigorously, and not probe such flowers again. Honeybees collect pollen from flowers of *A. vryheidensis*, but find the nectar too unpalatable to consume (Johnson *et al.*, 2006).

Fig. 2. Flowers of plant species with coloured nectar, illustrating the wide variety in flower form, colour and nectar colour. (A) *Nesocodon mauritianus* (Campanulaceae). (B) *Hoya diversifolia* (Apocynaceae), single flower, side view. (C) *Hoya diversifolia*, inflorescence. (D) *Aloe vryheidensis* (Asphodelaceae). (E) *Dombeya angulata* ssp. *rosea* (Malvaceae) – note also the secondary pollen presentation on the tip of the petals. (F) *Schwartzia brasiliensis* (Marcgraviaceae). (G) *Trochetia blackburniana* (Malvaceae). (H) *Schiedea obovata* (Caryophyllaceae). (I) *Grevillea robusta* (Proteaceae). (J) *Aloe castanea*. (K) *Jaltomata umbellata* (Solanaceae). (L) *Jaltomata weberbaueri*. (M) *Jaltomata paneroi*. (N) *Deplanchea tetraphylla* (Bignoniaceae). (O) *Fernandoa magnifica* (Bignoniaceae). (P) *Capsicum pubescens* (Solanaceae). (Q) Male *Phelsuma cepediana* gecko nectar feeding in a *Trochetia blackburniana* flower. (R) *Zosterops pallidus* nectar feeding on an *Aloe vryheidensis* inflorescence. Photographs by J. M. Olesen (A, M), P. Wallin (B), K. F. Yap (C), W. Barthlott (D), D. M. Hansen (E, G, Q), I. & M. Sazima (F), N. Kawakubo (H), N. Eden (I), M. Nepi (J), T. Mione (K), S. Leiva G. (L), A. Weber (N), C. Puff (O), A. Boatman (P), S. D. Johnson (R).

Table 2. Nectar properties of plant taxa with coloured nectar ('nd' = no data available)

Species	Nectar volume[1] (μl)	Sugar concentration[1] (%)	Sugar composition[2]
Aloe castanea	17–100[3]	6–18[3]	0.020 – HD
A. vryheidensis	27–70	6–17	nd
Phormium tenax	135–166[3]	15.8–20.3[3]	nd
Nesocodon mauritianus	2.2 ± 0.86[4]	11–25	HD
Schiedea lychnoides	18.3	nd	HR
S. obovata	16.6	nd	HR
S. trinerve	30.9	nd	HR
S. viscosa	6.3	nd	HR
Schwartzia brasiliensis	100–150	12.6 (5–20)	0.09 – HD
Calliandra calothyrsus	5–55	nd	nd
Erythrina humeana	nd	14.2	0–0.042 – HD
E. caffra	300	5.5–10	0–0.042 – HD
Melianthus comosus	41.7 ± 5.1	9.7 ± 0.2	0.020 – HD
M. dregeanus	60.3 ± 3.7	11.5 ± 0.4	nd
M. elongatus	41.9 ± 2.9	13.1 ± 0.4	nd
M. gariepinus	14.6 ± 1.8	12.7 ± 0.5	nd
M. major	81.0 ± 7.2	15.9 ± 5.0	HD
M. pectinatus	45.0 ± 4.1	13.5 ± 0.2	nd
M. villosus	60.0 ± 4.3	11.6 ± 0.1	nd
Deplanchea tetraphylla	280[5]	nd	HD
Dombeya a. ssp. *acutangula*	3.7 ± 1.5	18 – >50	nd
D. angulata ssp. *rosea*	8.5 (2–21)	7–11	nd
Trochetia blackburniana	30.9 (5–72)	22.6 (10–42)	0.030 – HD
T. boutoniana	49.3 (14–78)	30.2 (13–48)	0.036 – HD
T. granulata	46.7 (17–101)	13.3 (8.5–23)	HD
T. triflora	35.8 (15–63)	15.3 (10–19)	0.17 – HR
T. uniflora	61.1 (9–186)	21.6 (15–28)	0.027 – HD
Lumnitzera littorea	24–52	nd	nd
Puya alpestris	410	8.2	0.05–0.09 – HD
Banksia leptophylla	nd	22.0 ± 3.4	0.35 – HR
B. sphaerocarpa	nd	nd	1.10 – SD
B. telmatiaea	nd	nd	1.19 – SD
Grevillea robusta	19.1 ± 1.0 (9–37)	23.5 ± 1.5 (7–49)	0.11 – HR
Jaltomata biflora	0–47[6]	14–58	nd
J. paneroi	nd	nd	HD

[1] Measurements given as means ± S.D./S.E., or means with range in parentheses, or as a range.
[2] Classes of sugar composition as defined by Baker & Baker (1983): hexose–dominant, HD (S/H ratio < 0.1); hexose–rich, HR (0.1 > S/H ratio < 0.5); sucrose–rich, SR (0.5 < S/H ratio < 1.0); sucrose–dominant, SD (S/H ratio > 1.0).
[3] Range of mean values.
[4] Production per hour per flower.
[5] Indirect measure; the volume of water a 'nectar–lobe' will hold.
[6] Depending on sexual phase.

(b) Asparagales – Hemerocallidaceae – Phormium

Phormium is an endemic New Zealand genus with only two species. *Phormium tenax* grows widespread throughout New Zealand (P. B. Heenan, personal communication). The flowers are orange to dark red, large and tubular, and are borne in clusters on small sub-inflorescences along a main inflorescence stalk that can reach several meters in height. Nectar is produced in large quantities (Table 2), often forming visible drops at the mouth of the corolla tube (J. L. Craig, personal communication). Nothing has been mentioned about *P. tenax* nectar colour in the literature, but yellow colouration of the nectar has been observed in plants in the native range in New Zealand (J. L. Craig, personal communication), and in plants in a botanical garden in South Africa (J. Henning, pers. comm). However, colour-

ation of the nectar in *P. tenax* may be an exception, rather than the rule, as other researchers have only observed clear nectar (P. B. Heenan, personal communication). Nectar standing crop is higher in male-phase than in female-phase flowers (Craig & Stewart, 1988). Hence, any colouration in the nectar may be related to flower age; i.e. it may be a feature of nectar concentration by evaporation, perhaps combined with oxidative processes. The sister species, *P. cookianum*, has only been observed to have clear nectar in the field (P. B. Heenan, personal communication). The main pollinators of *P. tenax* are birds; specialised honeyeaters as well as more generalised nectarivorous species (Craig & Stewart, 1988), but two endemic *Hoplodactylus* gecko species have also been observed visiting the flowers in large numbers (Whitaker, 1987; Towns, 2002). *Phormium tenax* is a predominantly outcrossing species (Craig & Stewart,

1988), although the realised mating system is strongly influenced by local, inflorescence-level competition between selfed and outcrossed flowers (Becerra & Lloyd, 1992).

(c) *Asterales – Campanulaceae* – Nesocodon

Nesocodon mauritianus is a critically endangered Mauritian plant in a monotypic endemic genus, and is only found on vertical cliffs in five small populations. The four populations in the central and northern mountains are very small, with only a few plants each (J.-C. Sevathian, personal communication; V. Florens, personal communication). The largest known population, with some 110–130 plants, is found around the waterfall Cascade Cinq Cents Pieds in the south. The plants are small shrubs, growing on ledges and in crevices in the cliff. The flowers are large and borne singly (Fig. 2A). They last for as long as 10–11 days, with male phase lasting 6–7 days and female phase 3–5 days (J. M. Olesen, unpublished data from greenhouse plants). The red nectar has a pH as high as 9.2, and the red colour turns yellow at pH < 7. The red pigment is an aurone and the yellow pigment is a flavone or a 3-glucolysed flavonol, all of which are products of flavonoid biosynthesis. The only frequent flower visitor is an introduced bird, the red-whiskered bulbul, *Pycnonotus jocosus* (Olesen *et al.*, 1998). However, the area around Cascade Cinq Cents Pieds and the nearby Alexandra Falls was until the 1980s a stronghold of a critically endangered endemic bird, the Mauritius olive white-eye, *Zosterops chloronothos* (Cheke, 1987b). This bird would be a likely pollinator, as it is the most specialised nectarivore in the genus and it visits many other Mauritian plants for nectar (Gill, 1971; Safford, 1991; Hansen, Olesen & Jones, 2002). Furthermore, the endemic diurnal gecko, *Phelsuma ornata*, is common on the mountain slopes of the central and northern *N. mauritianus* populations. Mauritian *Phelsuma* geckos are known to be regular flower visitors and pollen vectors of many plant species (Nyhagen *et al.*, 2001; Olesen, Eskildsen & Venkatasamy, 2002; Hansen *et al.*, in press; C. N. Kaiser, personal communication); *P. ornata* is likely to play a role in the pollination of the northern *N. mauritianus* populations, but no studies have been made in these populations yet. Interestingly, recent studies have found that *P. ornata* geckos show a strong preference for coloured over clear nectar in artificial flowers (Hansen, Beer & Müller, 2006), and that *P. cepediana* geckos are efficient pollinators of another, unrelated Mauritian endemic plant with coloured nectar, *Trochetia blackburniana* (Malvaceae) (Hansen *et al.*, in press).

