

Morphology of oil-collecting pilosity of female *Rediviva* bees (Hymenoptera: Apoidea: Melittidae) reflects host plant use

Michael Kuhlmann^{a*} and Hilke Hollens^b

^aDepartment of Life Sciences, Natural History Museum, London, UK; ^bInstitute of Landscape Ecology, Westfälische Wilhelms-University of Münster, Münster, Germany

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The oil-collecting hair morphology and pilosity on female foretarsi for all 26 species of the southern African endemic bee genus *Rediviva* was studied and related to host plant use based on about 2700 flower visitation records. Four different types of tarsal pilosity and six principal hair types are identified. *Rediviva* bees collect floral oil from 12 plant genera representing the families Iridaceae, Orchidaceae, Scrophulariaceae and Stilbaceae, with *Diascia* being the most frequently used host. Differences in foretarsal pilosity reflect the availability of floral oil and elaiophore morphology of the principal host flowers. *Rediviva* species with short female forelegs exhibit a greater diversity of tarsal oil-collecting pilosity than long-legged species. This contradicts an earlier hypothesis that the pilosity of species with shorter legs might be less complex than in *Rediviva* with elongate forelegs.

Keywords: *Rediviva*; solitary bee; foretarsal pilosity; oil-collecting; flower relationships

Introduction

Floral oil-secretion and oil-collecting of bees is a unique pollination syndrome that was first described by Stefan Vogel in 1969 (summarized in Vogel 1974) and obviously evolved independently multiple times in plants and bees (Michez et al. 2009; Renner and Schaefer 2010). Oil flowers are most common in South America but are known from all continents (Vogel 1974, 1986, 1990; Buchmann 1987; Schaefer and Renner 2008) including between 1300 and 2400 plant species representing 10 families (Buchmann 1987; Vogel 2009). In southern Africa the pollination systems of oil-secreting flowers and oil-collecting bees of the genus *Rediviva* (Melittidae) was only discovered in 1984 (Vogel 1984; Whitehead et al. 1984) and is certainly one of the most fascinating ones. On the plant side the system comprises about 140 species in 14 genera of the families Scrophulariaceae, Stilbaceae, Orchidaceae and Iridaceae (Vogel 1984; Manning and Brothers 1986; Steiner 1989a; Steiner and Whitehead 1996; Manning and Goldblatt 2002; Pauw 2005, 2006) that get pollinated by 26 *Rediviva* species (Figure 1) (Whitehead and Steiner 2001; Whitehead et al. 2008; Kuhlmann 2012a).

Female *Rediviva* bees collect floral oil with their forelegs and it is either mixed with pollen for nest provisioning or used for lining brood cells (Whitehead and Steiner 2001; Pauw 2006; Whitehead et al. 2008; Kuhlmann Forthcoming 2014). In

