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New records of insect pollinators for South African asclepiads (Apocynaceae: Asclepiadoideae)

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Abstract

Studies of pollination in southern African asclepiads (aside from the stapeliads and members of the genus *Ceropegia*) are remarkably scarce given the diversity of asclepiad species in the region. In this study, we report new observations of insect flower visitors and their pollen loads for 15 species of South African asclepiads in the genera *Asclepias*, *Aspidoglossum*, *Miraglossum*, *Pachycarpus*, *Periglossum*, *Woodia* and *Xysmalobium*. Nectar properties are also presented for some species. Four specialized pollination systems are suggested by these observations: (1) pollination by wasps in the genus *Hemipepsis* (Hymenoptera: Pompilidae) in eight species, (2) pollination by chafer beetles (Scarabaeidae: Cetoniinae) in three species, (3) pollination by honeybees, *Apis mellifera* (Hymenoptera: Apidae) in two species, and (4) pollination by flies from various families in one species. The pollination system of *Asclepias crispa* remains unclear but appears to be one of generalized insect pollination. Future research is likely to confirm the preponderance of specialized pollination systems within this group of plants in southern Africa.

Keywords: Apocynaceae; Asclepiadoideae; Milkweed; Myophily; Pollination syndrome; Reproductive biology; Southern Africa; Spider-hunting wasp

1. Introduction

The pollination biology of southern African asclepiads (Apocynaceae subfamily Asclepiadoideae *sensu* Endress and Bruyns, 2000) is remarkably poorly studied compared with other regions, especially North America (see reviews by Wyatt and Broyles, 1994; Ollerton and Liede, 1997). The asclepiads have diversified tremendously in southern African grasslands, and South Africa is considered a centre of diversity and endemism for this group of plants (Victor et al., 2000). Approximately 600 species are currently described for southern Africa with 87% of these endemic to the region (Cowling and Hilton-Taylor, 1997; Victor et al., 2000). Knowledge of pollinator requirements is essential for conservation planning, especially given the high rates of habitat transformation in many of South Africa's grasslands.

Our current knowledge of the diversity of pollination systems in southern African asclepiads, apart from the succulent carrion-flower stapeliads and the genus *Ceropegia* (tribe Ceropegieae, see review by Meve and Liede, 1994; Ollerton et al., 2009), is somewhat limited. The earliest documented studies of asclepiad pollination in South Africa include descriptions of floral visitors to *Gomphocarpus*, *Periglossum* and *Woodia mucronata* (then known as *Xysmalobium linguaeforme*) in the Eastern Cape and on Table Mountain (Weale, 1873; Scott-Elliot, 1891). More recent studies have revealed a diversity of often specialized pollination systems within southern African asclepiads. These include specialized pollination by birds (Pauw, 1998), chafer beetles (Ollerton et al., 2003; Shuttleworth and Johnson, 2008), pompilid wasps (Shuttleworth and Johnson, 2006, 2008, 2009a,b,c), vespid wasps (Coombs et al., 2009) and possibly bees (Ollerton et al., 2003). Generalist insect pollination has also been described for several species (Liede and Whitehead, 1991; Ollerton et al., 2003). Nonetheless, pollination systems are known for a total of only 18 southern African asclepiad species excluding stapeliads and members of the genus *Ceropegia*.

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This study documents floral visitors (and likely pollinators) to a further 15 species of South African asclepiads in the genera *Asclepias*, *Aspidoglossum*, *Miraglossum*, *Pachycarpus*, *Periglossum*, *Woodia* and *Xysmalobium*. Rates of visitation to many of these species are typically low and visitor observations are consequently limited for some species. However, these have been included as they provide a valuable starting point for subsequent research. Furthermore, both *Woodia* species are listed as rare in the Red Data List of southern African plants (Hilton-Taylor, 1996) and knowledge of their pollinator requirements is essential for their conservation.

2. Methods

2.1. Study species and field sites

This study examined the pollination ecology of 15 perennial species of grassland asclepiad (Apocynaceae subfamily Asclepiadoideae *sensu* Endress and Bruyns, 2000) in the genera *Asclepias*, *Aspidoglossum*, *Miraglossum*, *Pachycarpus*, *Periglossum*, *Woodia* and *Xysmalobium* (Table 1; Figs. 1 and 2). Plant identifications were carried out with the assistance of Ashley Nicholas (University of KwaZulu-Natal, Westville) and were based on Langley (1980), Kupicha (1984), Smith (1988), Goyder (1998) and Nicholas (1999). Two of these species, *Woodia mucronata* and *W. verruculosa*, are listed as rare in the Red Data List of southern African plants (Hilton-Taylor, 1996). Voucher specimens of the species studied are deposited in the NU Herbarium (University of KwaZulu-Natal, Pietermaritzburg). This study was conducted over the course of five flowering seasons (between 2004 and 2009; see Table 1) at 12 sites in South Africa (Table 2).

