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Michael Kuhlmann^a

^a Department of Life Sciences, The Natural History Museum, London, UK

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Nest architecture and use of floral oil in the oil-collecting South African solitary bee *Rediviva intermixta* (Cockerell) (Hymenoptera: Apoidea: Melittidae)

Michael Kuhlmann*

Department of Life Sciences, The Natural History Museum, London, UK

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Nest architecture, use of floral oil for brood cell lining and pollen collecting are described for the first time for the genus *Rediviva*, using the South African endemic oil-collecting solitary bee species *Rediviva intermixta*. The nest consists of a dead-end vertical tunnel with a single brood cell located at the end of each of several horizontally branching lateral tunnels. Brood cells are lined with a thin layer of waxy material, presumably derived from chemically modified floral oil. *Rediviva intermixta* is a pollen generalist but relies on a small number of host plant species for oil-collecting. Brood cells are provisioned with pollen from at least six plant families, but with a preference for non-oil-producing Scrophulariaceae. The nesting biology and Dufour's gland size of the species are discussed and compared with the closely related genera *Melitta* and *Redivivoides* (non-oil-collecting) and *Macropis* (oil-collecting). The differences between *Macropis* and *Rediviva* suggest that oil-collecting in the two genera evolved independently.

Keywords: *Rediviva*; solitary bee; nesting biology; oil-collecting; floral host

Introduction

The bee genus *Rediviva* (26 described species, Whitehead and Steiner 2001; Whitehead et al. 2008; Kuhlmann 2012b) is endemic to South Africa and Lesotho and belongs to the tribe Melittini, which also includes *Melitta* (48 described species, Michez et al. 2012) and *Redivivoides* (seven described species, Kuhlmann 2012a) (Michez et al. 2009). For nest provisioning the females of *Rediviva* collect floral oil that is mixed with pollen from a range of oil-producing flowers, although *Diascia* (Scrophulariaceae) is the principal floral host (Whitehead and Steiner 2001; Pauw 2006; Whitehead et al. 2008). In several *Rediviva* species the forelegs are elongate, sometimes longer than the entire body, and the lengths of floral spurs and bee legs in some cases show co-variation at the population level, suggesting co-evolution (Steiner and Whitehead 1990, 1991). The sister-group of Melittini is the tribe Macropidini comprising the genera *Afrodasyypoda* (one described species, Michez et al. 2009), *Promelitta* (one described species, Michez et al. 2007) and *Macropis* (16 described species, Michez and Patiny 2005). Similar to *Rediviva*, females of *Macropis* also use floral oil that is exclusively collected from flowers of *Lysimachia* (Primulaceae) (Vogel 1986; Michez and Patiny 2005).

Melittidae are the most basal bees (Danforth et al. 2006, 2013), and Melittini and Macropidini, which together form the subfamily Melittinae, are likely to be the most

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

basal extant bee lineage within this family (Michez et al. 2009). Thus, *Rediviva*, *Macropis* and their relatives are a key group for understanding the evolution of oil-collecting in bees (Michez et al. 2009), as well as the origin and evolution of the high bee diversity in the Greater Cape Floristic Region (Kuhlmann 2009).

The origin of oil-collecting in bees has been much debated and this behaviour has evolved independently at least five times in the Centridini, Ctenoplectrini, Exomalopsini, Tetrapediini and Melittinae (Vogel 1974, 1986, 1990; Buchmann 1987; Renner and Schaefer 2010). For the most basal Melittidae, Michener (1981) and later Michez et al. (2009), based on the results of a phylogenetic study, discussed whether oil-collecting may have evolved only once in melittids or if there could be two independent origins in *Macropis* and *Rediviva*. Michez et al. (2009) showed that it is more parsimonious to assume that oil-collecting evolved independently in *Macropis* and *Rediviva*, a scenario that is congruent with the multiple origins of oil-collecting behaviour in other groups of bees. However, the differences in probability of an independent origin of oil-collecting in *Macropis* and *Rediviva* versus multiple losses in their non-oil-collecting relatives are small (Michez et al. 2009) so evidence from bee life history and in particular the use of floral oil may provide the information necessary to decide between the two scenarios.