*Corresponding author. Email: m.kuhlmann@nhm.ac.uk

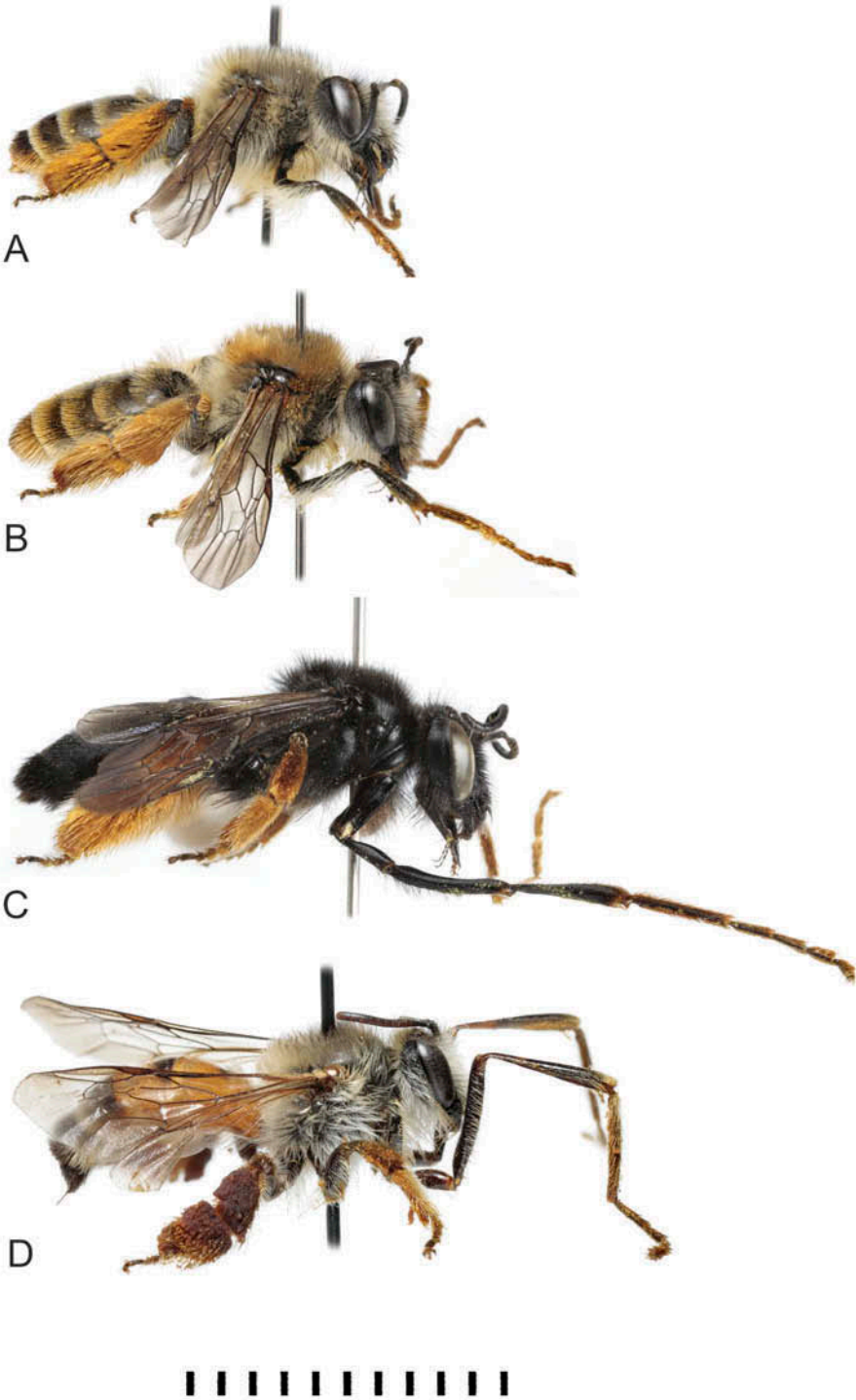


Figure 1. Female *Rediviva* bees in lateral view showing species-specific variation of foreleg length. (A) *R. alonsoae*; (B) *R. macgregori*; (C) *R. longimanus*; (D) *R. emdeorum*. Scale bar: 10 mm.

several *Rediviva* species the forelegs are elongate, sometimes longer than the entire body (Figure 1C–D), and in some cases the lengths of floral spurs and bee forelegs show co-variation at the population level, suggesting co-evolution (Vogel 1974; Steiner and Whitehead 1990, 1991). Floral oil is extracted from the host plants using the forelegs and is subsequently transferred to the hind legs for transport to the nest (Steiner and Whitehead 1990, 1991).

Although morphological adaptations for oil-collecting are quite well documented for many bee taxa, e.g. *Macropis* (Melittidae), *Ctenoplectra*, Centridini and Tapinotaspidini (Apidae) (Vogel 1974, 1986, 1990; Neff and Simpson 1981; Buchmann 1987; Vogel and Cocucci 1995; Roig-Alsina 1997; Cocucci et al. 2000), information about morphological adaptations of *Rediviva* is still patchy (Vogel 1986; Whitehead and Steiner 2001; Whitehead et al. 2008). More detailed observations are only available for three species but they already indicate that there is considerable morphological variation within the genus. *Rediviva gigas* has relatively unspecialized and simple oil-collecting setae restricted to the apical third of the forebasitarsus. Most of the hairs are strong and simple, slender and curved with the ones at the apical third partly being long with lanceolate tips and branched at the base (Whitehead and Steiner 1993; Steiner and Whitehead 1996). The foretarsi of *R. albifasciata* differ substantially as they are dorsally densely covered with fine, highly branched absorptive hairs and ventrally with strong and broad, slightly curved, blade-like scraping hairs (Steiner and Whitehead 2002). This species exclusively visits flowers of *Colpias mollis* and *Hemimeris racemosa* (Scrophulariaceae) where oil is provided in coated elaiophores that have to be ruptured to release the oil (Whitehead and Steiner 1994; Steiner and Whitehead 2002). Like in *R. albifasciata* the foretarsi of *R. emdeorum* (Figure 1D) are dorsally covered with fine and branched absorptive hairs but laterally and ventrally they are replaced by lamellar and apically pluridentate to blunt, spatulate hairs (Vogel 1984).