2.2. Floral visitors, pollen loads and visitor behaviour

Floral visitors were recorded for all species and, where possible, representative specimens were collected for subsequent identification (Table 1). Pollen loads were determined for all collected individuals using a dissecting microscope. In some instances individual insects were inspected for pollinaria in the field and released. Representative insect specimens are deposited in the Natal Museum (Pietermaritzburg). The behaviour of pollinators and mechanism of pollinarium attachment was noted for species where sufficient visits were observed. Pompilid wasps were identified using keys given in Arnold (1932), Day (1979) and Goulet and Huber (1993). Chafer beetles were identified using Holm and Marais (1992). Visits by the beetle *Atrichelaphinis tigrina* to *Pachycarpus concolor* were inferred from the presence of the highly distinctive *Pa. concolor* pollinaria on individual beetles that were collected on the sympatrically occurring asclepiad *Xysmalobium undulatum* as part of a separate study (see Shuttleworth and Johnson, 2008). Visitors identified as *Hemipepsis* spp. (Table 1) are all individuals of one of the following species: *H. capensis*, *H. errabunda* or *H. hilaris*. These wasps are familiar to the authors from previous fieldwork but can usually only be identified to species where the individuals were collected or photographed.

2.3. Nectar properties

Total nectar production over a 24 h period was measured for five of the study species (Table 3). Flowers were bagged for 24 h prior to nectar sampling except for *Pachycarpus campanulatus* where plants were collected and kept in vases in the laboratory overnight (nectar present at the beginning of the 24 h period was removed with capillary tubes). The volume and the concentration (percentage sucrose equivalent by weight) of nectar were measured with 20 µl capillary tubes and a Bellingham and Stanley (0–50%) hand-held refractometer. Means were calculated per flower for each plant and these values used to calculate a grand mean for the species (see Table 3 for sample sizes).

3. Results

3.1. Floral visitors, pollen loads and visitor behaviour

Floral visitors suggest four distinct pollination systems in the species studied (Table 1): (1) pollination by *Hemipepsis* wasps (Hymenoptera: Pompilidae) in *Asclepias macropus*, *Aspidoglossum glanduliferum*, *Miraglossum pulchellum*, *Pachycarpus campanulatus*, *Periglossum angustifolium*, *Woodia verruculosa*, *W. mucronata* and *Xysmalobium stockenstromense* (Fig. 1); (2) pollination by chafer beetles (Scarabaeidae: Cetoniinae) in *Pa. concolor*, *Pa. scaber* and *Pachycarpus* sp. nov. (Fig. 2); (3) pollination by honeybees (*Apis mellifera*, Hymenoptera: Apidae) in *Asc. dregeana* and *Asc. gibba* (Fig. 2); and, (4) pollination by flies in *X. parviflorum* (Fig. 2). The pollination system of *Asc. crispa* is unclear, but this species appears to be a generalist insect-pollinated species.

Pollinaria were found on representative visitors to 11 of the 15 (73%) plant species studied (see Table 1 for summary and placement of pollinaria on insects). For eight of these plant species, pollinaria were carried by visitors belonging to a single functional group.

Hemipepsis wasps approach flowers with a zigzag flight path typical of insects tracking an odour plume (Raguso, 2006). In *Pa. campanulatus*, the flowers face down and wasps land on the outside of the corolla and crawl inside the large flowers. Once inside, the shape of the corona lobes forces the wasps to hang from the central column in order to access nectar (Fig. 1b) and in so doing, pollinaria are attached to their claws. In *Asc. macropus*, nectar gathers in the upward facing cup formed by the corona lobes. The small size of the flowers means that wasps accessing nectar from a particular flower cling to adjacent flowers and get pollinaria from these flowers attached to their claws (Fig. 1a). In *Asp. glanduliferum*, wasps land on the small flowers and hang below them whilst lapping the nectar (Fig. 1c). Pollinia are presumably attached to their mouthparts, although this was not actually observed. Weale (1873) provides detailed descriptions of wasp behaviour on *W. mucronata* (Fig. 1e).