(d) *Caryophyllales – Caryophyllaceae* – Schiedea

Schiedea is a genus in the endemic Hawaiian subfamily Alsinoideae, comprising 34 species, four of which have black nectar (Table 1). These four species are divided into sections *Alsinidendron* and *Nothoschiedea*, which together are nested monophyletically within *Schiedea* (Wagner, Weller & Sakai, 2005). *Schiedea* is one of the most remarkable examples of adaptive radiation among Hawaiian angiosperms, with a large number of evolutionary shifts in morphology,

breeding systems, ecological adaptations and pollination biology (Weller & Sakai, 1990; Weller *et al.*, 1990; 1998). The four species with black nectar are found on two different islands in the Hawaiian archipelago (Table 1). The Kaua'i species are herbaceous vines, while the O'ahu species are woody shrubs and thus probably longer lived. In the greenhouse, the Kaua'i species live longer than one year, so they are not strict annuals (S. G. Weller, personal communication). The flowers are apetalous but have white or pale green petaloid sepals (Fig. 2H). Older taxonomical treatments of these species do not mention the black nectar (e.g. Mann, 1866; Sherff, 1944). The first published evidence of the coloured nectar is found in Weller & Sakai (1990), in which a colour photograph of *S. lychnoides* shows a large drop of black nectar on the tip of a petaloid sepal. Later, Weller, Sakai & Wagner (1995) reported that "nectar appears black when large amounts accumulate". In a new taxonomical revision of the genus the black nectar is finally mentioned in the description of the four species (Wagner *et al.*, 2005). The black nectar in *Schiedea* may be related to ornithophily (Weller *et al.*, 1998; Wagner *et al.*, 2005), but there are no observations of birds visiting the flowers. This is most likely due to the rarity of the plants in the wild, and the fact that much of the Hawaiian nectarivorous avifauna has gone extinct (Wagner *et al.*, 2005; S. G. Weller, personal communication).

(e) *Ericales – Marcgraviaceae* – Schwartzia

Schwartzia is a neotropical genus of shrubs with 14 species in the monophyletic subfamily Noranteoideae, which comprises four small genera. While morphologically well supported, recent molecular work suggests that the four genera may not be well delimited within Noranteoideae (de Roon & Dressler, 1997; Ward & Price, 2002; Dressler, 2004). *Schwartzia brasiliensis* is a scrambling, partly epiphytic shrub from Brazil. The branches of *S. brasiliensis* carry long, terminal, brush-like racemes of up to 40 cm in length, with 60–300 flowers, each of which has the cup-like nectary connected to the base of the peduncle (Fig. 2F) (Sazima, Buzato & Sazima, 1993; Dressler, 2004). The strikingly blue-coloured nectar in *S. brasiliensis* was reported by Sazima *et al.* (1993) and Pinheiro *et al.* (1995), and is produced in vast quantities in each nectary (Table 2). A nectary can hold 100–150 µL and produce 50 µL of nectar within a 3-hour period, and drops of overflowing nectar can often be observed on the nectaries (Fig. 2F) (Sazima *et al.*, 1993; Pinheiro *et al.*, 1995). The pigment causing the blue colouration of the nectar is an anthocyanin (Sazima *et al.*, 1993). The ruby-red long stalks and flowers, and the dark purple-brown nectaries, contrast well against green foliage (Sazima *et al.*, 1993), and, in turn, the blue nectar is easily visible against the dark nectaries (Fig. 2F). *Schwartzia brasiliensis* is visited and pollinated by a wide range of birds, including both hummingbirds and perching passerines (Sazima *et al.*, 1993; Pinheiro *et al.*, 1995), and even woodpeckers (Rocca *et al.*, in press). Based on foraging behaviour, Sazima *et al.* (1993) suggested that perching passerine birds were more likely to be efficient pollinators, than hovering hummingbirds. During night, when the flowers have already wilted, nocturnal insects and perhaps

bats forage on the remaining nectar, which in old nectaries can smell of cabbage (Sazima *et al.*, 1993).

(*f*) *Fabales – Fabaceae*

(*i*) *Calliandra.* This is a large, widespread tropical genus with about 200 species (Mabberley, 1997). Yellow nectar has been observed in *C. calothyrsus* over much of the species' native range (J. R. Chamberlain, personal communication), and also in naturalised and plantation trees in Western Kenya (Jensen, 2005) and the Philippines, where honey bees produce a green honey based on the yellow nectar (Estolas, 2004). The native range of *C. calothyrsus* stretches from southern Mexico to central Panama (Chamberlain, 1998), but the species is also widely used in many tropical countries for agroforestry, fodder and honey production (Palmer, Macqueen & Gutteridge, 1994; Chamberlain, 2000). The mimosoid flowers are small and green and are borne in large umbelliform clusters, but each flower has numerous red staminal filaments of 4–6 cm in length. Many different flower visitors have been observed in the native range of *C. calothyrsus*: bats, birds, large hawkmoths, honey bees and other insects. However, the nocturnal short anthesis of individual flowers means that the only efficient pollinators are bats and large hawkmoths (Palmer *et al.*, 1994; Chamberlain, 2000). If the plentiful nectar is left unharvested overnight, birds will feed on it in the morning until the flowers wilt and drop off, but by then the stigma is no longer receptive. Non-native honey bees and other insects also visit the flowers in the morning, but they all approach the nectar at the bottom of the flowers and never touch the fertile parts, and are thus unlikely pollinators (Chamberlain, 2000; Jensen, 2005).

(*ii*) *Erythrina.* A genus with 112 species, found both in paleotropical and neotropical regions (Bruneau, 1996; Mabberley, 1997). Coloured nectar was reported by Guillarmod, Jubb & Skead (1979) in three species of the two closely related small sections *Humeanae* and *Caffrae* (Krukoff & Barneby, 1974; Bruneau, 1996; 1997), but nothing more is known about coloured nectar in *Erythrina*. The flowers are usually grouped in large inflorescences, and are strongly zygomorphic, with most of the inner petals usually being enclosed by the large outer standard. Thus, the nectar is rarely visible from outside, and the relatively weak colours of the nectar are probably not visible against the bright red corollas (Table 1). The nectar colours reported by Guillarmod *et al.* (1979) may be due to local edaphic (e.g. pH or nutrient levels) or climatic factors in the areas where they investigated the plants, as other researchers have failed to notice any significant colouration of the nectar in these species (S. W. Nicolson, personal communication; F. Forest, personal communication). The genus is believed to be entirely ornithophilous, and flowers of most species produce large quantities of nectar. However, insects, lizards and mammals have also been observed visiting flowers, but mostly in very low numbers (Scott-Elliot, 1890; Raven, 1974; Toledo, 1974; Bruneau, 1997; Sazima, Sazima & Sazima, 2005). Guillarmod *et al.* (1979) report that the three species with col-

oured nectar are visited by a wide range of nectar-feeding bird species.

(*g*) *Gentianales – Apocynaceae* – Hoya

Hoya is a large, tropical genus with 200–300 currently recognised species. It is found throughout most of the Indo-Australian region. The centres of diversity are found in the Indonesian archipelago, with approximately 25 species in Malaysia, 74 in New Guinea and >30 species in the Philippines (Forster, Liddle & Liddle, 1998; Kleijn & van Donkelaar, 2001; Wanntorp, Kocyan & Renner, 2006; Wanntorp *et al.*, in press). *Hoya* belongs to the subfamily Asclepiadoideae, which has the most elaborate and complex floral structure of all eudicots (Endress, 1994). Most *Hoya* species grow as vines or arboreal shrubs, with flowers arranged in umbels. Apart from information on their habitat, almost nothing is known about their ecology. However, many species are popular as ornamental plants (waxflowers, porcelain flowers), and it is from dedicated hobby plant growers that we received much of the information on coloured nectar in this genus. Many *Hoya* species produce large amounts of nectar, which forms visible drops on the flat corollas of the flowers, including the ones with coloured nectar (Fig. 2B,C). Coloured nectar is only found in the five species of section *Amblyostemma* (Table 1), and Kloppenburg (1994) included "exuding a coloured honeydew" in his list of diagnostic characters (synapomorphies; specialised characters shared by two or more species, originating in their last common ancestor) for the section. Nothing is known about the nectar properties or pollination biology of any of the species in this section. The only study of pollination biology in *Hoya* is from Australia, in which Forster (1992) found *H. australis* to be pollinated by Lepidoptera. In fact, the asclepiads were thought to be strictly entomophilous (Ollerton & Liede, 1997), until Pauw (1998) elegantly demonstrated tongue-pollination by sunbirds in one species.

(*h*) *Geraniales – Melianthaceae* – Melianthus

Melianthus is a small South African genus with eight species in what has been called an enigmatic Southern African family, whose taxonomy and floral morphology have long puzzled botanists (Ronse Decraene *et al.*, 2001). The petals are small, fused and red or pinkish, and are mostly hidden in a cup formed by the large sepals. However, in some of the species, namely *M. elongatus*, *M. pectinatus* and *M. gariepinus*, the petals are large and showy enough to be considered as the main visual attractant of the flowers (J. Henning, personal communication). In some of the species, the large drop of dark nectar can be seen not only from the front of the flowers, but also from the sides because the sepals are pale, thin and translucent (Fig. 1). The dark nectar in *Melianthus* has been known at least since 1795 (see Section I), and has received anecdotal references in publications since then (e.g. Scott-Elliot, 1890; Dyer, 1952; Archer & Condy, 1997). It is unclear to what extent *Melianthus* species vary in nectar colour within and between species; whereas *M. comosus*, *M. elongatus* and *M. villosus* have all been

observed to have black nectar, most of the remaining species have brown nectar (J. Henning, personal communication). No thorough pollination study has been carried out, but both insects and birds have been observed visiting *Melianthus* species for nectar. Scott-Elliot (1890) reported that the "abundance of rich black honey which sometimes almost fills the cup" was eagerly sought by sunbirds, and Marloth (1925) remarked that "the nectar of *M. comosus* is so dark that the honey taken from the hives of bees which feed on it is quite black". Mabberley (1997) also includes, in his characteristic shorthand, the intriguing comment "fls rich in nectar (black, taken by sunbirds)".