The nesting biology of Melittinae is still poorly known, with information only available for five species from two of the six genera: *Macropis europaea* Warncke (= *M. labiata* (F.)) (Bouwman 1921; Malyshev 1929; Phipps 1948; Lieftinck 1957; Celary 2004), *Macropis fulvipes* (F.) (Malyshev 1929, 1935; Vogel 1986; Celary 2004; Schäffler and Dötterl 2011), *Macropis nuda* (Provancher) (Rozen and Jacobson 1980; Cane et al. 1983), *Melitta americana* (Smith) (Payette 2013) and *Melitta leporina* (Panzer) (Malyshev 1923, 1935; Türgari 1968; Celary 2006). Generally melittid bees nest in the ground with lateral tunnels leading to brood cells that are often horizontal and bilaterally symmetrical (Michener 2007). Michener (2007, p. 414) mentioned a lack of visible cell lining in Melittidae, except for among *Macropis* species, which line their cell walls with modified floral oil (Schäffler and Dötterl 2011). However, for *Melitta leporina*, Celary (2006) stated that brood cells are lined with secretions from the Dufour's gland. This observation is supported by the existence of a well-developed Dufour's gland in *Melitta leporina*, *Melitta haemorrhoidalis* (F.) and *Melitta americana* Smith (Tengö and Bergström 1976; Cane 1983; Celary 2006). The Dufour's gland produces the secretion used for cell lining in bees (Cane 1981) and hence is almost completely reduced in *Macropis* (Cane et al. 1983) as these bees use foreign material (i.e. floral oil) for lining their brood cells. However, it is unknown if all oil-collecting bees that use floral oil for cell lining have a reduced Dufour's gland because in some bees the gland's secretions are also used as pheromones (Cane 1983; Hefetz 1987) or larval food (Norden et al. 1980).

Here for the first time information is provided about the nesting biology for the oil-collecting bee genus *Rediviva*, in particular *Rediviva intermixta* (Cockerell). The information about the life history of this species allows the first comparison of nesting biology and use of floral oil between the two oil-collecting melittid genera *Macropis* and *Rediviva* and a non-oil-collecting *Melitta* species. Additionally, the Dufour's gland of South African species of *Melitta*, *Rediviva* and *Redivivoides* are dissected to test the hypothesis that Melittinae species using floral oil for cell lining should have

a reduced gland compared with the other species. The results shed light on the evolutionary origin of oil-collecting in melittid bees.

Material and methods

The study was carried out in the Nieuwoudtville Wild Flower Reserve (31°21'S, 19°08'E; 760 m) in the South African winter rainfall area. Climatically, the Nieuwoudtville area is semi-arid with a mean annual rainfall of 341 mm (Snijman and Perry 1987). The reserve falls within the vegetation type of the Nieuwoudtville dolerite renosterveld (Mucina and Rutherford 2004) and is renowned for its high diversity of geophytes and annual plants (Manning and Goldblatt 1996).

Fieldwork was conducted during the flowering season from August to September of 2002, 2004 and 2007 depending on opportunity (discovery of nests, availability of *R. intermixta* females). In 2002 and 2004 females of *R. intermixta* when visiting flowers were captured using a sweep net during warm and sunny weather, mainly between 11.00 and 16.00 h, for the analyses of female scopal pollen loads. Nests were excavated in 2002 and 2007 and brood cells were taken to the laboratory for further investigation and documentation.