Table 1
Insect visitors and their pollen loads for fifteen species of asclepiad.

Species and flowering times [a] (Estimated observation time/no. of seasons in which observed)	Visitors	No. observed (No. collected)	No carrying pollinaria (No. checked)	Pollinarium placement	Localities [b]	Flowering season
Asclepias crispa P.J.Bergius var. *plana* N.E.Br.	Coleoptera					
December–January	Scarabaeidae: Cetoniinae					
(1 h/1)	*Atrichelaphinis tigrina* (Olivier, 1789)	1 (0)	1 (1)	Hairs	S	2006/2007
	Diptera					
	Tabanidae					
	Tabanus sp. 1	4 (1)	1 (1)	Claws	S	2006/2007
	Calliphoridae					
	Calliphoridae spp.	10 (0)	None checked		S	2006/2007
	Sarcophagidae					
	Sarcophagidae spp.	5 (0)	None checked		S	2006/2007
Asclepias dregeana Schltr. var. *calceolus* (S.Moore) N.E.Br.	Coleoptera					
October–December	Scarabaeidae: Cetoniinae					
(4 h/2)	*Cyrtothyrea marginalis* (Swartz, 1817)	4 (3)	0 (3)		W	2008/2009
	Diptera					
	Calliphoridae					
	Calliphoridae sp. 1	1 (0)	0 (1)		W	2007/2008
	Hymenoptera					
	Apidae					
	Apis mellifera Linnaeus, 1758	17 (2)	1 (1)	Claws, proboscis	W	2007/2008; 2008/2009
Asclepias gibba (E.Mey.) Schltr. var. *gibba*	Coleoptera					
July–February	Scarabaeidae: Cetoniinae					
(3 h/2)	*Atrichelaphinis tigrina*	0 (1 [c])	1 (1)	Claws	M	2006/2007
	Diptera					
	Calliphoridae					
	Calliphoridae sp. 2	1 (1)	0 (1)		M	2006/2007
	Hymenoptera					
	Apidae					
	Apis mellifera	4 (2)	3 (3)	Claws	M	2006/2007; 2007/2008
Asclepias macropus (Schltr.) Schltr.	Coleoptera					
January–February	Scarabaeidae: Cetoniinae					
(20 h/3)	*Atrichelaphinis tigrina*	33 (13)	0 (13)		W, LB	2005/2006; 2007/2008
	Diptera					
	Sarcophagidae					
	Sarcophagidae spp.	2 (0)	None checked		W	2007/2008
	Hymenoptera					
	Tenthredinidae					
	Tenthredinidae sp. 1	1 (0)	None checked		W	2005/2006
	Pompilidae					
	Hemipepsis errabunda (Dalla Torre, 1897)	3 (3)	0 (3)		GC	2004/2005
	H. capensis (Linnaeus, 1764)	14 (14)	3 (14)	Claws	W, SP, GC	2004/2005; 2005/2006; 2007/2008
	H. hilaris (Smith, 1879)	14 (9)	2 (9)	Claws	W	2004/2005; 2005/2006; 2007/2008
	Hemipepsis spp.	53 (0)	None checked		W	2004/2005; 2005/2006; 2007/2008;
Aspidoglossum glanduliferum (Schltr.) Kupicha	Hymenoptera					

(continued on next page)

Table 1 (*continued*)