(i) Lamiales – Bignoniaceae

(i) *Deplanchea*. A genus with five species, ranging from Sumatra to New Caledonia. *Deplanchea tetraphylla* is a large tree, found in New Guinea, the Aru Islands, and North East Queensland, Australia (Avé, 1984). It is apparently the only species in the genus with coloured nectar, which it presents in a most spectacular and specialised manner. Its large yellow flowers are clustered in large, circular and flat inflorescences at the end of upper branches. Each flower is strongly zygomorphic with a lower central corolla lobe forming a spoon-like hollow where the dark-brown nectar accumulates (Fig. 2N; Weber & Vogel, 1986). Known flower visitors include birds (Brown & Hopkins, 1995) and mammals (Jackson, 2001). Weber & Vogel (1986) concluded that birds were most likely to be the main pollinators throughout most of the range of *D. tetraphylla*. Furthermore, they stated that the easy, open access to the nectar is suggestive of pollination by relatively short-beaked, generalised nectar-feeding birds, such as lorikeets. In Australia, birds and large butterflies visit the flowers in great numbers (G. Sankowsky, personal communication). Weber & Vogel (1986) suggested that the brown pigment in the nectar was a melanin. Furthermore, they remarked that in New Guinea, younger flowers were seen with honey-coloured nectar, while older flowers had darker brown nectar.

(ii) *Fernandoa*. A genus with 14 species with a paleotropical distribution stretching from Africa and Madagascar to China, South-east Asia and Sumatra (Mabberley, 1997). *Fernandoa magnifica* is a large central-eastern African tree. It often flowers while leafless; inflorescences consist of cymes of 4–10 upwards-turned, large campanulate flowers (Dale & Greenway, 1961). The flowers are red at the top, grading through orange to yellow at the base, where copious amounts of dark brown, almost black nectar forms a small pool (Fig. 2O). Pollinators are unknown, but the flowers have an unpleasant, cabbage-like smell (C. Puff, personal communication, M. Hyde; personal communication), which may be indicative of bat-pollination (Knudsen & Tollsten, 1995). However, the large, colourful flowers also suggest that birds may be attracted to the flowers and act as pollinators, and there are plant species that are pollinated by both bats and birds (Sazima, Sazima & Buzato, 1994; Muchhala, 2003). Almost nothing is known about nectar colour in the rest of the genus, but the Malagasy *F. madagascariensis* has 6–7 cm large ornithophilous flowers with small amounts of clear nectar (J. M. Olesen, personal observations).

(j) Lamiales – Lamiaceae – Leucosceptrum

Leucosceptrum is a very small genus with three species, found from the Himalayas to China (Mabberley, 1997). *Leucosceptrum canum* is a common species, with small, cream-white flowers arranged in dense, terminal spikes. Nothing is noted about its dark brown nectar in the literature, the only information is from an observation in a commercial nursery in the Indian Himalayas (G. M. Pradhan, personal communication). The species is known as a honey plant (Li & Hedge, 1994), and Cowan & Cowan (1929) remarked that, "a quantity of sweet juice exudes from the flowers, and this is sucked by Paharia herdsmen, and by many birds". The former are probably less efficient than the latter as pollinators, though, and it can therefore be assumed that the plant is ornithophilous. A study on the species in China (Caihuan *et al.*, 2004) identified a yellow pigment from the flowers as an amine, but it is not clear whether the pigment analysed was from the floral parts or the nectar.

(k) Malvales – Malvaceae

(i) *Dombeya*. A large, widespread genus with about 225 recognised species in Africa, Madagascar and some of the Indian Ocean islands (Mabberley, 1997). The evolutionary hotspot and likely origin of *Dombeya* is in Madagascar (including the Comoros Islands) with approximately 190 species. The Ethiopian *D. kefaensis*, the Malagasy *D. cacuminum* and the Mascarene *D. elegans*, *D. acutangula* ssp. *acutangula*, *D. acutangula* ssp. *palmata* and *D. acutangula* ssp. *rosea* are the only known *Dombeya* with coloured nectar. In the taxonomical description of *D. kefaensis*, Friis & Bidgood (1998) mention a dark orange nectar stain at the base of each petal, and in their Fig. 2 the dark red nectar is clearly seen, contrasting with the pale cream petals. Malagasy *D. cacuminum* plants in cultivation elsewhere have been reported to produce abundant musky-scented yellow nectar (Llamas, 2003). Another rare floral trait, secondary pollen presentation on the tip of the petals, has been reported for this species (Prenner, 2002). Together, these two floral traits could suggest a combination of bird- and bat pollination for *D. cacuminum* (Llamas, 2003). In a revision of continental African *Dombeya* species, Seyani (1991) lamented the fact that virtually nothing is known about their pollination biology. However, there have been some studies of the reproductive biology of *Dombeya* spp. on the island of La Réunion (Gigord, Lavigne & Shykoff, 1998; Gigord, Picot & Shykoff, 1999; Humeau & Thompson, 2001 and references therein), with a few of those studies providing anecdotal observations on flower visitors. In two studies of *D. acutangula* ssp. *acutangula*, Gigord *et al.* (1998, 1999) mention insects and birds visiting the flowers that produce large quantities of nectar. There is no reference to the yellow colour of the nectar in any of the studies mentioned above, but it is always strikingly yellow when present (L. Gigord, personal communication). The majority of *Dombeya* species have flowers with either white or pinkish corollas, and many have large, showy inflorescences with rather small flowers. The small, white-flowered species are probably pollinated mainly by insects, whereas

larger, pinkish and red ones such as *D. lastii* may be bird pollinated (Seyani, 1991). Indeed, *D. goetzenii* with pale pink flowers that are deep red at the base of the staminal tube (Dale & Greenway, 1961) is visited by several sunbird species (Cheke & Mann, 2001).

(*ii*) *Trochetia.* An endemic Mascarene genus encompassing six species of shrubs and small trees; five species in Mauritius and one in La Réunion. All six species have coloured nectar, and show a remarkable variation in flower morphology and colour among species (Fig. 2G; Table 1; Friedmann, 1987). Their proposed closest relatives include several Malagasy Dombeyoid genera (Friedmann, 1987). The most commonly reported pollinators of the Mauritian *Trochetia* species are two nectarivorous endemic bird species: the Mauritius grey white-eye, *Zosterops mauritianus*, has been observed visiting *T. blackburniana*, and the Mauritius olive white-eye, *Z. chloronothos*, has been observed on *T. uniflora* and has repeatedly been suggested as the main pollinator of *T. blackburniana* (Gill, 1971; Staub, 1988; Safford, 1991; Hansen *et al.*, 2002). Furthermore, *Z. chloronothos* has been suggested as a pollinator of the endangered *T. boutoniana* (Staub, 1988). In La Réunion, both endemic species of *Zosterops* have been observed visiting *T. granulata* (Gill, 1971; D. M. Hansen, personal observations). An anecdotal observation of an endemic diurnal gecko visiting a flower of *T. blackburniana* (Staub, 1988) has recently been confirmed by a study which shows that Mauritian *Phelsuma* geckos are important pollinators of *T. blackburniana* (Fig. 2Q; Hansen *et al.*, in press). *Phelsuma* geckos have been confirmed to visit a wide range of other Mauritian endemic plant species (Nyhagen *et al.*, 2001; Olesen *et al.*, 2002; D. M. Hansen, personal observations; C. N. Kaiser, personal communication), and in a recent study *P. ornata* geckos strongly preferred coloured over clear nectar in experimental artificial flowers (Hansen *et al.*, 2006). More studies on how *Phelsuma* geckos interact with Mauritian plants with coloured nectar in the wild are needed to assess the effect of coloured nectar on reproductive success. *Trochetia blackburniana* may be well suited for such studies, as its nectar naturally varies from clear to deep yellow or orange, even within small populations, while variation in nectar colour of flowers on the same plant seems to be smaller (D. M. Hansen, personal observations).

Dombeya and *Trochetia* both belong to the subfamily Dombeyoideae. It seems curious that the occurrence of coloured nectar within Dombeyoideae in Madagascar, the evolutionary hotspot of the subfamily, should be restricted to *D. cacuminum*. It is very likely that further field studies will reveal coloured nectar in more of the Malagasy Dombeyoid genera or species. Given the wide distribution of many *Dombeya* species in Africa (Seyani, 1991), it is also likely that coloured nectar will be found in additional African species.

(*l*) *Myrtales – Combretaceae –* Lumnitzera

Lumnitzera is a genus with only two species, both of which are widespread in mangrove forests from East Africa to Western Pacific and tropical Australia (Tomlinson, 1986).

Lumnitzera littorea has terminal inflorescences with small, red flowers, exerted stamens and a cup formed by the calyx, allowing for abundant nectar to accumulate (Table 2). The flowers thus fit well into the general ornithophilous syndrome, and are predominantly visited by sunbirds and honeyeaters, but also by bees and wasps (Tomlinson, 1986). Yellow nectar in *L. littorea* has only been reported from Guam (H. Skovsgaard, personal communication), but nothing is known about nectar colour anywhere else in this species' wide range. However, the nectar of plants of the sister species, *L. racemosa*, growing in the Fairchild Botanical Garden, Florida, USA, was observed to be clear (P. B. Tomlinson, personal communication).