The nesting sites were in loamy dolerite soil surrounded by some dolerite rocks and several medium-sized shrubs in the dolerite hills of the Nieuwoudtville Wild Flower Reserve. The nesting area was sparsely vegetated and exposed to the sun. The flora included *Zygophyllum foetidum* Schrad. and J.C. Wendl. (Zygophyllaceae), *Felicia australis* (Alston) E. Phillips, *Osteospermum acanthospermum* (D.C.) Norl., *Rhynchosidium pumilum* (L.f.) D.C., *Senecio* sp., *Ursinia anthemoides* (L.) Poir. (Asteraceae), *Lotononis maximiliani* Schltr. ex De Wild. (Fabaceae), *Diascia cardiosepala* Hiern, *D. 'floribunda'*, *Hemimeris racemosa* (Houtt.) Merrill, *Hemimeris centrodes* Hiern, *Nemesia leipoldtii* Hiern (Scrophulariaceae), *Galenia sarcophylla* Fenzl, *Tetragonia* spec. (Aizoaceae), *Oxalis pes-caprae* L., *Oxalis obtusa* Jacq. (Oxalidaceae), *Erodium cicutarium* (L.) L'Hér (Geraniaceae), *Bulbinella latifolia* Kunth (Asphodelaceae), *Cyanella hyacinthoides* L. (Tecophilaeaceae) and *Albuca maxima* Burm.f. (Hyacinthaceae).

The pollen host plants of *R. intermixta* were identified by analysing the content of 15 female scopal pollen loads and larval food provision of two brood cells excavated in 2002. After the degree of filling of the female scopae was noted, the pollen was gently removed with an insect pin and embedded in Kaiser's glycerol gelatine on microscope slides. Pollen samples were identified by light microscopy at a magnification of 400 × with the help of a pollen reference collection representing all plants flowering at the wider study site. The pollen composition was investigated by identifying 400 pollen grains randomly chosen from each sample (Westrich and Schmidt 1986; Müller and Kuhlmann 2008; Timmermann and Kuhlmann 2008). Reference specimens of *R. intermixta* and pollen samples are deposited in the collection of the author.

Scanning electron microscopy was carried out using a Leo 1455VP. The back-scattered 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.

The Dufour's glands of single female specimens of *Melitta arrogans* Smith, *Rediviva longimanus* Michener and *Redivivoides variabilis* Kuhlmann preserved in ethanol were dissected.

Results

Nest architecture

The nest entrance was funnel-shaped and 12 mm in diameter but narrowed within 10 mm to a final width of 6 mm for the circular tunnel. The entrance possessed a 1-cm high tumulus of 3.5 cm length and 2 cm width. A female *R. intermixta* was still actively using its nest when it was dug up. When viewed from the top (Figure 1A) the nest extended over an area of about 12 × 15 cm. The tunnel descended almost vertically to a depth of 22 cm and then terminated in a dead-end (Figure 1B). Each of the four brood cells was located at the end of a lateral tunnel of 2–12 cm length, 10–14 cm below the surface. Three brood cells were provisioned and contained larvae of different sizes with lateral access tunnels tightly refilled with soil material while cell 2 was not provisioned and the tunnel was still open (Figure 1B).

The brood cells in this nest were vertical, but brood cells have been found to be slightly tilted in the nests of other females. The cells were evenly round in cross-section (diameter 7.0 mm medially and 5.5 mm at the upper and lower end of the cell) and elongate oval in longitudinal section (10.5 mm length) (Figure 1C). The cell closure consisted of soil material with a spiral structure on the inside. The closures were slightly concave on the inside, had a diameter of 5.5 mm and were 0.5 mm thick in the middle (1.3 mm laterally). Except for the cell closure and the upper end of the wall next to it (Figure 2C) the wall of the brood cell was lined