Species and flowering times [a] (Estimated observation time/no. of seasons in which observed)	Visitors	No. observed (No. collected)	No carrying pollinaria (No. checked)	Pollinarium placement	Localities [b]	Flowering season
September–January (2 h/2)	Pompilidae					
	Hemipepsis capensis [d]	2 (0)	None checked		W	2008/2009
	Hemipepsis sp.	1 (0)	Not checked		W	2007/2008
Miraglossum pulchellum (Schltr.) Kupicha	Hymenoptera					
October–January (30 min/1)	Pompilidae					
	Hemipepsis capensis	1 (1)	0 (1)		BN	2005/2006
Pachycarpus campanulatus (Harv.) N.E.Br. var. *campanulatus*	Hymenoptera					
November–February (4 h/2)	Pompilidae					
	Hemipepsis capensis	8 (4)	4 (5)	Claws	BN, W	2005/2006; 2007/2008
	H. hilaris	2 (2)	0 (2)		BN, W	2005/2006
	Halictidae					
	Halictidae sp. 1	1 (1)	0 (1)		W	2005/2006
Pachycarpus concolor E.Mey.	Coleoptera					
October–April	Scarabaeidae: Cetoniinae					
(20 h/3)	*Atrichelaphinis tigrina*	1 (25 [e])	26 (26)	Tibiae, tarsi	M	2005/2006; 2006/2007; 2007/2008
Pachycarpus scaber (Harv.) N.E.Br.	Hemiptera					
October–January	Lygaeidae					
(8 h/2)	Lygaeidae sp. 2	2 (0)	None checked		B	2008/2009
	Coleoptera					
	Scarabaeidae: Cetoniinae					
	Cyrtothyrea marginalis	131 (26)	4 (32)	Palps	B	2007/2008; 2008/2009
	Leucocelis adspersa (Fabricius, 1801)	8 (2)	0 (2)		B	2008/2009
	L. amethystina (MacLeay, 1838)	8 (2)	0 (2)		B	2007/2008
	L. haemorrhoidalis (Fabricius, 1775)	1 (1)	0 (1)		B	2007/2008
	L. rubra (Gory and Percheron, 1833)	2 (2)	0 (2)		B	2008/2009
	Scarabaeidae: Rutelinae					
	Rutelinae sp. 1	18 (7)	1 (7)	Mouthparts	B	2007/2008; 2008/2009
	Elateridae					
	Elateridae sp. 1	2 (0)	None checked		B	2007/2008
	Curculeonidae					
	Curculeonidae sp. 1	12 (2)	0 (2)		B	2007/2008
	Diptera					
	Diptera spp.	30 (0)	None checked		B	2007/2008
	Calliphoridae					
	Chrysomya chloropyga (Wiedemann, 1818)	1 (1)	0 (1)		B	2008/2009
	Calliphoridae sp. 3	2 (2)	0 (2)		B	2007/2008
	Muscidae					
	Orthellia sp. 1	10 (2)	0 (2)		B	2007/2008; 2008/2009
	Muscidae spp.	2 (0)	None checked		B	2007/2008
	Sarcophagidae					
	Sarcophaginae sp. 1	8 (3)	0 (3)		B	2007/2008; 2008/2009
	Hymenoptera					
	Tiphiidae					
	Tiphia sp. 1	1 (1)	0 (1)		B	2007/2008
	Pompilidae					
	Pepsinae sp. 1	1 (1)	0 (1)		B	2008/2009
	Apidae					
	Apis mellifera	1 (0)	None checked		B	2007/2008

Table 1 (*continued*)

Species and flowering times [a] (Estimated observation time/no. of seasons in which observed)	Visitors	No. observed (No. collected)	No carrying pollinaria (No. checked)	Pollinarium placement	Localities [b]	Flowering season
Pachycarpus sp. nov. [f]	Hemiptera					
November–December	Lygaeidae					
(3 h/2)	Lygaeidae sp. 1	1 (1)	0 (1)		Hi	2008/2009
	Coleoptera					
	Scarabaeidae: Cetoniinae					
	Atrichelaphinis tigrina	5 (3)	1 (3)	Tarsus	Hi	2008/2009
	Diptera					
	Diptera spp.	20 (0)	None checked		Hi	2007/2008
Periglossum angustifolium Decne.	Hymenoptera					
January–March	Pompilidae					
(6 h/1)	*Hemipepsis errabunda*	2 (2)	2 (2)	Mouthparts	M	2005/2006
	Hemipepsis spp.	9 (0)	7 (9)	Mouthparts	M, LB	2005/2006
Woodia mucronata (Thunb.) N.E.Br.	Coleoptera					
December–January	Scarabaeidae: Cetoniinae					
(1 h/1)	*Atrichelaphinis tigrina*	1 (0)	None checked		Ho	2007/2008
Red Data: Rare	Hymenoptera					
	Pompilidae					
	Hemipepsis spp.	5 (0)	None checked		Ho	2007/2008
Woodia verruculosa Schltr.	Hymenoptera					
October–February	Pompilidae					
(3 h/1)	*Hemipepsis capensis*	1 (1)	1 (1)	Mouthparts	M	2007/2008
Red Data: Rare	*Hemipepsis* sp.	1 (0)	Not checked		M	2007/2008
Xysmalobium parviflorum Harv. ex Scott-Elliot	Diptera					
October–April	Calliphoridae					
(3 h/1)	Calliphoridae sp. 4	3 (1)	2 (2)	Mouthparts	G	2007/2008
	Muscidae					
	Orthellia sp. 1	50 (3)	0 (3)		G	2007/2008
	Scathophagidae					
	Scathophaga sp. 1	1 (4)	1 (1)	Mouthparts	G	2007/2008
Xysmalobium stockenstromense Scott-Elliot	Hymenoptera					
November–January	Pompilidae					
(2 h/2)	*Hemipepsis capensis*	1 (1)	0 (1)		Se	2008/2009
	Hemipepsis spp.	5 (0)	None checked		Ho	2007/2008