(*m*) *Poales – Bromeliaceae –* Puya

Puya is a terrestrial bromelioid genus with almost 200 species that are mainly found on the slopes of the Andes Mountains from Chile to Columbia (Smith & Downs, 1974). Recent molecular taxonomical work assigned *Puya* as a monophyletic sister genus to the subfamily Bromelioideae (Terry, Brown & Olmstead, 1997; Givnish *et al.*, 2004). The subgenus *Puya* comprises eight species with large, terminal, columnar, and multibranched inflorescences (Hornung-Leoni & Sosa, 2004); the most well known being the Peruvian *P. raimondii* – the 'Queen of the Andes' – which grows to 10–12 m in total height (Sgorbati *et al.*, 2004). *Puya alpestris* is confined to Chile, and is smaller, with an inflorescence of 1–1.5 m and up to 2 m total height (Hornung-Leoni & Sosa, 2006). Each branch on the inflorescence carries several large flowers of a striking blue colour with bright orange pollen. Nectar is produced in vast quantities, and sometimes it drips out of the flowers. In the wild, the nectar has been observed to be varying in colour from pale pink to a red-wine like colouration (C. Hornung-Leoni, personal communication). In plants grown in gardens in California and in the UK it has been reported to be of a blue colour (Dortort, 2003; D. Poole, personal communication). In all species of subgenus *Puya*, the terminal half of each branch is sterile, with only bracts and no flowers. This was proposed by Johow (1898) to be an adaptation to pollination by perching nectar-feeding birds, which are the main pollinators of the subgenus – as opposed to the subgenus *Puyopsis*, which is mainly hummingbird-pollinated and lacks such perches. This dichotomy is reflected in the nectar composition as well: nectars from subgenus *Puyopsis* are sucrose-rich and of relatively high concentration, while nectars from subgenus *Puya* are relatively dilute and hexose-rich (Table 2; Scogin & Freeman, 1984; Baker & Baker, 1990). Observed pollinators of *P. alpestris* include the Austral blackbird, *Curaeus curaeus*, and *Castnia eudesmia*, a large diurnal moth that also passes its larval and pupal stages on *Puya alpestris*, and which is known occasionally to drive off other moths and birds (!) from the flowers (Gourlay, 1950; Ortiz-Crespo, 1973). Nothing is known about what causes the blue colouration of the nectar, but an unusual floral anthocyanin, delphinidin 3,7,3'-triglucoside, has been identified as the main petal colour pigment (Scogin & Freeman, 1984; Scogin, 1985), and it could be related to the nectar colouration as well. Coloured

nectar is not known from any other Bromeliaceae, and a recent study of nectar from 110 bromeliad species from 16 genera, including five *Puya* species, found all of these to be clear (T. Krömer, unpublished data).

(n) Proteales – Proteaceae

(i) *Banksia*. An Australian genus with 73 species (Mabberley, 1997). Five *Banksia* species from the *Sphaerocarpa* group (series *Abietinae*) were reported to have an initially yellow nectar, which turns olive to dark green, almost black, and gelatinous during anthesis (Lamont, 1980; Markey & Lamont, 1995). The dark nectar is easily seen deep in the inflorescence, between the long filaments (Fig. 1 in Lamont, 1980). The nectar of another species, *B. nutans*, remains a translucent yellow throughout anthesis. At first this was assumed to be a secondary effect of a presence of cyanobacteria, but a subsequent analysis rejected this hypothesis (Markey & Lamont, 1995). What causes the colouration of the nectar is still unknown (B. B. Lamont, personal communication). However, it is likely to be a chemical process in the nectar itself, as a colour change also occurs in freshly secreted yellow nectar after storage in sterile tubes (Markey & Lamont, 1995). The inflorescences of all *Banksia* species in series *Abietinae* are spherical, relatively close to the ground, and produce large volumes of nectar. Observed pollinators and flower visitors include honeyeaters, ants, flies and beetles. The strong, musky smell of the flowers of these species also suggests nocturnal mammals, and scats have often been found on inflorescences, lending further credibility to this hypothesis (Markey & Lamont, 1995; B. B. Lamont, personal communication). Indeed, several non-flying mammals, e.g. the honey possum, are efficient pollinators of Australian plants, including several *Banksia* species (Carthew & Goldingay, 1997; Wooller & Wooller, 2003).

(ii) *Grevillea*. A large Australasian genus with 261 species, many of which are ornithophilous (Mabberley, 1997). Ornamental *Grevillea robusta* plants in South Africa and Kenya have been reported to have yellow nectar, and red nectar has been observed in a greenhouse plant in Germany (Kalinganire *et al.*, 2001; Nicolson, 1993; 1995; J. Henning, personal communication), but curiously nobody has reported coloured nectar from its native range in Australia (R. O. Makinson, personal communication). The red colouration at the base of the petals makes the yellow nectar seem almost orange (Fig. 2I). There are many observations of nectar-feeding birds on the flowers of *G. robusta* in its native range (Makinson, 2000), and native flying foxes (*Pteropus*, Macrochiroptera) have also been observed visiting the flowers (R. O. Makinson, personal communication).

(o) Solanales – Solanaceae

(i) *Capsicum*. Also known as chilli-peppers, *Capsicum* is a neotropical genus with 20–27 recognised species. Chilli peppers have been cultivated in many parts of South America for 7000–8500 years, and are now grown in many parts of the world (Walsh & Hoot, 2001). The genus is closely related to *Jaltomata* (Vogel, 1998). Yellow nectar is found in species from the earliest diverging branches of the phylogeny of the genus, in the two closely related groups *Eximium* and *Baccatum*, and in the unassigned species *C. pubescens* (Walsh & Hoot, 2001). The yellow nectar is visible as well-defined drops on the cream-white corolla of *C. baccatum*. In the purple-flowered species *C. pubescens* and *C. eximium* the yellow nectar contrasts against white spots near the centre of the corolla, and is also clearly visible (Fig. 2P). Despite the current widespread cultivation of at least one of the *Capsicum* species with coloured nectar (*C. baccatum* varieties), nothing has previously been published about the yellow nectar it very often produces. The only flower visitors that have been observed on plants with coloured nectar in the field are ants (W. H. Eshbaugh, personal communication). Based on the current understanding of the phylogenetic relationships within the genus (Walsh & Hoot, 2001) it is likely that more *Capsicum* species might produce yellow nectar, namely *C. cardenasii* and *C. tovarii* (W. H. Eshbaugh, personal communication). Self-incompatibility in the genus seems to be facultative; plants typically exhibit self-incompatibility for a period, but if outcrossing does not occur, plants will 'allow' self-pollination and produce a small amount of fruit toward the end of the fruiting season (W. H. Eshbaugh, personal communication).

(ii) *Jaltomata*. *Jaltomata* is a diverse neotropical genus of 46 species of perennial herbs and shrubs, and is distributed from Arizona, USA, to Bolivia, the Galápagos Islands and the Greater Antilles. A subset of the species that grow in Peru and Bolivia produce orange to red nectar; all other species produce clear nectar. These species represent some of the most striking examples of coloured nectar; for example, Bitter (1924) quoted Weberbauer's vivid description of how *J. umbellata* secretes "blood red juice ... which often fills the whole tube" that can be seen through the pale green corolla – similar to red wine in a glass (Fig. 2K). *Jaltomata umbellata* and *J. aspera* grow in the Lomas formation, a fog-fed desert habitat of the west coast of South America with a high level of endemism (Dillon, 1997). The remaining *Jaltomata* species with coloured nectar grow in higher and moister habitats, at altitudes up to 3800 m (Table 1). The species with coloured nectar show marked variation in flower shape (Table 1), and have corollas that remain open at night. Among the *Jaltomata* species with clear nectar, some species have corollas that remain open at night, and others have corollas that close in the late afternoon and open again the next day. Coloured nectar tends to be produced in greater volumes than clear nectar, but this trend is not absolute. *Jaltomata paneroi*, *J. umbellata*, *J. ventricosa* and *J. weberbaueri* all produce copious red or orange nectar, whereas *J. antillana*, *J. confinis*, *J. grandiflora*, *J. procumbens*, *J. repandidentata* and *J. sinuosa* produce clear nectar in minute amounts. Quantitative nectar data are only known for one species with coloured nectar, *J. biflora* (Table 2). The nectar in *J. biflora* is usually clear but can turn amber or orange in colour as the flower ages (Mione, Mugaburu & Connolly, 2001). Nothing is known about the pollination biology of

Jaltomata, including the species with coloured nectar. Bitter (1921) quoted a correspondence with Weberbauer, in which he suggested that the red nectar of *J. aspera* attracts small flies for pollination. Bitter (1921) did not state whether Weberbauer had seen the flies or was speculating, but the size of flowers and the large distance from the nectar to the reproductive surfaces (Fig. 2L) make it unlikely that small flies could act as pollinators. Later, Mione & Anderson (1996) speculated that the red nectar in *Jaltomata* was related to hummingbird pollination, based on floral morphology and the red colouration common among hummingbird flowers (e.g. Proctor, Yeo & Lack, 1996).

IV. DISCUSSION

Our review demonstrates that coloured nectar is geographically and taxonomically widespread, but also relatively rare and poorly documented. However, it is very likely that many more plant species have coloured nectar, and that it has so far been under-reported in the scientific literature. Nevertheless, the information we have presented allows us to discuss environmental and ecological patterns, in addition to the evolution of coloured nectar.

(1) Environmental and ecological correlates of coloured nectar

The occurrence of coloured nectar seems to be correlated with three factors. Firstly, vertebrate pollination: many plants with coloured nectar are known to or have been hypothesised to be vertebrate-pollinated, mainly by birds (Table 1). Secondly, insularity: *Nesocodon mauritianus*, *Trochetia* spp., *Dombeya acutangula* ssp. *acutangula* and ssp. *rosea*, *D. cacuminum*, as well as the *Schiedea* spp. are all island endemics, while the majority of the other species are found in insular mainland areas, isolated either by altitude (e.g. most *Jaltomata* spp. and *Puya alpestris* in the Andes Mountains, *Leucosceptrum canum* in the Himalayas, and *Dombeya kefaensis* in Ethiopia), habitat (*Jaltomata umbellata* and *J. aspera* grow in the Peruvian Lomas formations – vegetation islands surrounded by hyperarid desert) or by biogeographical history (i.e. *Aloe* spp. and *Melianthus* spp. in Southern Africa, *Hoya* spp. in insular Asia, and *Banksia* spp. and *Grevillea robusta* in Australia). Thirdly, most plants with coloured nectar occur at high or relatively high altitudes (Table 1) – e.g. for a plant in Mauritius, 600–800 m is a high altitude, as the maximum height of the island is 828 m.

There are some notable exceptions to the second and third factors listed above, including *Hoya*, where some species with coloured nectar occur in mainland Asia, and all *Hoya* species with coloured nectar are lowland plants. Also, *Grevillea robusta* is found from sea level to higher altitudes, as is *Calliandra calothyrsus*, *Fernandoa magnifica*, *Deplanchea tetraphylla*, *Phormium tenax* and some of the *Melianthus* species (Table 1). Lastly, being a mangrove forest plant, *Lumnitzera littorea* is only found at sea level.