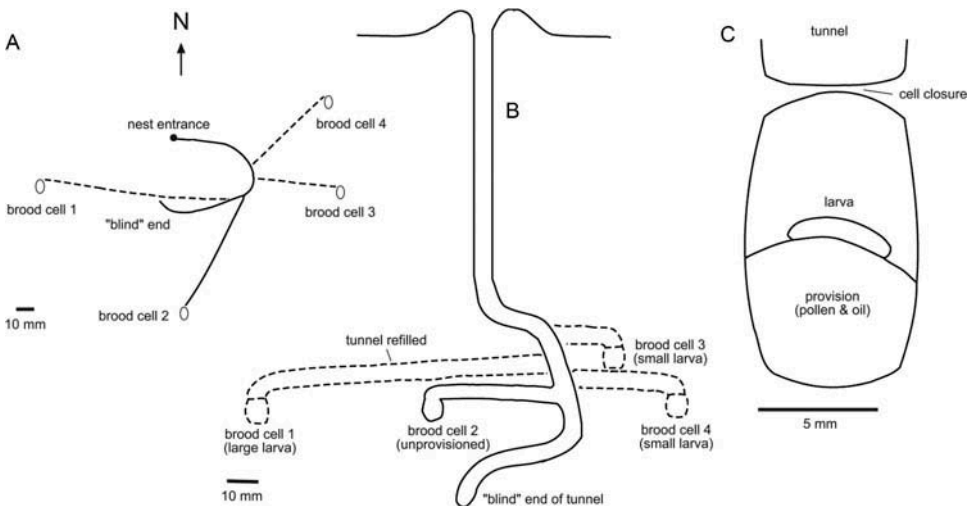


Figure 1. Nest of *Rediviva intermixta*: (A) nest in top view; (B) nest in lateral view; (C) brood cell in lateral view.

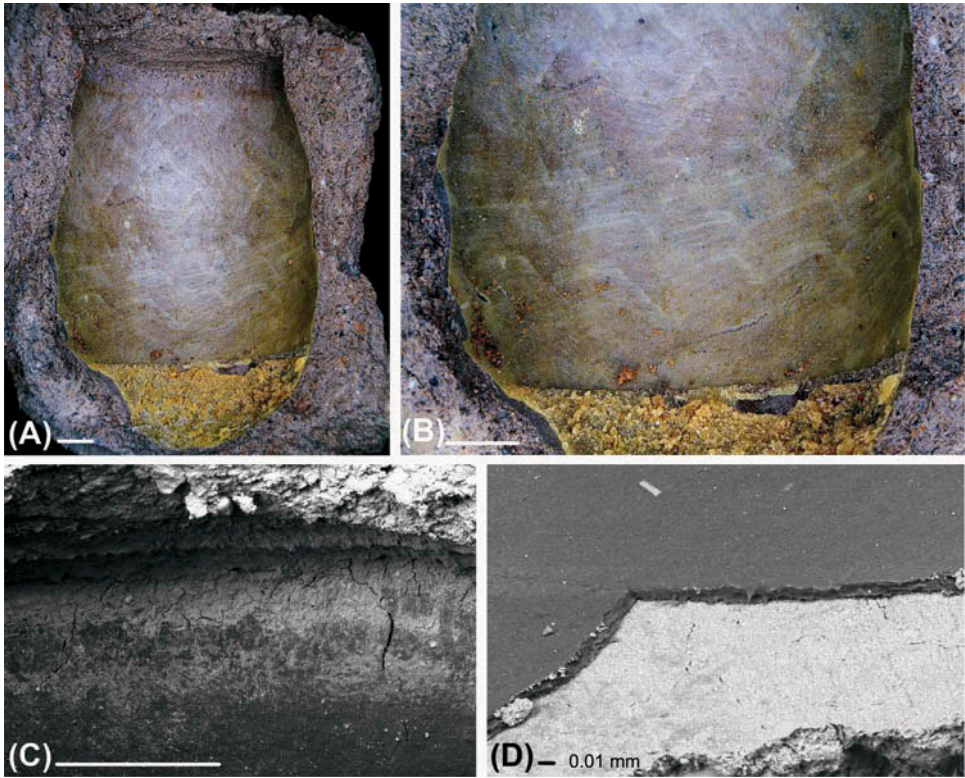


Figure 2. Brood cell of *Rediviva intermixta*: (A) opened brood cell in lateral view (pollen removed); (B) lower part of brood cell with brush marks on the cell lining; (C) scanning electron microscopy (SEM) of the upper end of the brood cell just below the closure where the cell lining (dark grey) becomes thinner and disappears towards the top (= brown margin in Figure 2A); (D) SEM of waxy layer of cell lining (dark grey) on top of smoothed soil on the inside of the brood cell. The waxy layer forms the inner surface of the brood cell as shown in Figure 2B. Scale bar 1 mm.