Plants of the *Rediviva* pollination system secrete floral oil in different ways, suggesting that variation of female foreleg pilosity might reflect this diversity, as known from Neotropical Tapinotaspidini (Cocucci et al. 2000). Among the about eight genera of oil-secreting Orchidaceae, species of the genera *Corycium*, *Disperis* and *Pterygodium* dominate in South Africa (Steiner 1989a; Pauw 2006; Steiner et al. 2011). Oil is secreted at the lip appendage of the flower, mostly from patches of glandular trichomes (trichome elaiophores) or sometimes specialized cells of the epidermis (epithelial elaiophores) (Steiner 1989a; Pauw 2006). Female *Rediviva* bees rub their front legs over the oil film to absorb and collect it with their tarsi (Steiner 1989a; Pauw 2006).

Oil-production was only recently discovered in the South African *Tritoniopsis parviflora*; this is the only record of oil-secretion in any African member of the Iridaceae (Manning and Goldblatt 2002). Like in some orchids, *T. parviflora* secretes oil from epithelial elaiophores (Manning and Goldblatt 2002). The oil covers central parts of the perianth and forms a thin film that is collected by *R. gigas*, which is the principal pollinator of this species (Manning and Goldblatt 2002, 2005).

The most speciose group of oil-producing plants in southern Africa is formed by seven genera of the families Scrophulariaceae and Stilbaceae, encompassing some 100 species: *Alonsoa*, *Colpias*, *Diascia*, *Hemimeris* (Scrophulariaceae), *Anastrabe*, *Bowkeria* and *Ixianthes* (Stilbaceae) (Buchmann 1987; Whitehead and Steiner 2001; Pauw 2006; Whitehead et al. 2008).

In the most speciose genus, *Diascia*, which comprises about 73 species (Steiner 2011), floral oil is mainly secreted within shallow pouches that in some species have

evolved into long spurs (Figure 2B, E–F). The oil is released as small droplets by trichome elaiophores consisting of large, blackish, hemispherical hairs (Vogel 1974, 1984; Hilliard and Burtt 1984; Manning and Brothers 1986). The floral oil of six perennial *Diascia* species from eastern South Africa was analysed by Dumri et al.