Furthermore, there may be cases where intercorrelations can explain some of the patterns. For example, bird pollination and altitude are correlated, as birds are important pollinators in many high-altitude tropical ecosystems (Cruden, 1972; Wolf & Gill, 1986; Kessler & Krömer, 2000). Similarly, it is likely that there is an intercorrelation between insularity and vertebrate pollination. Bird- and non-bird vertebrate pollination may be more prevalent on islands than in comparable mainland areas, due to a depauperate invertebrate pollinator fauna on islands (Elmqvist *et al.*, 1992; Feinsinger, Wolfe & Swarm, 1982; Olesen, 2003; Olesen & Valido, 2003).

(2) Coloured nectar and vertebrate pollination

One straightforward interpretation of coloured nectar across all taxa is to see it as a visual floral cue to potential pollinators. In this study, we often find coloured nectar to be associated with observed or hypothesised ornithophily. Hence, it is tempting to interpret this floral trait as another example of visual floral adaptation to ornithophily. However, whether or not different floral traits fit neatly into clearly defined pollination syndromes has recently been the subject of debate, and some researchers have argued that syndromes are not very useful predictors of pollinators (reviewed by Fenster *et al.*, 2004). Nevertheless, there are many studies that find syndromes to be valid and useful, at least to predict flower visitors or functional groups of most efficient pollinators at higher taxonomic levels (e.g. Bruneau, 1997; Lange, Scobell & Scott, 2000; Temeles & Kress, 2003; Hargreaves, Johnson & Nol, 2004; Wilson *et al.*, 2004). Fenster *et al.* (2004) conclude that pollination syndromes are of great use in understanding the ecology and evolution of plant-pollinator interactions, and suggest that pollinators can be organised into functional groups according to the selection pressures they exert. Since many taxa with coloured nectar are visited by birds, or have been hypothesised to be visited by birds (Table 1), we can ask the question: do the observed nectar colours correspond to typical bird-colours of flowers? For yellow and especially orange and red, the answer is yes (e.g. Proctor *et al.*, 1996). For darker nectar colours, especially black, the answer may also be yes if we substitute flower colour with fruit colour, as black is the most frequent fruit colour among bird-dispersed plant species in the tropics (Herrera, 2002; van der Pijl, 1982; Wheelwright & Janson, 1985; Willson & Whelan, 1990).

Furthermore, where known, most coloured nectars are hexose-dominated (Table 2), which could be an adaptation to generalised bird pollinators in habitats with a general dearth of pollinators, such as islands and montane areas (Cruden, 1972; Wolf & Gill, 1986; Barrett, 1996; Olesen & Jordano, 2002; Anderson, 2003). Generalised nectar-feeding birds often lack the specific enzymatic activity required to digest sucrose, and can thus only utilise the simpler hexose sugars (e.g. Martínez del Rio, Baker & Baker, 1992).

Therefore, it is conceivable that several different generalised avian pollinators in insular or montane habitats can

exert a relatively uniform selective pressure on one or more floral traits. For example, in the Canary Islands many unrelated plant lineages show a remarkable evolutionary flexibility in relation to nectar sugar composition. It has been hypothesised that this could be caused by selective pressures exerted by several generalist nectar-feeding passerine birds (Dupont *et al.*, 2004).

However, birds are not the only vertebrates associated with coloured nectar. In Mauritius, at least one and possibly two or three *Trochetia* species are pollinated by endemic diurnal *Phelsuma cepediana* geckos (Hansen *et al.*, in press), and two of the three *Nesocodon mauritianus* populations are found on cliffs, which harbour *Phelsuma ornata* geckos that are also well-known flower visitors (Nyhagen *et al.*, 2001; Olesen *et al.*, 2002), and which react strongly to coloured nectar as a visual signal for reward (Hansen *et al.*, 2006). Furthermore, *Phormium tenax* in New Zealand is visited by endemic geckos, albeit nocturnal species. A recent review demonstrated that lizard pollination was almost exclusively an island phenomenon (Olesen & Valido, 2003). Hence, further studies may reveal even more lizard pollinators for island plants with coloured nectar. Lastly, some coloured nectar plants are also visited and pollinated by nocturnal mammals (Table 1; *Deplanchea tetraphylla*, *Fernandoa magnifica*, *Calliandra calothyrsus*, *Dombeya cacuminum* and *Banksia* spp. – and *Trochetia triflora* may have been pollinated by one of the two extinct small Mauritian fruitbat species, *Pteropus subniger* and *P. rodricensis*). While it is more difficult to envisage a visual function of coloured nectar during night, it may be related to diurnal pollinators for some of these species (*D. tetraphylla*, *F. magnifica* and *Banksia* spp.), or it may serve functions other than pollinator attraction or be a non-functional trait (see below).

(3) Coloured nectar and insect pollination

Obviously, coloured nectar could also function as a visual cue to flower visiting or pollinating insects. Small, insect-pollinated flowers are probably even more unlikely to have had any colouration of their nectar documented than the relatively large flowers displayed by most of the plant species in our review. This could explain the bias towards large, vertebrate-pollinated flowers in our current knowledge of coloured nectar. We have a very incomplete knowledge of flower visitors for many of the plant species with coloured nectar, and some of the plants are likely to be mainly insect-pollinated (*Hoya* spp. and *Capsicum* spp.). These species are thus ideal candidates for studies investigating the potential functional significance of coloured nectar for insect pollinators or flower visitors.

(4) Coloured nectar as an honest signal

Thorp *et al.* (1975) suggested that the UV-reflectance of some nectars could be interpreted as a visual cue for flower-visiting insects, especially bees, allowing them to evaluate the presence and perhaps the abundance of nectar. Similarly, Weber & Vogel (1986) suggested a functional significance of coloured nectar in the human visible spectrum. They interpreted the dark nectar against the yellow corolla in *Deplanchea tetraphylla* as a visual signal,

a nectar guide, in addition to its primary function as a reward. Olesen *et al.* (1998) also suggested this link between signal and reward, and having observed birds visiting *Nesocodon mauritianus*, they speculated further that the coloured nectar could be interpreted not only as a visual cue, but additionally as an honest signal, leading to increased pollination efficiency (the idea was originally suggested to J. M. Olesen by W. S. Armbruster). However, they rejected this possibility, since – to their knowledge – coloured nectar had not evolved in other regions and taxa. With our review we demonstrate that the opposite is true: coloured nectar has evolved independently and repeatedly in many geographical regions and in many plant taxa. This pattern of convergence suggests the possibility of a common selective pressure, such as the need for an honest signal (*sensu* Zahavi, 1975, 1977) to flower visitors, allowing them to judge the presence and size of the reward before flower visitation, and to adjust their behaviour accordingly.

Recently, another little-studied nectar trait, scent, was proposed to be a potential honest signal (Raguso, 2004b). He argued that scented nectar could facilitate remote detection of the nectar by potential pollinators, as well as providing an assessment of nectar quantity in individual flowers. A similar argument has been put forward in relation to the potential function of pollen odours by Dobson & Bergström (2000), but they did not discuss the potential for honest signalling here. Scent may not always be a precise signal, as it strongly depends on environmental conditions. However, compared to visual signals that rely on an unobstructed straight line between sender and receiver, scent signals could be more efficient, as these can also be percieved without a straight line between sender and receiver. Additionally, some floral oils are known to be coloured (Buchmann & Buchmann, 1981; Buchmann, 1987), and this could act as a visual honest signal in a parallel way to coloured nectar. Lastly, being a harvestable floral resource like nectar, pollen has also been shown to function as a visual signal (reviewed in Lunau, 2000), but unlike nectar, pollen in individual anthers is not a renewable floral resource. Once an anther has dehisced, it can produce no more pollen. However, temporal patterns of anther dehiscence during anthesis of individual flowers or inflorescences do provide a plant with some control over the amount of pollen available for harvest (Lunau, 2000). Hence, in some plant species, pollen may well function as an honest signal, too.

In general, for a signal to be honest, it has to infer some cost, a 'handicap', upon the signaller (Grafen, 1990; Zahavi, 1975; 1977). In coloured nectar plants, the cost can be at least twofold: firstly, colour compounds may be costly to produce. Here, the cost might be directly related to the production of the signal. However, until we have more knowledge on which processes or substances cause colouration of nectar, the biochemical cost of producing coloured nectar is impossible to calculate. Secondly, the cost can be seen as the number of visits that a flower does not receive when the nectar has been depleted and the signal is absent. In this scenario, contrary to conventional honest signalling theory, it is not the production or

presence of a signal that is costly; it is rather the absence of the signal that is costly, as the flowers will not receive further visits until the signal has been replenished. Because signal and reward are coupled, an additional cost of having coloured nectar could be the loss of the plant's ability do deceive its pollinators and manipulate their movement patterns.

The benefit of coloured nectar to the pollinator is clear: it directs foraging towards rewarding flowers and promotes avoidance of visits to empty flowers, thus reducing foraging costs. The benefit to the plant is more complex. At first glance, coloured nectar could seem to be disadvantageous to the plants; penalising them because they receive fewer visits when the nectar is missing. However, as mentioned above, signal and reward are coupled in coloured nectar, and this could lead to rapid positive reinforcement of 'correct' pollinator behaviour. This would increase floral constancy, and hence also increase pollination efficiency. Furthermore, it is interesting to note that most of the plants with coloured nectar have inflorescences consisting of several to many flowers (e.g. *Hoya* spp., *Aloe* spp., *Schwartzia brasiliensis*, *Leucosceptrum canum*, *Deplanchea tetraphylla*, *Schiedea* spp., *Dombeya* spp., *Grevillea* spp., and *Banksia* spp.). Here, coloured nectar could facilitate a rapid orientation of the pollinators towards rewarding flowers 'in need of' pollen removal or pollen deposition. In turn, this would minimise geitonogamy, and lead to increased outcrossing (de Jong, Waser & Klinkhamer, 1993). A parallel can be drawn to pollinators responding to colour changes in floral parts when flowers are no longer offering rewards; sometimes this colour change is even triggered by a pollinator visiting a flower and harvesting the rewards (Casper & Pine, 1984; Weiss, 1991; Weiss, 1995 and references therein).