with a yellowish-brown waxy and waterproof substance (tested with a droplet of water) that was easily chipped off when the brood cell was opened (Figure 2A). The lining was about 10 μm thick and was spread out over the compacted and smoothed cell wall (Figure 2D). The cell lining was covered with what looked like light-coloured brush marks (Figure 2B). Their size exactly matched that of a brush-like fringe of hairs at the apical end of the female hind basitarsus that is used for storage and transport of floral oil and pollen (Figure 3A–C). The brood cell provision was a bright yellowish pollen mass with a moist oily sheen and a pasty consistency filling slightly less than the lower half of the brood cell. The surface of the provision was convex, probably even more so before the larva started feeding, whereas the lower part conformed to the cell shape. The larva was feeding on top of the pollen mass (Figure 1C). No glucose could be detected in the provision (glucose test strip used).

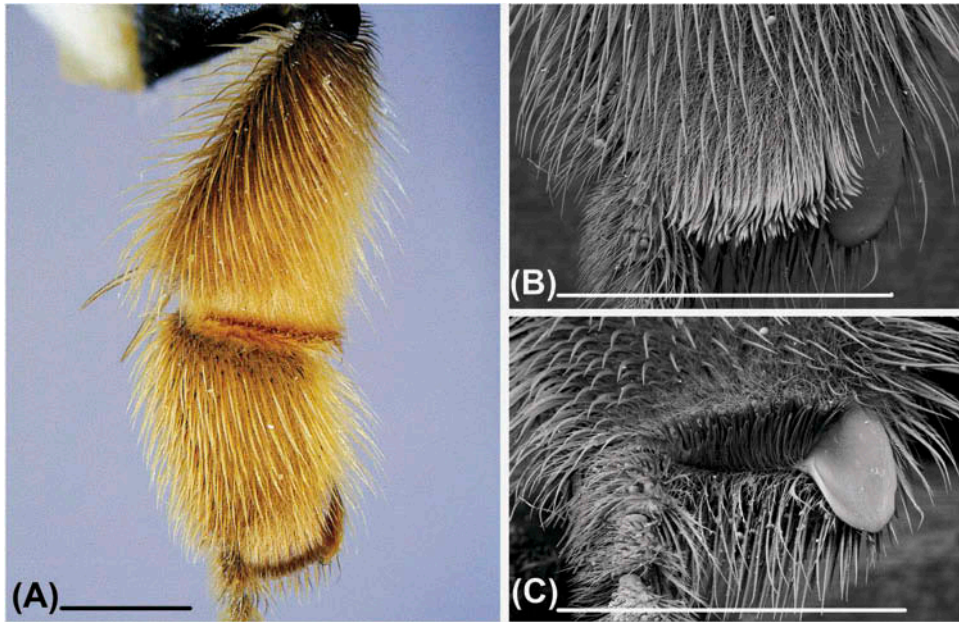


Figure 3. Hindleg of female *Rediviva intermixta*: (A) tibia and basitarsus in dorsal view showing specialized hairs for transporting floral oil; (B) scanning electron microscopy (SEM) of apical end of hind basitarsus showing the hair brush in dorsal view; (C) SEM of apical end of hind basitarsus showing the hair brush from below. Scale bar 1 mm.

Host plants

A total of 17 pollen samples were used for pollen analyses, including 15 samples from female scopal loads and two from brood cells. *Rediviva intermixta* collected pollen from at least six different plant families (Table 1) with pollen from Scrophulariaceae being dominant (69.8% of total pollen) followed by Fabaceae (14.3%) and Zygophyllaceae (10.2%). Pollen from these plant families and in particular Scrophulariaceae was frequently collected and dominated the pollen content of single

Table 1. Composition of 17 pollen samples of *Rediviva intermixta*.