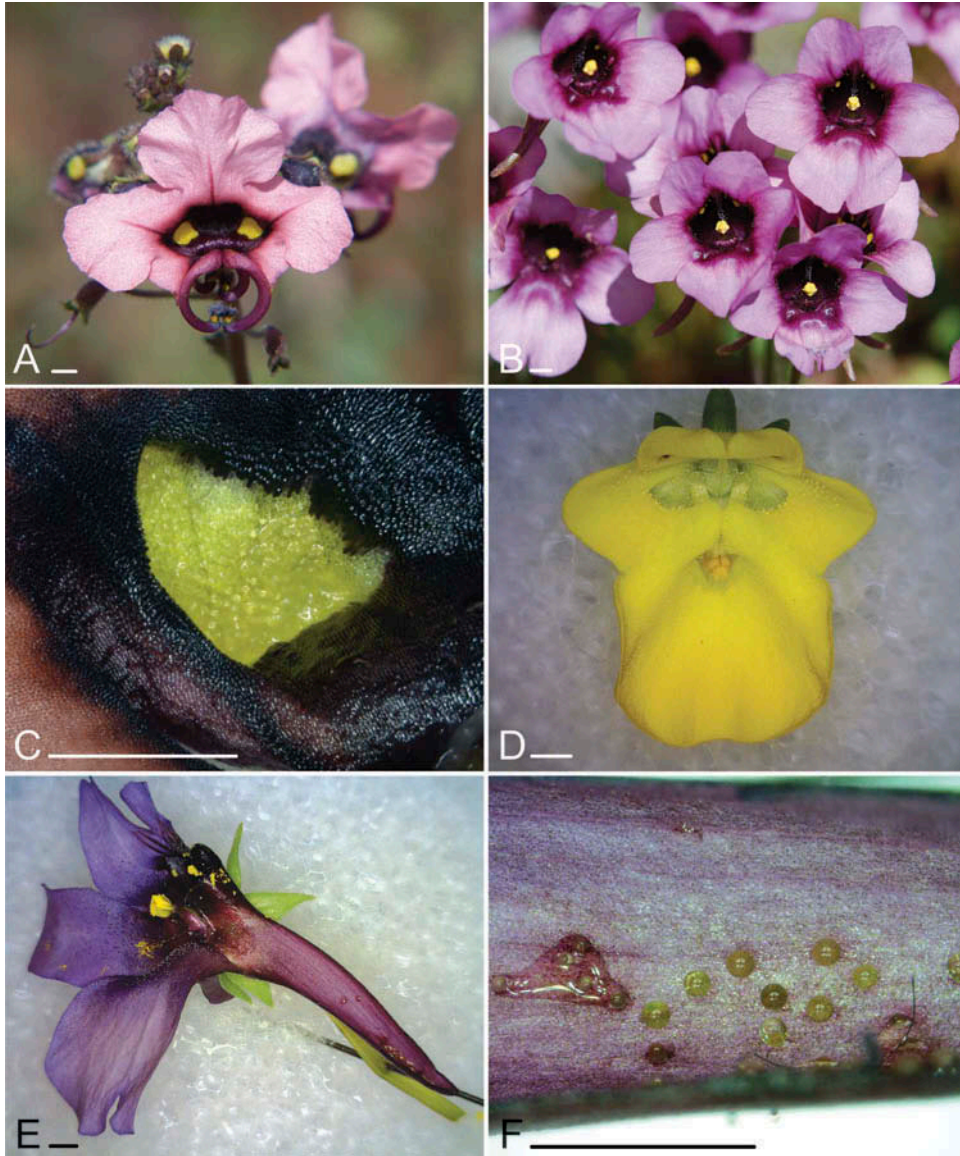


Figure 2. Oil-secreting flowers of the family Scrophulariaceae (*sensu stricto*). (A) *Alonsoa unilabiata*; (B) *Diascia 'floribunda'*; (C) *A. unilabiata*, detail of oil-containing pouch; (D) *Hemimeris racemosa*, flower around openings of spurs with hemispherical oil droplets covered by a cuticle; (E) *Diascia insignis*, longitudinal section of flower with oil droplets in apex of opened floral spur; (F) *D. insignis*, detail of dissected floral spur with oil droplets on top of trichome elaiophores. Scale bars: 1 mm.

(2008) and was found to mostly contain partially acetylated acylglycerols of (3R)-acetoxy fatty acids. Like in *Diascia* floral oil is also freely released in *Alonsoa unilabiata* (Figure 2A, C) (Steiner 1989b, 1996) and, thus, is easily available for oil-collecting *Rediviva* females. In the monotypic *Colpias mollis* the lower inside surface of the corolla is lined with trichome elaiophores. At the apical end of the elaiophores oil is secreted in form of hemispherical droplets that are covered by a cuticle which, in contrast to the previous two genera, has to be ruptured to release the oil (Steiner and Whitehead 2002). In the approximately four *Hemimeris* species the oil droplets are also covered with a cuticle. The trichome elaiophores are mostly located inside and around the entrances of the short spurs and are openly accessible to oil-collecting bees (Figure 2D) (Whitehead and Steiner 1985; Pauw 2005).

In order to gather oil from the three plant genera of the Stilbaceae bees have to enter the large flowers and collect the oil from the lower parts of their inner corolla wall instead of just using their legs for extracting oil from the relevant floral parts, as in the other plant genera. In *Bowkeria* oil is secreted in small droplets by numerous trichome elaiophores that are located in a large glandular field in the lower part of the corolla (Vogel 1974; Whitehead and Steiner 1992). A comparable situation is found in the very large flowers of the monotypic *Ixianthes retzioides*, where flattened spherical trichome elaiophores occur that are very similar in structure to those of *Bowkeria verticillata* (Steiner 1993; Steiner and Whitehead 1996). In both plant genera oil droplets are coated by a cuticle, like in *Colpias* and *Hemimeris*, that has to be ruptured to release the oil (Steiner and Whitehead 2002). No details have been available about oil-secretion in the closely related monotypic *Anastrabe integerrima* (Whitehead and Steiner 1992) but the situation appears to be similar to *Bowkeria* (Vogel 1974).

The diversity of floral hosts used by *Rediviva* and the specialized flower visitation behaviour suggests morphological adaptations for oil-collecting not only with respect to foreleg length but also regarding the pilosity of foretarsi. Manning and Brothers (1986) proposed that the pubescence of species with shorter legs might be less complex than in *Rediviva* with elongate forelegs. The goals of this paper are: to investigate and describe the pilosity of foretarsi in the females of all 26 *Rediviva* species using scanning electron microscopy (SEM); to find out if interspecific differences exist in relation to host plant use and foreleg length; and to identify possible reasons for morphological differentiation.

Materials and methods

A total of 2717 flower visitation records of females of 25 *Rediviva* species captured from label data were obtained from the collections database of the South African Museum, Cape Town. All specimens in the database were identified by the leading expert of *Rediviva* taxonomy, V.B. Whitehead, and digitized by experienced staff, thus are reliable. No observations were electronically available for *R. macgregori* so they were extracted from Whitehead and Steiner (2001).