In many plants with coloured nectar the signal value of the nectar increases over time. That is, the longer a flower is not visited – and thus the nectar not harvested – the stronger the signal becomes, and in turn the flower might become more attractive to visitors. This can work in at least three different ways that are not mutually exclusive: firstly, in cases where the nectar is strongly coloured and easily seen – the larger the drops, the greater the reward and the stronger the attraction (e.g. *Leucosceptrum canum*, and *Aloe*, *Jaltomata* and *Hoya* spp.). Secondly, the strength of the signal can increase with nectar volume. This is the case in *Schiedea* spp., where the nectar appears black only when a large drop has formed; in small amounts, or spread out thinly, it is a dirty grey and almost translucent (Weller *et al.*, 1995; S. G. Weller personal communication). The same is true for *Trochetia blackburniana*, *T. granulata* and *T. triflora* where the yellow and amber colours of the nectar darken considerably against the corolla with increasing volume. Finally, the nectar colour can change over time. In some of the *Hoya* species, the nectar is initially secreted as a clear or almost clear liquid, which then changes into dark brown or red, perhaps as a result of oxidation (K. F. Yap, personal communication). The same process has been observed in some of the *Aloe* species (Johnson *et al.*, 2006; Nicolson & Nepi, 2005; Reynolds, 1940), in *Jaltomata biflora* (Mione *et al.* 2001), in *Banksia* spp. (Markey

& Lamont, 1995), and in some *Deplanchea tetraphylla* flowers (Weber & Vogel, 1986).

However, it is not only the colour of the signal which is important – far more important could be the contrast between signal and background (Burns & Dalen, 2002; Endler, 1992; Schmidt, Schaefer & Winkler, 2004; Hansen *et al.*, 2006). Why, then, do some species with coloured nectar also have strikingly coloured corollas, which could weaken the contrast between nectar and flower? We find this in *Jaltomata weberbaueri*, where the corolla is a bright violet, in contrast to the pale colours in other *Jaltomata* species with coloured nectar. A red corolla with yellow or red nectar is also seen in *Trochetia boutoniana*, *T. uniflora* and *T. blackburniana*. In these species, however, the base of the corolla is often much paler, thus providing a stronger contrast exactly where the nectar drops accumulate (Fig. 2G; Hansen *et al.*, 2006). The same pattern is also seen in *Aloe* section *Anguialoe*. The most extreme case is perhaps *Capsicum pubescens*, where the corolla is almost entirely dark purple, except for five white spots near the centre – which is exactly where the yellow nectar accumulates into visible drops (Fig. 2P). The presence of conspicuous colours in both corolla and nectar may act in a complementary way (Raguso, 2004a). The coloured petals attract visitors from a distance and the coloured nectar then 'fine-tunes' visitor behaviour by guiding them to rewarding flowers. This may be especially important for plant species with large inflorescences with many flowers – which many coloured nectar plants have. Of course, another explanation is that the state is transitory, evolving towards colourful corollas with colourless nectar or *vice versa*.

Overall, these patterns could explain why coloured nectar has evolved repeatedly in habitats with a depauperate pollinator fauna, such as islands and montane areas, where competition for pollinators may be fierce. The relatively long 'shelf-life' of nectar in flowers in such habitats – i.e. potentially it is not 'harvested' that often – may further increase the need to protect this resource against nectar thieves and microbial infestation (see below).

(5) Other functions of coloured nectar

Floral traits related to pollinator attraction may of course also attract herbivores or nectar robbers (Irwin, Adler & Brody, 2004). Thus, pigments causing colouration of nectar could also be related to defensive or deterring functions, protecting the nectar crop against nectar-thieving ants (Galen, 1983; Stephenson, 1981, 1982), mites (Colwell, 1995), bees (Johnson *et al.*, 2006; Irwin & Brody, 1999) or long-billed nectar-robbing birds (Johnson *et al.*, 2006). Coloured nectar could thus act as a double 'floral filter', keeping inefficient pollinators or nectar robbers at bay, while simultaneously serving as a visual signal for reward to legitimate pollinators – and indeed, this is what Johnson *et al.* (2006) found to be the case for *Aloe vryheidensis* (see Section III.3.*a*). Another unusual nectar-based floral filter is found in *Combretum lanceolatum* (Combretaceae) from Brazil, where the nectar is presented in gelatinous drops that cannot be utilised by flower-visiting insects (Sazima *et al.*, 2001).

Lastly, colour pigments in nectar could serve as agents against microbial infestation (Janzen, 1977; Pichersky & Gershenzon, 2002). Anti-microbial function has been demonstrated for proteins in floral nectars, especially against fungi that could spoil the nectar crop or attack the gynoecium (Carter & Thornburg, 2004; Naqvi *et al.*, 2005). Indeed, Olesen *et al.* (1998) found anti-bacterial properties in the aurone responsible for the red colouration of nectar in *Nesocodon mauritianus*. Also, all *Melianthus* species have very toxic vegetative parts, and extracts from leaves and stems of *Melianthus comosus* have been found to have anti-bacterial activity (Kelmanson, Jäger & van Staden, 2000). While it seems that honey made from *Melianthus* nectar is not toxic to humans (Marloth, 1925), the nectar may still exhibit anti-bacterial properties. Future studies of coloured nectar should investigate potential anti-microbial properties by using bioassays or by screening for compounds with known anti-microbial properties – even though the latter approach could lead to non-detection of hitherto unknown compounds, or of compounds that may be common, but which are not easily screened (Adler, 2000).

The blood-red nectar of *N. mauritianus* provides a cautionary tale: without any ecological evidence, Rosenkranz & Klopman (1999) used a model-based approach to speculate further that the aurone responsible for the red colouration of *N. mauritianus* nectar was a deterrent against endemic Mauritian mammalian nectar robbers. This cannot be the case, as there are no extant or extinct native non-flying mammals in Mauritius (Cheke, 1987a), and the endemic fruitbats – if they ever visited flowers that close to the ground – would most likely be efficient pollen vectors. This example stresses the importance of detailed regional ecological and natural history information when interpreting the potential functions of coloured nectar for a particular plant species. Generally, we need to be cautious in interpreting coloured nectar as adaptive *per se*, whether it is as a signal to attract or deter a certain group of flower-visiting animals, or as an anti-microbial function. We must evaluate each case based on field observations and experimental evidence on a species-by-species basis.

(6) Non-functional explanations

There are also non-functional explanations for the presence of coloured nectar is some species. For example, in *Melianthus* spp. and *Schwartzia brasiliensis*, the entire plant and the inflorescence, respectively, has dark pigmentation, and the dark colour of the nectar may simply be a non-adaptive or pleiotropic by-product of pigment biosynthesis elsewhere in the plant. A similar argument can be made for *Puya alpestris*, whose petals sport the same blue colour as the nectar, at least in plants grown in gardens, but we need more detailed studies of the plant and its nectar in the wild, where it may be darker and of a more red colouration (C. T. Hornung-Leoni, personal communication). Furthermore, it has recently been investigated how both herbivores and pollinators may select for nectar traits – that is, how traits that are related to both pollinator attractance and herbivore deterrence can be evolutionarily

tightly linked (Adler & Bronstein, 2004; Herrera *et al.*, 2002) – and in some species coloured nectar could be an example of such correlated evolution. For *Erythrina*, the unusually high content of amino acids in the nectars of passerine-pollinated *Erythrina* species (Baker & Baker, 1982) could account for the weak colouration of the nectar in the three species, but more investigations across the genus and across individual species' geographical ranges are needed. For *Calliandra calothyrsus* with nocturnal anthesis, it also seems unlikely that the yellow colour of the nectar has any function related to how pollinators perceive the flowers visually.

(7) Evolution of coloured nectar

The topology of the angiosperm phylogeny (Stevens, 2001 onwards) suggests that coloured nectar has evolved independently at the level of order at least 13 times (Fig. 3), and 15 times at the level of family (Table 1). For the majority of taxa with coloured nectar there are no species-level phylogenies available, and thus we cannot answer questions about single *versus* multiple origins of coloured nectar within these taxa, or speculate on when the trait arose within a lineage. One exception is *Schiedea*, where all four species with coloured nectar form a monophyletic group nested within a well-resolved phylogeny (Soltis *et al.*, 1996; Weller *et al.*, 1995; Wagner *et al.*, 2005). In this case it is most parsimonious to assume that coloured nectar arose once within the clade, most likely in a species from Kaua'i, the older of the two islands where coloured nectar occurs. For *Nesocodon mauritianus*, recent molecular phylogenetic work shows it to be nested within the genus *Heterochaenia* with three species found on the neighbouring island of La Réunion (J. M. Olesen & B. K. Ehlers, unpublished data). The flowers of *H. ensifolia* and *H. rivalsii* have clear nectar, but nectar colour is unknown in *H. borbonica*. Here, we can hypothesise a relatively recent origin of the evolution of coloured nectar, as La Réunion is approximately two million years old (McDougall, 1971). As Mauritius is about eight million years old (McDougall & Chamalaun, 1969), it is thus most likely that *N. mauritianus* is a recent addition to the Mauritian flora, and that coloured nectar evolved here after colonisation from La Réunion during a relatively short time.