Family	Host plant species	% (all loads)	Presence in samples	Min.–max./ load (%)
Scrophulariaceae	<i>Nemesia leipoldtii</i> (93.2%) <i>Diascia</i> sp. (6.8%)	69.8	17 (100.0%)	3–100
Fabaceae	various genera	14.3	8 (47.1%)	2–66
Zygophyllaceae	<i>Zygophyllum foetidum</i>	10.2	7 (41.2%)	3–84
Oxalidaceae	<i>Oxalis pes-caprae</i>	2.1	9 (53.0%)	2–11
Asteraceae	various genera	1.6	4 (23.5%)	2–10
Iridaceae	various genera	0.9	4 (23.5%)	2–6
Unidentified		1.1	3 (17.6%)	5–8

pollen loads whereas pollen of other families was only occasionally collected and usually in small amounts. The distinctly bright orange coloured and readily identifiable pollen of *Nemesia leipoldtii* (Scrophulariaceae) was particularly frequently collected. Importantly, *Nemesia* is very common at this site but does not produce floral oil (Table 1). At the study site *R.intermixta* mainly visited *Diascia cardiosepala*, *Hemimeris centrodes* and sometimes *Hemimeris racemosa* for collecting floral oil but their pollen was almost completely missing in female scopal pollen loads (4.7% of total pollen).

Dufour's gland

The Dufour's gland of *Melitta arrogans* is very well developed, large and shaped like an inverted 'U'. Its size is similar to that of *Colletes validus* Cresson as illustrated in Lello (1971) and when stretched is about 1.5 times as long as the metasoma. The Dufour's glands of both *Rediviva longimanus* and *Redivivoides variabilis* are only about one-quarter of the size (about one-third of the length of their metasoma) of the gland in *Melitta arrogans*, but are still several times larger than those in *Macropis nuda*, which is tiny and only about one-tenth of the length of its metasoma (Cane et al. 1983, Figure 1B).

Discussion

Nest architecture

The nest architecture of *R.intermixta* shows some parallels with but also differences from both *Melitta* and *Macropis*, which may shed some light on the evolutionary origin of oil-collecting in melittid bees.

The nest architecture of *R.intermixta* is largely identical with that of *Melitta leporina*, reflecting the sister-group relationship of *Melitta* and *Rediviva* (Michez et al. 2009). However, there are also some notable differences: in *Melitta* the brood cells have a weakly flattened bottom (slightly more round in *R.intermixta*) (Celary 2006), are in a horizontal position or slightly inclined downwards (vertical or slightly tilted in *R.intermixta*), and the cell wall is lined with secretions of the Dufour's gland instead of modified floral oil (Malyshev 1923; Celary 2006). Although direct evidence (i.e. chemical analysis of brood cell lining and Dufour's gland secretion; Cane 1981) is missing it seems reasonable to assume that, like in *Macropis*, floral oil is used for brood cell lining in *Rediviva* given the striking similarity of hind leg morphology and the close phylogenetic relationship of both genera. However, further studies are required to establish this and to clarify the function of the Dufour's gland in *Rediviva*.

The nest architecture of *Macropis* differs considerably in a number of points from that of *R.intermixta* despite the fact that both collect floral oil and seem to use it in much the same way. Nests of *Macropis* are very shallow and brood cells are at most 2–4 cm below the surface (*R.intermixta*: 10–15 cm and deeper), main tunnels are mostly horizontal (*R.intermixta*: vertical), cells are usually arranged in linear series of two, sometimes three to four cells at the end of a lateral tunnel (*R.intermixta*: single brood cell at the end of each lateral), cells are horizontal to tilting about 45 degrees and brood cells have a weakly flattened bottom like in *Melitta leporina* (Malyshev

1929; Rozen and Jacobson 1980; Vogel 1986; Celary 2004). In both, *Macropis* and *Rediviva*, side tunnels are soil-filled after cell provisioning has finished.