[a] Flowering times taken from Pooley (1998) and Nicholas (1999), except for *Asclepias crispa* and *Woodia mucronata* which were inferred from our observations.
[b] B=Baynesfield, BN=Bushman's Nek, G=Gilboa Estate, GC=Giant's Castle, Hi=Highflats, Ho=Hogsback, LB=Lion's Bush Farm, M=Midmar Nature Reserve, S=Sinangwana, SP=Sani Pass, Se=Sentinel, W=Wahroonga Farm.
[c] This individual was captured carrying *Asclepias gibba* pollinaria, but was not directly observed visiting flowers.
[d] These individuals were identified from photographs.
[e] These individuals were collected on the sympatrically occurring asclepiad, *Xysmalobium undulatum*.
[f] This is a recently discovered species (M. Glenn, J. Lamb, A. Nicholas and A. Shuttleworth, unpubl. data).

Visits to *Pachycarpus concolor* and *Pachycarpus* sp. nov. were too limited to enable visitor behaviour to be described. In *Pa. concolor*, the widely spaced anther wings (forming the guide rails; Fig. 1f) combined with the placement of pollinaria on the tibiae and tarsi of visiting beetles suggests that the entire leg of the insect is trapped whilst accessing nectar. In *Pa. scaber*, the corona lobes curve back over the central column (Fig. 2b) and nectar gathers between ridges at the base of the corona lobe. Visiting beetles are thus forced to access the nectar from between the corona lobes (Fig. 2b). In doing so the palps are trapped between the guide rails and pick up the pollinaria.

In *Asc. dregeana*, flowers are suspended in an umbelliform inflorescence which faces down. Honeybees fly into the flowers from below and hang from the central column whilst probing for nectar. During this process, pollinaria are attached to the

Fig. 1. Plants pollinated by *Hemipepsis* wasps. (a) Female *H. capensis* visiting *Asclepias macropus*, Wahroonga Farm; (b) Male *H. capensis* visiting *Pachycarpus campanulatus*, Bushman's Nek. Note the pollinaria attached to tarsal claws (indicated by arrows); (c) Female *H. capensis* visiting *Aspidoglossum glanduliferum*, Wahroonga Farm; (d) Male *H. errabunda* visiting *Periglossum angustifolium*, Midmar Nature Reserve. Note the pollinaria attached to the mouthparts (indicated by arrow); (e) *Hemipepsis* sp. visiting *Woodia mucronata*, Hogsback; (f) *Xysmalobium stockenstromense* inflorescence. All scale bars = 10 mm.

claws as these get trapped between the guide rails (Fig. 2a). Observations of visits to *Asc. gibba* were insufficient to describe pollinator behaviour.

In *X. parviflorum*, the flowers are small and nectar appears to gather in the bottom of the cup formed by the corolla lobes (Fig. 2e). Flies visiting the flowers probe the base of the corolla, during which pollinaria are attached to their mouthparts and proboscides (Fig. 2e).

3.2. Nectar properties

Pachycarpus concolor and *Pa. scaber* (both chafer-pollinated) produced large amounts (3.7 and 6.6 µl respectively) of nectar with a concentration of 37% and 28% respectively (Table 3). *Pa. campanulatus* (*Hemipepsis* wasp pollinated) produced less nectar with a lower concentration (Table 3). The two honeybee-pollinated species (*Asc. dregeana* and

Fig. 2. Plants pollinated by honeybees, chafer beetles and flies. (a) *Apis mellifera* visiting *Asclepias dregeana*, Wahroonga Farm. Note the pollinaria attached to the tarsal claws and proboscis (indicated by arrows); (b) *Cyrtothyrea marginalis* visiting *Pachycarpus scaber*, Baynesfield; (c) *Asclepias gibba* flowers, Midmar Nature Reserve; (d) *Pachycarpus* sp. nov. flower, Highflats; (e) Calliphoridae sp. 4 visiting *Xysmalobium parviflorum*, Gilboa Estate. Note pollinarium attached to the proboscis (indicated by arrow); (f) *Pachycarpus concolor* flowers, Midmar Nature Reserve. All scale bars = 10 mm.