Although no well-resolved species-level phylogenies exist for the other taxa with coloured nectar, it is still possible to make inferences about evolutionary events in some of the lineages. In *Hoya*, coloured nectar is found in all five species in the section *Amblyostemma* (Kloppenburg, 1994). This suggests that coloured nectar arose only once in *Hoya*. However, further phylogenetic studies are needed to confirm the monophyly of this section (Wanntorp *et al.*, 2006, Wanntorp *et al.*, in press). Similarly, the *Banksia* species with coloured nectar are all found in one group, *Sphaerocarpa*, in the series *Abietinae* (George, 1999). However, as our knowledge about nectar in this series is incomplete (Markey & Lamont, 1995), and as there is no species-level phylogeny, we cannot deduce anything about single or multiple origins of coloured nectar. In *Jaltomata*, Mione *et al.* (1994) constructed a phylogeny of parts of the

genus, but only two species producing coloured nectar were included. These were members of an unresolved lineage, of which all other species produced clear nectar. Thus, no statement about single *versus* multiple origins of coloured nectar can be inferred here either. Mione & Anderson (1996) speculated that if coloured nectar only evolved once in *Jaltomata*, it could be seen as a key character. Together with long-distance bird dispersal of the brightly coloured berries, it could have fuelled an adaptive radiation of *Jaltomata* species with coloured nectar into various habitats and altitudes.

Similarly, the evolution of black nectar in four *Schiedea* species could be seen as a novel way of attracting birds to provide outcrossing services. The four species with coloured nectar are all autogamous (self-pollinating) and in one case even cleistogamous (the flowers never open) (Weller *et al.*, 1995). However, many other *Schiedea* species show very high levels of inbreeding depression (Culley *et al.*, 1999; Norman *et al.*, 1995; Rankin, Weller & Sakai, 2002; Sakai, Karoly & Weller, 1989; Sakai *et al.*, 1997) and inbreeding depression was recently demonstrated for *S. viscosa* (Weller *et al.*, 2005).

Some of the other taxa with coloured nectar are members of small genera (*Capsicum, Leucosceptrum, Deplanchea, Schwartzia, Fernandoa*, and *Lumnitzera*), where almost nothing is known about nectar colour in their respective congeners. Thus, in these cases it is also impossible to state anything about evolutionary events.

In summary, it is either known or suspected that coloured nectar has arisen only once in most lineages. It is not possible, however, to generalise on whether nectar colour is an evolutionarily labile or conservative floral trait. Contrary to the flexibility of floral morphology displayed within most angiosperm lineages, another nectar trait, sugar composition, has been considered a conservative trait (Baker & Baker, 1983; Baker *et al.*, 1998; Nicolson & van Wyk, 1998; van Wyk & Smith, 1996). Thus, we could assume nectar colour to be a conservative trait as well. However, a recent analysis of nectar sugar composition in putative ornithophilous species from the Canary Islands and their closest entomophilous relatives has demonstrated a remarkable evolutionary flexibility in sugar ratios (sucrose:hexose), possibly as a response to selective pressures from generalised avian pollinators (Dupont *et al.*, 2004). Bruneau (1997) reported similar flexibility in sugar ratios and nectar amino acid concentrations in *Erythrina* (Fabaceae), both of which had changed repeatedly to reflect hummingbird- or passerine pollination, irrespectively of phylogenetic relationships. In general, it is thus possible to view nectar colour also as an evolutionarily labile trait, and to interpret shifts in nectar colour as being a result of selective pressures exerted by pollinators. However, phylogenetic inertia rather than continued selective pressures from pollinators could account for the persistence of coloured nectar once it has evolved in a lineage.

Obviously, for a pollinator to exert selective pressure on the colour of nectar, there must be variation in this floral trait in the first place. The vast majority of floral nectars are as clear as water. Therefore, one important question begs answering: how did the original variation in nectar colour in the species with coloured nectar arise? As discussed above, nectar may be coloured for several different reasons – or for no reason at all. Hence, any initial colouration of nectar may have been related to non-signalling functions or be purely pleiotropic in origin. At the moment, we know too little about the ecology and evolution of most taxa with coloured nectar. Only with several species- and lineage-specific studies can this question be addressed, and potential general trends investigated.

V. CONCLUSIONS AND FUTURE DIRECTIONS

(1)   We have shown that coloured nectar is a widespread phenomenon, which is possibly correlated with one or more of several factors: vertebrate pollinators, insularity, and altitude. We believe that the occurrence of coloured nectar is even more widespread than this review suggests. However, coloured nectar is probably often overlooked by taxonomists describing new species, especially if the description is only based on herbarium material. We would thus like to call on workers in plant taxonomy, plant ecology and related fields to pay attention to coloured nectar in their study species and study areas. As shown, coloured nectar may be especially prevalent in vertebrate-pollinated, insular and/or montane taxa. Future reports of additional taxa with coloured nectar will enable us to investigate environmental and ecological correlates with more accuracy, as well as facilitate the testing of current hypotheses and development of new hypotheses on the function and evolution of this spectacular floral trait. With comparative methods, the evolution and maintenance of coloured nectar in lineages could be investigated – but species-level phylogenies are currently only available for a small number of lineages containing species with coloured nectar. Furthermore, future investigations of species with coloured nectar should aim to cover as much of a species' geographical range as possible; some species show variation in expression of nectar colour within a species, and only a broad sampling will elucidate the potential importance of local climatic and edaphic factors, and other nectar properties, such as pH.

(2)   Most importantly, there is a great need for experimental studies which address one or more of the hypotheses for the presence of colour pigments in nectar. In relation to the signalling hypothesis, we need studies of plants with coloured nectar and their interactions with flower visitors and pollinators, investigating whether coloured nectar can act as a visual cue and potentially as an honest signal. Experimental approaches could include manipulating nectar colour and amount in real or artificial flowers, and investigating the response of free-ranging or captive flower visitors (*cf.* Hansen *et al.*, 2006; Johnson *et al.*, 2006). Furthermore, future studies should include a biochemical analysis of the nectar to determine the identity of the pigments responsible for the colouration. There is also a need for experimental investigations of other functions of the colour pigments, especially as a defence against microbial infestation, and deterring of flower visitors that are inefficient pollinators or nectar robbers. Ultimately, to demonstrate adaptivity and fitness advantages of coloured nectar in relation to any ecological function, we need experiments in

the field that assess the effect of coloured nectar on reproductive success – i.e. fruit- or seed set.

(3) Already, there is some experimental evidence that coloured nectar can have ecological functions: firstly, in the case of *Aloe* section *Anguialoe*, experiments show that the phenolics which impart the dark colouration of the nectar are distasteful to certain flower visitors that are morphologically unsuitable as pollinators, while at the same time visually attracting birds that are effective as pollinators (Johnson *et al.*, 2006). Secondly, experiments with lizard pollinators in Mauritius show that they strongly prefer coloured nectar to clear nectar in artificial flowers (Hansen *et al.*, 2006).

(4) A caveat in any study of coloured nectar as a visual signal is the 'perception space' (Chittka & Brockmann, 2005) of the flower visitor species that may react to the presence of coloured nectar. Flower visitors are likely to perceive flower- and nectar colour differently to the way humans do, and interpretations of coloured nectar as a visual signal for a certain flower visitor should take the specific visual capabilities of that species into account. A good example of this is our inability to perceive colours in the UV range, whereas many insects, birds and lizards are able to perceive these colours. Hence, future research should also assess nectar colours in the UV range (Thorp *et al.*, 1975). Moreover, as already mentioned, the contrast between colours rather than a preference for specific colours may be important (Hansen *et al.*, 2006; Schmidt *et al.*, 2004). Measurements of nectar and flower colours with a spectrometer (e.g. Ollerton *et al.*, 2003) could be used to quantify colours in a 'perception space'-neutral manner, and comparisons of Euclidian distances (e.g. Schmidt *et al.*, 2004) between flower and nectar colours thus obtained could be made to investigate the importance of colour identity *versus* contrast.

(5) In a review of sexual selection, Andersson & Iwasa (1996) pointed out that sexual selection and signalling studies so far had been a major research area in zoology only, but that future studies could benefit from applying sexual selection and signalling theory in botany as well. Similarly, honest signalling in animals has been an active research area for a long time (see Maynard-Smith & Harper, 2001 and references therein), but it has to our knowledge only been suggested three times previously in plants. Firstly, in relation to nectar scent (Raguso, 2004b) in parallel to our argument in this review. Secondly, in the positive correlation between floral bract size and resin award size in *Dalechampia ipomoeifolia* (Euphorbiaceae) blossoms, and how pollinating bees select flowers based on bract size rather than reward size (Armbruster, Antonsen & Pelabon, 2005). Interestingly, in relation to coloured *versus* clear nectar, Armbruster *et al.* (2005) speculate that while the resin in *D. ipomoeifolia* is clear, it is brightly coloured in many other *Dalechampia* species, and that coloured resin in those species could act as an honest signal without the need for additional honesty via bract size. Thirdly, honest signalling in plants has been proposed in the recent 'autumn colouration' hypothesis of Hamilton & Brown (2001). This hypothesis states that the vibrant autumn leaf colours of deciduous trees are honest signals to deter phytophagous insects, and it has already created substantial debate and led to experimental approaches and calls for more research on colour patterns in plants in general (Atkinson, 2001; Holopainen & Peltonen, 2002; Wilkinson *et al.*, 2002; Hagen, Folstad & Jakobsen, 2003; Schaefer & Wilkinson, 2004; Archetti & Leather, 2005; Schaefer & Rolshausen, 2006). Furthermore, compared to signalling between animals, signals from plants to animals lend themselves well to study, due to a relative constancy in time and space, and a lower complexity and simpler dynamics (Schaefer, Schaefer & Levey, 2004). We propose that plants with coloured nectar and their flower visitors are an excellent study system to investigate honest signalling in plants. Comparative studies in a phylogenetic framework of species with and without coloured nectar would be particularly useful, addressing both ecological and evolutionary aspects of coloured nectar.

(6) In summary, future research on coloured nectar has the potential not only to increase our basic knowledge about this fascinating floral trait, but also to contribute significantly to the diverse fields of signalling theory, nectar biochemistry, pollination biology and the evolutionary ecology of mutualisms.