The brood cell lining of *Macropis* was described in great detail by Rozen and Jacobson (1980) for *Macropis nuda* and for *Macropis fulvipes* by Malyshev (1929) and Vogel (1986). Although both *Macropis* and *Rediviva* use chemically modified floral oil for brood cell lining there are some differences in the texture. For *Macropis* the inner surface of the lining is described as ‘slightly rugose’ (Malyshev 1929, p. 101), ‘little rough’ (Celary 2004, p. 84) or ‘uneven’ (Rozen and Jacobson 1980, p. 3) while it is almost completely smooth in *Rediviva* even when viewed under the scanning electron microscope (Figure 2A–D). Rozen and Jacobson (1980) and Vogel (1986) both describe the brood cell wall as about 1 mm thick and penetrating the soil surrounding the cell while the inner lining consisting of the pure waxy material was 50 µm thick (Vogel 1986). In contrast, in *R. intermixta* brood cells the waxy material was only found to be a thin 10-µm layer applied to the surface of compacted soil and not penetrating it (Figure 2D). Further, occasionally, *Lysimachia* pollen and fragments of the bees’ pilosity were found in *Macropis* cell lining (Vogel 1986) whereas this was not the case in *R. intermixta*. These discrepancies suggest that the actual process of lining the cell and the mechanism and speed of floral oil solidification might be quite different in both genera although the morphology of female hind legs supposedly used for cell lining in both *Macropis* (Vogel 1986; Schäffler and Dötterl 2011) and *Rediviva* is largely identical (Kuhlmann 2012a).

Host plants

For the oil-collecting *Rediviva* bees, the situation regarding flower visitation is complex because they need flowers for collecting oil, pollen and nectar. For nectar collection a wide range of different flowers from various families is visited (Whitehead and Steiner 2001), whereas at the study site *R. intermixta* almost exclusively used three species, *Diascia cardiosepala*, *Hemimeris centrodes* and *Hemimeris racemosa*, for floral oil. This observation agrees with data from Whitehead and Steiner (2001), who report that *R. intermixta* collects oil on 14 different species, with *H. racemosa* (55.1%), *H. centrodes* (21.1%) and *D. cardiosepala* (9.1%) being the dominant host plants.

Interestingly, there is little overlap between the plant species used for oil and pollen collecting. Although Scrophulariaceae are a major constituent of *R. intermixta* female scopal pollen loads (Table 1), pollen was rarely collected from oil-producing *Diascia* and *Hemimeris* but instead was mainly from the genus *Nemesia* (93.2% of all Scrophulariaceae pollen). *Nemesia* is closely related to both *Diascia* and *Hemimeris* (all belong to Hemimerideae) but it does not produce floral oil (Oxelman et al. 2005; Datson et al. 2008). Pollen of Scrophulariaceae is collected by a range of bee species from different families but usually it is only a minor component in scopal pollen loads (Kuhlmann and Eardley 2012) even in Melittidae (Michez et al. 2008). A notable exception is *Redivivoides*, a genus derived from *Rediviva* and which has secondarily lost its ability to collect oil, highlighting the close relationship of the two genera (Michez et al. 2009). *Redivivoides* species have been frequently observed on Scrophulariaceae flowers, and they are likely to collect most of their pollen on them (Kuhlmann 2012a).

With respect to floral oil *R.intermixta* and other species of the genus are certainly specialists, relying on a small number of host plants for oil-collecting (Whitehead and Steiner 2001; Pauw 2006; Whitehead et al. 2008). However, based on pollen analysis of female scopal pollen loads, *R.intermixta* was classified as ‘polylectic with a preference for Scrophulariaceae’ (Kuhlmann and Eardley 2012), emphasizing the fact that the level of specialization has to be defined separately for different floral resources (oil, pollen, nectar). A more generalized pollen-collecting habit in *Rediviva* species in general is remarkable given that most species in Melittidae are pollen specialists (Michez et al. 2008).