Asc. gibba) produced smaller amounts of nectar, but the concentration of *Asc. dregeana* nectar (54%) was considerably higher than that of *Asc. gibba* (36%; Table 3).

4. Discussion

The results of this study suggest that most of the asclepiad species studied have pollination systems which are highly specialized at the level of functional group. These groups are *Hemipepsis* pompilid wasps (for eight species of asclepiads), chafer beetles (for three species), honeybees (for two species) and flies (for one species) (Table 1). However, confirmation of the pollinator spectrum for some of the study species requires a larger sample of flower visitors and these results should thus be considered to be preliminary.

Table 2
Details of study sites and estimated population sizes for plants species.

Site name (province)[a]	Coordinates	Altitude (masl)	Habitat	Species (no. of plants)
Baynesfield (KZN)	29°45′13.3″ S; 30°21′29.9″ E	810	Rocky grassland	*Pachycarpus scaber* (c. 40)
Bushman's Nek, Drakensberg (KZN)	29°50′28.1″ S; 29°12′07.2″ E	1861	Montane grassland	*Miraglossum pulchellum* (c. 30) *Pachycarpus campanulatus* (c. 20)
Giant's Castle, Drakensberg (KZN)	29°13′06.0″ S; 29°33′18.0″ E	1600	Montane grassland	*Asclepias macropus* (c. 5)
Gilboa Estate (KZN)	29°16′30.7″ S; 30°16′45.0″ E	1607	Montane grassland	*Xysmalobium parviflorum* (c. 10)
Highflats (KZN)	30°16′10.3″ S; 30°12′09.3″ E	976	Annually mown grassland	*Pachycarpus* sp nov. (c. 30)
Hogsback (EC)	38°28′0.4″ S; 26°55′20.9″ E	1418	Montane grassland	*Woodia mucronata* (c. 15) *Xysmalobium stockenstromense* (c. 20)
Lion's Bush Farm (KZN)	29°24′25.1″ S; 29°56′19.6″ E	1476	Montane grassland	*Asclepias macropus* (c. 5) *Periglossum angustifolium* (c. 5)
Midmar Nature Reserve (KZN)	29°32′15.8″ S; 30°10′13.1″ E	1088	Moist montane grassland	*Asclepias gibba* (c. 30) *Pachycarpus concolor* (c. 45) *Periglossum angustifolium* (c. 10) *Woodia verruculosa* (c. 40)
Sani Pass, Drakensberg (KZN)	29°37′16.0″ S; 29°23′15.0″ E	1900	Montane grassland	*Asclepias macropus* (c. 5)
Sentinel, Drakensberg (FS)	28°42′54.0″ S; 28°53′43.0″ E	2400	Montane grassland	*Xysmalobium stockenstromense* (c. 15)
Sinangwana (EC)	31°44′41.9″ S; 29°22′50.8″ E.	132	Coastal grassland	*Asclepias crispa* var *plana* (c. 30)
Wahroonga Farm (KZN)	29°36′35.9″ S; 30°07′59.4″ E	1350	Moist montane grassland	*Asclepias dregeana* (c. 20) *Asclepias macropus* (c. 10) *Pachycarpus campanulatus* (c. 10)

[a] KZN = KwaZulu-Natal province, EC = Eastern Cape province, FS = Free State province.

Pollination by *Hemipepsis* pompilid wasps is now known for several South African asclepiads and these insects appear to be especially important as asclepiad pollinators within the region (Ollerton et al, 2003; Shuttleworth and Johnson, 2006, 2008, 2009a,b,c). Visitor observations and pollen load data are reasonably comprehensive for *Asclepias macropus* (Fig. 1a), *Pachycarpus campanulatus* (Fig. 1b) and *Periglossum angustifolium* (Fig. 1d), and these three species are clearly pollinated exclusively by these wasps (Table 1). Pollination by *Hemipepsis* wasps has not previously been described in the genus *Asclepias* but specialized pollination by these wasps is known in four other *Pachycarpus* species (*Pa. appendiculatus*, *Pa. asperifolius*, *Pa. grandiflorus* and *Pa. natalensis*; see Ollerton et al, 2003; Shuttleworth and Johnson, 2006, 2009a,c). The role of *Hemipepsis* wasps as the pollinators of *Pe. angustifolium* is consistent with early observations by Weale (1873) of visits by "a large black and yellow wasp … *Pallosoma*, one of the Pepsidae" to *Periglossum* in the Eastern Cape. The genus *Pallosoma* Lepeletier 1845 referred to by Weale (1873) is a synonym for *Hemipepsis* Dahlbom 1844 (Arnold, 1932). In addition, *Pe. angustifolium* pollinia have been found inserted between the guide rails of another exclusively *Hemipepsis* wasp pollinated species (*Xysmalobium orbiculare*) at a site near Midmar Nature Reserve (Shuttleworth and Johnson, 2009b; A. Shuttleworth, unpubl. data).