Scanning electron microscopy (SEM) of pilosity on foretarsi was carried out using a Leo 1455VP. The backscattered electron images were taken under low vacuum (variable pressure) of uncoated specimens. In this mode electron-poor organic material appears darker than electron-rich material (e.g. soil dust particles) consisting of heavier chemical elements. SEM images of foretarsi were visually examined for hair morphology and *Rediviva* species with identical pilosity patterns grouped together.

Information about foreleg lengths of females of all *Rediviva* species were taken from Whitehead and Steiner (2001), Whitehead et al. (2008) and Kuhlmann (2012a). Legs were defined as ‘short’ when their length was less than that of the body and ‘long’ when they were longer.

Results

For the 26 described *Rediviva* species the pilosity of female foretarsi and visitation records of oil-secreting flowers were investigated, with 17 species having short and nine species long forelegs (Table 1). Fundamentally, six hair types can be found on female *Rediviva* foretarsi:

- (a) unbranched strong and slender, sometimes curved hairs (Figure 3D);
- (b) highly branched absorptive hairs (Figure 3A, E);
- (c) lamellar apically pluridentate hairs (Figure 3A);

Table 1. Host plant visitation records of female oil-collecting *Rediviva* bees in relation to the pilosity of their foretarsi.

Foretarsi pilosity (N records)	<i>Rediviva</i> species (foreleg length) (N records)	% Host plant genera (N species)
Type I (467) (Figure 3A)	<i>R. alonsoae</i> (short) (47)	85.4% <i>Diascia</i> (25)
	<i>R. aurata</i> (short) (105)	10.5% <i>Alonsoa</i> (1)
	<i>R. emdeorum</i> (long) (65)	4.1% <i>Hemimeris</i> (4)
	<i>R. intermedia</i> (short) (38)	
	<i>R. micheneri</i> (long) (71)	
	<i>R. nitida</i> (short) (115)	
Type II (1151) (Figure 3B)	<i>R. ruficornis</i> (short) (25)	
	<i>R. autumnalis</i> (long) (27)	91.4% <i>Diascia</i> (33)
	<i>R. brunnea</i> (short) (20)	3.8% <i>Bowkeria</i> (3)
	<i>R. colorata</i> (long) (11)	3.2% <i>Hemimeris</i> (3)
	<i>R. longimanus</i> (long) (253)	1.1% orchids (7)
	<i>R. macgregori</i> (long)	0.5% <i>Alonsoa</i> (1)
	<i>R. neliana</i> (long) (604)	
	<i>R. pallidula</i> (long) (147)	
	<i>R. peringueyi</i> (short) (36)	
	<i>R. rhodosoma</i> (short) (24)	
	<i>R. steineri</i> (short) (3)	
Type III (984) (Figure 3C, E)	<i>R. transkeiana</i> (long) (9)	
	<i>R. whiteheadi</i> (short) (17)	
	<i>R. albifasciata</i> (short) (57)	60.2% <i>Hemimeris</i> (4)
	<i>R. intermixta</i> (short) (198)	21.0% <i>Bowkeria</i> (2)
	<i>R. parva</i> (short) (316)	17.9 % <i>Diascia</i> (19)
Type IV (115) (Figure 3D, F)	<i>R. rufipes</i> (= <i>bicava</i>) (short) (201)	0.6% <i>Colpias</i> (1)
	<i>R. rufocincta</i> (short) (212)	0.3% <i>Alonsoa</i> (1)
	<i>R. gigas</i> (short) (12)	65.2% <i>Bowkeria</i> (1)
	<i>R. saetigera</i> (short) (103)	24.3% <i>Anastrabe</i> (1)
		7.0% orchids (1)
		2.6% <i>Ixianthes</i> (1)
		0.9% <i>Tritoniopsis</i> (1)

- (d) pluridentate to blunt spatulate hairs (Figure 3B);
- (e) broad and slightly curved blade-like scraping hairs that are partly reinforced at their rear edge (Figure 3C, E); and
- (f) strong simple hairs with lanceolate tips and branched at the base (Figure 3F);

Transitional forms exist between all hair types (Figure 3A–B, E) except for the ones with lanceolate tips that are only known from *R. gigas* (Figure 3F).