VI. ACKNOWLEDGEMENTS

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VIII. APPENDIX 1: TABLE REFERENCES

References for Table 1

Aloe alooides	Glen & Hardy, 1995; S. D. Johnson, unpublished data; B.-E. van Wyk, personal communication; B. Loison, personal communication.
A. castanea	Reynolds, 1940; Glen & Hardy, 1995; Nicolson & Nepi, 2005; S. D. Johnson, unpublished data.
A. vryheidensis	Reynolds, 1940; Dyer, 1941; Glen & Hardy, 1995; van Wyk & Smith, 1996; S. D. Johnson, unpublished data.
A. spicata	Dyer, 1931; Reynolds, 1940; Glen & Hardy, 1995; S. D. Johnson, unpublished data.
Phormium tenax	Craig & Stewart 1988; Isacch, 2002; J. Henning, personal communication; J. L. Craig, personal communication; P. B. Heenan, personal communication.
Nesocodon mauritianus	Olesen *et al.*, 1998; Wyse Jackson, 1990.
Schiedea lychnoides	Weller & Sakai, 1990; Weller *et al.*, 1995; Wagner *et al.*, 2005; S. G. Weller, personal communication.
S. obovatum	Weller *et al.*, 1995; Wagner *et al.*, 2005; S. G. Weller, personal communication.
S. trinerve	Weller *et al.*, 1995; Wagner *et al.*, 2005; S. G. Weller, personal communication.
S. viscosum	Weller *et al.*, 1995; Wagner *et al.*, 2005; S. G. Weller, personal communication.
Schwartzia brasiliensis	Sazima *et al.* 1993; Pinheiro *et al.* 1995; M. Rocca & M. Sazima, personal communication.
Calliandra calothyrsus	Palmer *et al.*, 1994; MacQueen & Hernández, 1997; Chamberlain, 1998, 2000; Jensen, 2005; Estolas, 2004.
Erythrina caffra	Guillarmod *et al.*, 1979; Cheke & Mann, 2001, Scott-Elliot, 1890.
E. humeana	Guillarmod *et al.*, 1979; Cheke & Mann, 2001.
E. zeyheri	Guillarmod *et al.*, 1979.
Hoya diversifolia	Hoffmann *et al.*, 2002; D. Liddle, personal communication; R.D. Kloppenburg, personal communication.
H. excavata	D. J. Liddle, personal communication; R.D. Kloppenburg, personal communication.
H. kerrii	Hoffmann *et al.*, 2002; D. J. Liddle, personal communication; R. Pettersson, personal communication; C. Burton, personal communication.
H. meliflua	Hoffmann *et al.*, 2002; R.D. Kloppenburg, personal communication; D. J. Liddle, personal communication.
H. obovata	Hoffmann *et al.*, 2002; D. J. Liddle, personal communication.
Melianthus comosus	Scott-Elliot, 1890; H. P. Linder, unpublished data; J. Henning, personal communication.
M. dregeanus	Tansley & Schelpe, 1984; H. P. Linder, unpublished data; J. Henning, personal communication.
M. elongatus	H. P. Linder, unpublished data; J. Henning, personal communication.
M. gariepinus	Archer & Condy, 1997; Tansley & Schelpe, 1984; H. P. Linder, unpublished data., unpublished data; J. Henning, personal communication.
M. insignis	Dyer, 1959; Tansley & Schelpe, 1984; H. P. Linder, unpublished data.
M. major	Scott-Elliot, 1890; H. P. Linder, unpublished data; J. Henning, personal communication.
M. pectinatus	Tansley & Schelpe, 1984; H. P. Linder, unpublished data; J. Henning, personal communication.
M. villosus	Dyer, 1952; H. P. Linder, unpublished data; J. Henning, personal communication
Deplanchea tetraphylla	Avé, 1984; Weber & Vogel, 1986; Brown & Hopkins, 1995; Jackson, 2001.
Fernandoa magnifica	Weber & Vogel, 1986; Beentje, 1994; Diniz, 1988; C. Puff personal communication.
Leucosceptrum canum	Cowan & Cowan,1929; Li & Hedge, 1994; Grierson & Long, 1999; G.M. Pradhan, personal communication.
Dombeya a. ssp. *acutangula*	Gigord *et al.*, 1998, 1999; L. Gigord, personal communication.
D. a. ssp. *palmata*	L. Gigord, personal communication.
D. a. ssp. *rosea*	Friedmann, 1987; D. M. Hansen, personal observations.
D. cacuminum	Prenner, 2002; Llamas, 2003.
D. elegans	Friedmann ,1987; L. Gigord, personal communication.
D. kefaensis	Friis & Bidgood, 1998, 2001.
Trochetia blackburniana	Friedmann , 1987; Olesen *et al.*, 1998; D.M. Hansen & C.B. Müller, unpublished data.
T. boutoniana	Friedmann , 1987; Olesen *et al.* 1998; D.M. Hansen & C.B. Müller, unpublished data.
T. granulata	Friedmann, 1987; D.M. Hansen & C.B. Müller, unpublished data.
T. parviflora	Friedmann, 1987; D.M. Hansen & C.B. Müller, unpublished data.
T. triflora	Friedmann, 1987; D.M. Hansen & C.B. Müller, unpublished data.
T. uniflora	Friedmann, 1987; D.M. Hansen & C.B. Müller, unpublished data.
Lumnitzera littorea	Tomlinson , 1986; H. Skovgaard, personal communication.
Banksia grossa	Markey & Lamont ,1995; George, 1999; B. B. Lamont, personal communication.
B. incana	Markey & Lamont, 1995; George, 1999; B. B. Lamont, personal communication.
B. leptophylla	Markey & Lamont, 1995; George, 1999; B. B. Lamont, personal communication.
B. nutans	Markey & Lamont, 1995; George, 1999; Wooller & Wooller, 2003; B. B. Lamont, personal communication.
B. sphaerocarpa	Lamont, 1980; Markey & Lamont, 1995; George, 1999; B. B. Lamont, personal communication.
B. telmatiaea	Markey & Lamont, 1995; George, 1999; B. B. Lamont, personal communication.
Grevillea robusta	Skead, 1967; Nicolson, 1993, 1995; Kalinganire, 2000; Makinson, 2000; R. O. Makinson, personal communication.
Capsicum baccatum	Eshbaugh, 1970; 1975; W. H. Esbaugh, personal communication.
C. pubescens	Eshbaugh, 1975; W. H. Esbaugh, personal communication; A. Boatman, personal communication.

References for Table 1: (*cont.*)

C. eximium	Eshbaugh, 1975; W. H. Esbaugh, personal communication.
Jaltomata aspera	Bitter, 1921; T. Mione, unpublished data.
J. biflora	Mione *et al.*, 2001; T. Mione, unpublished data.
J. herrerae	Mione & Leiva, 1997; T. Mione, unpublished data.
J. paneroi	Mione & Leiva, 1997; T. Mione, unpublished data.
J. umbellata	Mione *et al.*, 1993; T. Mione, unpublished data.
J. ventricosa	Mione *et al.*, 1993; T. Mione, unpublished data.
J. weberbaueri	T. Mione, unpublished data.
J. sp. *"contumacencis"*	T. Mione, unpublished data.
J. sp. *"642"*	T. Mione, unpublished data.
J. sp. "647"	T. Mione, unpublished data.
J. sp. "669"	T. Mione, unpublished data.
J. sp. *"711"*	T. Mione, unpublished data.

References for Table 2:

Aloe castanea	Nicolson & Nepi, 2005.
A. vryheidensis	S. D. Johnson *et al.*, unpublished data.
Phormium tenax	Craig & Stewart 1988.
Nesocodon mauritianus	Olesen *et al.*,1998; J. M. Olesen, unpublished data.
Schiedea lychnoides	Weller *et al.*, 1998.
S. obovata	Weller *et al.*, 1998.
S. trinerve	Weller *et al.*, 1998.
S. viscosa	Weller *et al.*, 1998.
Schwartzia brasiliensis	Sazima *et al.* 1993; Pinheiro *et al.* 1995.
Calliandra calothyrsus	Jensen, 2005.
Erythrina humeana	van Wyk, 1993; S. W. Nicolson, personal communication.
E. caffra	van Wyk, 1993; S. W. Nicolson, personal communication.
Melianthus comosus	Baker *et al.*, 1998; H. P. Linder, unpublished data; J. Henning, personal communication.
M. dregeanus	H. P. Linder, unpublished data; J. Henning, personal communication.
M. elongatus	H. P. Linder, unpublished data; J. Henning, personal communication.
M. gariepinus	H. P. Linder, unpublished data; J. Henning, personal communication.
M. major	Nicolson, 2002; H. P. Linder, unpublished data; J. Henning, personal communication.
M. pectinatus	H. P. Linder, unpublished data; J. Henning, personal communication.
M. villosus	H. P. Linder, unpublished data; J. Henning, personal communication.
Deplanchea tetraphylla	Weber & Vogel, 1986.
Dombeya a. ssp. *acutangula*	L. Gigord, personal communication.
D. angulata ssp. *rosea*	D. M. Hansen, unpublished data.
Trochetia blackburniana	D. M. Hansen & C.B. Müller, unpublished data.
T. boutoniana	D. M. Hansen & C.B. Müller, unpublished data.
T. granulata	D. M. Hansen & C.B. Müller, unpublished data.
T. triflora	D. M. Hansen & C.B. Müller, unpublished data.
T. uniflora	D. M. Hansen & C.B. Müller, unpublished data.
Lumnitzera littorea	H. Skovgaard, personal communication.
Banksia leptophylla	Nicolson & van Wyk, 1998; Markey & Lamont, 1995.
B. sphaerocarpa	Nicolson & van Wyk, 1998.
B. telmatiaea	Nicolson & van Wyk, 1998.
Grevillea robusta	Baker *et al.*, 1998; Kalinganire *et al.*, 2001.
Jaltomata biflora	Mione *et al.*, 2001.
J. paneroi	J. M. Olesen & D. M. Hansen, unpublished data.

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