Table 3
Nectar properties for five of the asclepiad species studied.

Plant	Volume (μl)	Concentration (%)	Locality[a]
	Mean ± SE per flower per plant (no. of flowers/ no of plants)	Mean ± SE per flower per plant (no. of flowers/ no of plants)	
Asclepias dregeana	0.7 ± 0.46 (28/3)	54 ± 0.3 (12/2)	W
Asc. gibba	0.2 ± 0.04 (50/16)	36 ± 1.8 (20/10)	M
Pachycarpus campanulatus	0.9 ± 0.21 (12/5)	21 ± 2.2 (7/5)	BN
Pa. concolor	3.7 ± 1.23 (35/20)	37 ± 4.4 (25/15)	M
Pa. scaber	6.6 ± 1.63 (30/6)	28 ± 1.9 (30/6)	M

[a] BN = Bushman's Nek, M = Midmar Nature Reserve, W = Wahroonga Farm.

Observations of visitors to flowers of *Aspidoglossum glanduliferum*, *Miraglossum pulchellum*, *Woodia verruculosa*, *W. mucronata* and *Xysmalobium stockenstromense* were more limited (Table 1). However, *Hemipepsis* wasps were the only insects observed to visit these plants (except for a single chafer beetle on *W. mucronata*) and the floral characteristics of these species (see Fig. 1) appear to be consistent with a guild of cryptic flowers that are pollinated by *Hemipepsis* wasps (Ollerton et al., 2003; Johnson, 2005; Johnson et al., 2007; Shuttleworth and Johnson, 2006, 2008, 2009a,b,c,d). Pollination by *Hemipepsis* wasps is known for two other *Miraglossum* species (*M. verticillare* and *M. pilosum*) and two other *Xysmalobium* species (*X. orbiculare* and *X. undulatum*; Ollerton et al, 2003; Shuttleworth and Johnson, 2008, 2009b). *Hemipepsis* wasps have also been observed visiting *M. anomalum* (S.D. Johnson, unpubl. data). Weale (1873) provides detailed descriptions of the behaviour of "*Pallosoma*" (now *Hemipepsis*) wasps on "? *Xyomalobium* [sic.] *linguaeforme* ?" in the Eastern Cape. "*Xyomalobium linguaeforme*" presumably refers to *Xysmalobium linguaeforme* Harv ex. Weale which has subsequently been classified as *Woodia mucronata* (Victor et al., 2000, 2003). The results of our study, supplemented with Weale's (1873) observations, suggest that *Woodia mucronata* is indeed a *Hemipepsis* wasp specialist and it seems likely that *W. verruculosa* is similarly reliant on *Hemipepsis* wasps.

Specialized pollination by chafer beetles (Scarabaeidae: Cetoniinae) has been described in three South African

asclepiads (*Asclepias woodii*, *Sisyranthus trichostomus* and *Xysmalobium involucratum*; Ollerton et al., 2003). We suggest that specialized chafer pollination systems also occur in the genus *Pachycarpus*. Our observations for *Pa. scaber* are relatively comprehensive and this species appears to be pollinated almost exclusively by the chafer *Cyrtothyrea marginalis* (Fig. 2b) although a single monkey beetle (Scarabaeidae: Rutelinae) was also found to be carrying pollinia (Table 1). Visitor observations to *Pa. concolor* and *Pachycarpus* sp. nov. (Fig. 2d, f) were more limited, but suggest that these species are pollinated primarily by the chafer beetle *Atrichelaphinis tigrina*.

Apart from chafer beetles, *Pachycarpus* sp. nov. was also visited by a large number of flies (Table 1). However, we believe the delicate nature of the flies' legs makes them unlikely to systematically remove and insert pollinaria on the large and relatively robust flowers (Fig. 2d), although we cannot rule out the possibility that flies may contribute to the pollination of this species. *Pachycarpus* sp. nov. is currently known from only a single site near the village of Highflats in KwaZulu-Natal (M. Glenn, J. Lamb, A. Nicholas and A. Shuttleworth, unpubl. data) and its pollinator requirements should be assessed for its conservation.