Based on the morphology and composition of hairs on the foretarsi four different species-specific types of tarsal pilosity could be identified:

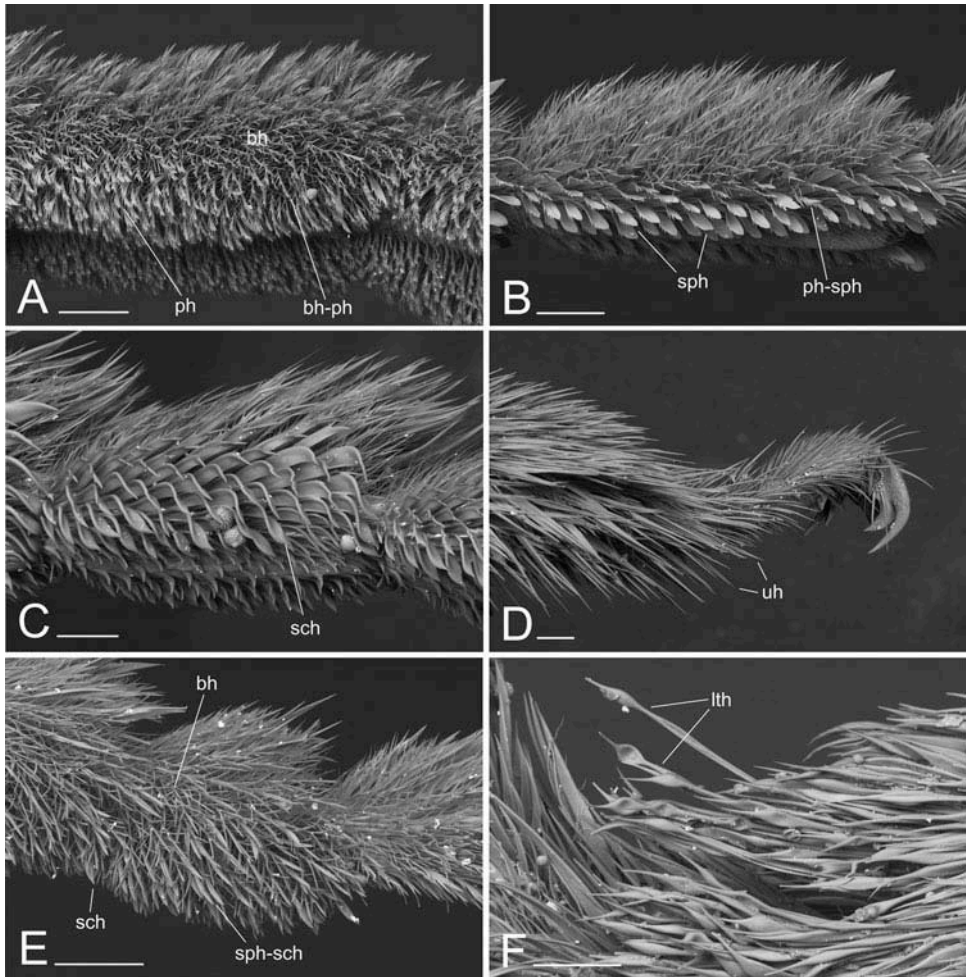


Figure 3. Backscattered SEM images of female *Rediviva* tarsomeres of forelegs in lateral view. (A) *R. nitida* (type I); (B) *R. macgregori* (type II); (C) *R. intermixta* (type III); (D) *R. saetigera* (type IV); (E) *R. parva* (type III); (F) *R. gigas* (type IV). Scale bar 0.1 mm. Abbreviations: uh, unbranched strong and slender hairs; bh, highly branched absorptive hairs; ph, lamellar apically pluridentate hairs; sph, pluridentate to blunt spatulate hairs; sch, broad and slightly curved blade-like scraping hairs; lth, strong simple hairs with lanceolate tips, branched at the base.

Type I: In the seven species assigned to this type (Table 1) foretarsi are predominantly covered with finely branched absorptive hairs with lamellar hairs mainly found on the ventral side (Figure 3A). *Rediviva* species with type I foreleg pilosity have short to long legs and only occur in the winter rainfall area of the Greater Cape Floristic Region (GCFR) of western South Africa.

Type II: Twelve *Rediviva* species belong to tarsal pilosity type II (Table 1), which is characterized by abundant fine absorptive hairs on the dorsal side intermixed with spatulate hairs and sometimes intermediate lamellar to spatulate hairs that dominate ventrally (Figure 3B). Species with this tarsal pilosity have short to long legs and are found across the entire range of the genus.

Type III: Legs of this type are found in five species (Table 1). They show a mixture of absorptive hairs intermixed with simple unbranched, strong, sometimes slightly broadened to pluridentate hairs dorsally while the ventral side is densely covered with strong blade-like scraping hairs (Figure 3C). Within this group of species *R. parva* is unusual because the proportion of strong simple hairs is conspicuously lower and scraping hairs are smaller, including transitions to spatulate hairs (Figure 3E). Type III tarsi are only found on short-legged species occurring across the entire range of *Rediviva*.