Dufour’s gland

The dissection of a female *Melitta arrogans* confirms that bees of the genus *Melitta* seem to have a very well developed Dufour’s gland, which is used for brood cell lining, as already observed for *Melitta leporina*, *Melitta haemorrhoidalis* and *Melitta americana* (Tengö and Bergström 1976; Cane 1983; Celary 2006).

The relatively large Dufour’s gland in both *Rediviva* and *Redivivoides* match that of bee genera that use Dufour’s gland secretions for brood cell lining (Lello 1971) and, so, came as a surprise. *Rediviva* collects floral oil that is partly used for lining brood cells so the expectation was for a greatly reduced Dufour’s gland, like in *Macropis* (Cane et al. 1983). *Redivivoides* derived from *Rediviva* and secondarily lost its ability to collect floral oil (Michez et al. 2009) so it was expected that due to its phylogenetic position the Dufour’s gland might also be reduced. Importantly, although bees of the genus *Redivivoides* do not collect floral oil (Kuhlmann 2012a), the details of their nesting biology are not known. As *Rediviva* and *Redivivoides* have Dufour’s glands of similar size but differ with respect to oil-collecting, it remains to be explored if either in both genera the gland has no function with respect to brood cell lining or if it serves a similar function in both genera regarding cell lining, larval food or both. In contrast, the significant differences in size of the Dufour’s gland in *Macropis* and *Rediviva* suggest that the gland serves different functions in these genera, although both collect and seem to use floral oil for brood cell lining in much the same way.

In *Macropis fulvipes*, oil is brushed onto the brood cell wall with the hind leg and afterwards females lick the oily surface (Schäffler and Dötterl 2011). *Lysimachia* floral oil stays liquid for a long time and would be absorbed by the soil without leaving brush marks, so presumably the oil is chemically modified by the bees’ saliva (Vogel 1986; Schäffler and Dötterl 2011). A similar mechanism leading to a solidification of liquid oil into a waxy substance (polymerization?) lining the brood cell wall can be assumed for *Rediviva* as the chemistry of floral oils in *Lysimachia* and *Diascia* is similar (Cane et al. 1983; Dumri et al. 2008). Salivary gland products are probably involved in the polymerization of liquid Dufour’s gland secretions used for cell lining in many bees (Albans et al. 1980); hence, a similar function in oil-collecting bees seems plausible. No observations have been made so far on how *Rediviva* females apply floral oil on the brood cell wall, but given the similarity in brush mark patterns and hind leg morphology, it is presumably done in the same way as in *Macropis*. Chemical modification of the floral oil is also likely to be necessary to make the lining solid in *Rediviva* brood cells, but the mechanism is not clear. As assumed for *Macropis*, it could either be done by applying saliva to the oil (Schäffler and

Dötterl 2011), or secretions of the Dufour's gland may be involved, which would explain why the gland is significantly larger in *Rediviva* than in *Macropis* (Cane et al. 1983). Alternatively, in both *Rediviva* and *Macropis* saliva might be involved in the chemical modification of floral oil, and the larger size of the Dufour's gland in *Rediviva* might point to a role in pheromone production as is known from other bees (Cane 1983; Hefetz 1987).

Conclusions

The data on the nesting biology and Dufour's gland size of *Rediviva* provided here can be used to further explore the evolutionary origin of oil-collecting in melittid bees. The different sizes and presumably functions of Dufour's glands in *Macropis* and *Rediviva* and the differences in nest architecture and brood cell lining support the view that oil-collecting evolved independently in *Macropis* and *Rediviva* as suggested by Michez et al. (2009). Hence, the almost complete congruence of female hind leg morphology and pilosity in both genera (Kuhlmann 2012a) is presumably caused by convergent evolution and does not indicate a close phylogenetic relationship.

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