In the case of *Pa. concolor*, only a single visit by *A. tigrina* was observed. However, a large number of these beetles were collected on the sympatric *X. undulatum* and found to be carrying *Pa. concolor* pollinaria (Table 1). Furthermore, the pollinaria on these beetles were frequently reduced to just the corpusculum suggesting successful insertion of individual pollinia in *Pa. concolor* flowers. *Pachycarpus concolor* pollinia are considerably larger than the stigmatic grooves on *X. undulatum* flowers and were thus unlikely to have been inserted into the grooves of these flowers. Furthermore, *Pa. concolor* pollinia were never discovered inserted in *X. undulatum* flowers from Midmar Nature Reserve when these were being inspected for removal and insertion rates of pollinia in a separate study (see Shuttleworth and Johnson, 2008). The flowers of *X. undulatum* are very attractive to *A. tigrina* beetles (Shuttleworth and Johnson, 2008) and the presence of a large *X. undulatum* population alongside the population of *Pa. concolor* at Midmar Nature Reserve may partly explain the low visitation rates of *A. tigrina* to *Pa. concolor* at this site (Table 1).

Pollination by bees (honeybees and halictids) has been suggested for *Aspidonepsis diploglossa* and *Asc. cucullata* (Ollerton et al., 2003). Our observations suggest that *Asc. dregeana* (Fig. 2a) and *Asc. gibba* (Fig. 2b) are pollinated primarily by honeybees (Table 1). Honeybees were the most abundant of the visitors to both species and appeared to be the most important pollen vectors (Table 1). However, a single chafer beetle (*A. tigrina*) was collected carrying *Asc. gibba* pollinia and these beetles may also contribute to the pollination of this species.

Myophily in asclepiads has typically been associated with the succulent stapeliads and members of the genus *Ceropegia* (Asclepiadoideae: Ceropegieae *sensu*; Endress and Bruyns, 2000; see review by Meve and Liede, 1994; Ollerton et al., 2009). Our observations suggest that *X. parviflorum* is pollinated exclusively by flies (Fig. 2e). This is consistent with the results of pollinator observations reported for this species by Johnson et al. (in press). This therefore represents the first record of myophily outside of the stapeliads and the genus *Ceropegia* in a southern African asclepiad. *Xysmalobium parviflorum* has a very powerful faecal odour (resulting from the production of high levels of *p*-Cresol by the flowers; A. Shuttleworth, unpubl. data) and flies are undoubtedly attracted by the strong odour of these flowers.

The pollination system of *Asclepias crispa* remains unclear. Pollinaria were found on a chafer beetle (*A. tigrina*) and on a tabanid fly suggesting that this species may have a more generalized pollination system than other species examined in this study (Table 1). However, visitor observations were limited and further research is required to determine the pollinator profile of this species.

The chafer-pollinated species reported here (*Pa. scaber* and *Pa. concolor*) produce large amounts of nectar (3–7 μl per flower) with a concentration of ±30% sugar (Table 3). These volumes are greater than those recorded for chafer-pollinated species by Ollerton et al. (2003) although the concentrations are comparable. The *Hemipepsis* wasp pollinated *Pa. campanulatus* produced a relatively low amount (less than 1 μl per flower) of dilute (21%) nectar (Table 3), in contrast with other *Hemipepsis* pollinated species which typically (but not always, see Ollerton et al., 2003; Johnson, 2005) produce copious amounts of very concentrated nectar (Ollerton et al., 2003; Shuttleworth and Johnson, 2006, 2008, 2009a,b,c,in press). The honeybee-pollinated *Asc. dregeana* and *Asc. gibba* produced low amounts of moderately concentrated nectar (Table 3), comparable with the putatively bee-pollinated species suggested by Ollerton et al. (2003).

The majority of the pollination systems documented in this study appear to be highly specialized. This contrasts with studies of North American asclepiads which typically have generalized pollination systems (cf. Fishbein and Venable, 1996). This study also adds several new species to a growing list of South African plants that are pollinated exclusively by *Hemipepsis* wasps. The high morphological diversity that has developed among southern African asclepiads suggests that future research is likely to reveal further interesting pollination systems within this diverse group of plants.

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