Type IV: This type of foretarsal pilosity was only observed in two species (Table 1). Their tarsal pilosity is dominated by unbranched strong, slender hairs while absorptive hairs are largely missing (Figure 3D). In *R. gigas* simple hairs with lanceolate tips and branched at the base are located at the apex of the forebasitarsus (Figure 3F) which is unique for the genus. Both species are short-legged and occur in the winter or summer rainfall area of South Africa.

With respect to foreleg length short-legged *Rediviva* species exhibit all types of tarsal pilosity while long-legged species either have pilosity of type I (two species) or type II (seven species).

Based on label data female *Rediviva* bees were recorded visiting the oil-secreting flowers of 68 species from 12 genera, representing the families: Iridaceae (one genus, one species), Orchidaceae (four genera, eight species), Scrophulariaceae and Stilbaceae (seven genera, 59 species). *Diascia* (Scrophulariaceae) was the most speciose host plant genus (48 species). Overall the most frequently visited flowers are those of *Diascia*, attracting 60.6% of the total visits, followed by *Hemimeris* (23.6%). Scrophulariaceae (i.e. *Alonsoa*, *Diascia*, *Hemimeris*) in total account for 86.2% of all oil-flower visitations, while Stilbaceae (*Anastrabe*, *Bowkeria*, *Ixianthes*) with 13.0%, Orchidaceae (0.8%) and Iridaceae (<0.1%) are less commonly visited.

However, there are significant differences in flower preferences of *Rediviva* species when pilosity of foretarsi and foreleg length is considered (Table 1). Species with tarsal pilosity types I and II both have a strong preference particularly for *Diascia* but also other flowers, like *Alonsoa* and orchids, with openly released oil that can be easily mopped up. Combined they account for 95.9% (type I) and 93.0% (type II) of all flower visits. Flowers where oil droplets are coated by a cuticle, as in *Colpias*, *Hemimeris* and Stilbaceae, are preferentially visited by *Rediviva* species equipped with type III tarsal pilosity (81.8% of all visits) that rupture the elaiophores to release the oil. These species are also able to exploit openly released oil of *Diascia* and *Alonsoa* flowers (18.2% of all visits). The two *Rediviva* species with type IV tarsal pilosity visit a mix of the generally uncommon non-Scrophulariaceae, including floral hosts such as *Anastrabe*, *Ixianthes* and *Tritoniopsis* (combined 27.8% of all visits) that

are not used by others. Favoured host plants are the three genera of Stilbaceae with a total of 92.1% of all visits.

With respect to foreleg length *Rediviva* species show marked preferences (Table 1). While short-legged species visit the full range of oil-secreting flowers, long-legged species are far more specific, having a clear preference for *Diascia* (93.8% of all recorded visits) with *R. autumnalis*, *R. emdeorum*, *R. micheneri*, *R. pallidula* and *R. transkeiana* only recorded from this genus. *Bowkeria* (3.2% of all recorded visits) is exclusively visited by *R. colorata* while *Alonsoa* (0.5%), orchids (1.2%) and *Hemimeris* (1.4%) are only of marginal relevance for the three remaining species, *R. longimanus*, *R. macgregori* and *R. neliana*. The strong preference for *Diascia* among long-legged *Rediviva* is down to the fact that extremely long spurs only exist in this genus.

Discussion

The hair types found on female *Rediviva* foretarsi have also been observed in identical or similar form on the oil-collecting organs of other bee genera, suggesting convergent evolution and a similar function (Vogel 1974, 1986, 1990; Neff and Simpson 1981; Buchmann 1987; Vogel and Cocucci 1995; Roig-Alsina 1997; Cocucci et al. 2000; Kuhlmann 2012b). Remarkable exception is the simple hairs with lanceolate tips and branched base of unknown function that are exclusively known from *R. gigas* (Whitehead and Steiner 1993; Steiner and Whitehead 1996).

Although most hair types of *Rediviva* foretarsi are common in other oil-collecting bees, the way they form a pilosity pattern is different for most genera. An equivalent to *Rediviva* type I and II foretarsal pilosity is only known from *Macropis* (Vogel 1986). To some extent they also resemble the pilosity of the tarsal pads of two *Centris* species collecting oil on *Monttea aphylla* (Miers) Benth. & Hook. f. (Plantaginaceae) in Argentina (Simpson et al. 1990). The mechanism of absorbing floral oil by exploiting capillary forces acting on fine branched and more flattened lamellar and spatulate hairs was described in detail by Vogel (1984, 1986) and Simpson et al. (1990).

Scraping hairs in combination with absorptive pilosity of type III are known in a similar form from *Lanthonomelissa* (Roig-Alsina 1997; Cocucci et al. 2000). In *R. albifasciata* these blade-like hairs are used to rupture the elaiophores of the host plants to release the oil (Steiner and Whitehead 2002). A similar function is assumed for *Lanthonomelissa* and its host plants of the genus *Sisyrrinchium* (Iridaceae) (Cocucci et al. 2000).

The unbranched, strong and slender hairs of type IV with absorptive hairs largely missing (Whitehead and Steiner 1992, 1993; Steiner and Whitehead 1996) seem to be exclusive for *Rediviva* and are similar to those of the genus *Melitta* that does not collect floral oil. The apparent lack of extensive specialized pilosity on the foretarsi of *R. saetigera* and *R. gigas* is puzzling. Whitehead and Steiner (1993) and Steiner and Whitehead (1996) mention that *R. gigas* has an isolated position within the genus, showing a number of plesiomorphies suggesting it might occupy a basal position as a transitional form to non-oil-collecting ancestors. No comprehensive phylogenetic analysis of *Rediviva* has yet been published. However, the available information based on larger phylogenies including two (Michez et al. 2009) and three (Dellicour et al. 2014) *Rediviva* species respectively suggest that the relatively unspecialized and

largely unmodified oil-collecting pilosity on the foretarsi might indeed represent a basal state. In both studies *R. saetigera* came out at the base of the *Rediviva*–*Redivivoides* clade but more data are required to understand the evolution of oil-collecting pilosity as well as the elongation of female forelegs in general.

A dated phylogeny of *Rediviva* would also be required for understanding how rapidly hair morphology and pilosity patterns can evolve and adapt to new floral hosts. Oil-producing Scrophulariaceae and Stilbaceae are of relatively recent origin (*c.*28 Ma and >17 Ma respectively; Datson et al. 2008; Renner and Schaefer 2010) suggesting, in combination with the existence of intermediate hair types, that hair morphology and pilosity patterns might be able to evolve and change rapidly when they come under selection.

Manning and Brothers (1986) hypothesized that the foretarsal pilosity of short-legged *Rediviva* might be less complex than in species with elongate forelegs. Based on the results of the present study this hypothesis can be rejected because all four pilosity types are represented in bees with short forelegs, while only types I and II were found in long-legged species. *Rediviva* with elongate forelegs are almost exclusively visiting long-spurred *Diascia* species that openly release oil which can be easily mopped up. These bees are certainly derived, thus, do not have the presumably basal unspecialized hairs of type IV and they do not need the scraping hairs of pilosity type III for oil-collecting.

Functional relationships of foreleg pilosity and flower morphology as found here for *Rediviva* have been documented for a number of different oil-collecting bees and their host plants, but are mainly based on studies especially dedicated to investigating interactions (Vogel 1974, 1986, 1990; Neff and Simpson 1981; Buchmann 1987; Vogel and Cocucci 1995; Cocucci et al. 2000). When flower visitation records are analysed, as in the present paper, it has to be considered that not all of them necessarily represent real interactions but might be incidental observations without a functional relationship (Kuhlmann and Eardley 2012). Long-legged *R. longimanus*, for example, can occasionally be seen visiting short-spurred *Alonsoa* and *Diascia* species, but for sterical reasons the species is unable to collect oil from these flowers with its extremely long forelegs (Hollens 2010). *Rediviva intermixta* with its specialized scraping hairs for rupturing coated oil droplets has a strong preference for *Hemimeris* flowers but also often visits *Diascia* whose oil is openly available. The species is capitalizing on an easy-to-use source of floral oil other than its principal host plants (Hollens 2010).

Another observational bias in the dataset used here can be caused by host plants that are rare and little investigated. They can be under-represented or even completely missing in the record, as found for *R. peringueyi*. Based on label information this species has been exclusively collected on Scrophulariaceae, which are certainly the most important source of floral oil. Only later was it recognized that *R. peringueyi* is the principal or even exclusive pollinator of 15 orchid species that can be rare but are frequently visited by this species (Pauw 2006; Pauw and Bond 2011; Pauw and Hawkins 2011).

The preferences reported here are accurate, at least for the frequently visited host plants, given the large number of observations (>2700), the host plant associations and the presumed functional relationships of the bees' tarsal pilosity and flower morphology. However, more studies focusing on *Rediviva* oil-collecting are required to understand the functional details of the interactions.

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