Convergent evolution of pollen transport mode in two distantly related bee genera (Hymenoptera: Andrenidae and Melittidae)

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Abstract— Purposeful transport of pollen represents a key innovation in the evolution of bees from predatory wasps. Most bees transport pollen on specialized hairs on the hind legs or ventral metasoma in one of three ways: moist, dry, or “glazed,” which combines dry and moist transport. The evolutionary pathway among these three transport modes is unclear, though dry transport has been hypothesized to be ancestral. We address this hypothesis using museum specimens and published records of the bee genera *Perdita* (Andrenidae) and *Hesperapis* (Melittidae), two distantly related groups whose pollen transport modes appear to have converged. Most species in both genera transport moistened pollen; glazed and dry transport are limited to derived clades of specialists on floral hosts in Asteraceae and Onagraceae, with specialization on Asteraceae associated with more elaborate scopal hairs. The associations between transport mode, host plant, and hair type may be due to the sticky pollenkit of asteraceous pollen grains and the viscin threads of Onagraceae pollen, which provide alternates to the binding properties of nectar. These findings suggest that the hypothesis that dry transport is ancestral in bees should be reexamined.

Apoidea / glaze / *Hesperapis* / *Perdita* / scopae

1. INTRODUCTION

Female bees collect pollen at flowers and transport it to the nest where it serves as the primary protein source for their progeny. Although past research has explored the various adaptations of bees to gather pollen (e.g., Thorp 1979; Müller 1996a, b; Müller and Bansac 2004), fewer studies have addressed how pollen is transported to the nest. Although a few bee taxa transport pollen internally in the crop, most transport it either on the ventral metasoma (e.g., most Megachilidae) or, more commonly, on the hind legs (Michener

2007). Transport on the hind legs is facilitated by structural elaborations, mostly of the tibia and basitarsus, to include either hair brushes (scopae) or flattened plates (corbiculae).

Pollen is packed on the hind legs and transported in one of three modes: moistened with nectar or oils (Figure 1a, b), dry (Figure 2c, d), or “glazed,” a combination of dry and moist collection (Figure 1c, d). A glazed pollen load is initially packed dry and is then capped with nectar during the latter part of the foraging trip (Thorp 2000; Eickwort et al. 1986; Norden et al. 1992). Although most bee species transport dry pollen, five of the seven bee families also contain genera with species that transport either moistened or glazed pollen: Andrenidae, Apidae, Halictidae, Melittidae, and Stenotritidae (Malyshev 1936; Houston and Thorp 1984; Westerkamp 1996; Thorp 2000; Michener 2007).

The evolutionary sequence of external pollen transport among the three modes is presently

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Fig. 1 Lateral views of moist and glazed transport. **a** Moist transport of Loasaceae pollen by *Perdita perplexa* Timberlake on simple hairs. **b** Moist transport of Asteraceae pollen by *P. n. sp. 2* aff. *laticincta* on simple hairs. **c** Glazed (25% dry) transport of Asteraceae pollen by *Hesperapis hurdi* Timberlake on branched hairs. **d** Glazed (80% dry) transport of Asteraceae pollen by *P. albonotata* Timberlake on corkscrew-shaped hairs.

unsettled. Traditionally, primitive bees were thought to transport pollen internally in the crop (Malyshev 1936; Jander 1976; Michener et al. 1978; Michener 1979). More recent hypotheses propose that primitive bees transported pollen dry on plumose hairs that covered most of the body (Roberts and Vallespir 1978; Radchenko and Pesenko 1996; Michener 2007). This hypothesis is presumably supported by the branched body hairs and plumose hindleg hairs found on the oldest known bee fossil (~100 Myr), a single male *Melittosphex burmensis* Danforth and Poinar (Danforth and Poinar 2011). Alternatively, others

have hypothesized that plumose hairs originated as an adaptation for temperature and water regulation rather than pollen transport (Engel 2001, Michener 2007). The paucity of bees in the fossil record (Michez et al. 2012) offers little additional help in disentangling the evolution of pollen transport or of hair traits.

Bee genera that contain some species that transport moist pollen and others that transport pollen dry are particularly apt to shed light on the evolutionary sequence of pollen transport modes especially when phylogenies are available for comparison. Two examples are the genera *Perdita*

Fig. 2 Dry transport of Onagraceae pollen. **a** Sparse, simple scopal hairs of *P. pallida* Timberlake. **b** Denser and longer scopal hairs of *Perdita vespertina* Griswold & Miller. **c** Dry transport Onagraceae pollen on *P. pallida*. **d** Closeup of **c** showing viscin threads binding pollen together.

(Andrenidae) and *Hesperapis* (Melittidae) (Timberlake 1954; Stage 1966), which are distantly related (Cardinal and Danforth 2013; Hedtke et al. 2013), yet have several similarities: They are restricted to North America (Michener 2007; Michez et al. 2007), are most diverse in the arid west (Michener 2007), and are comprised almost exclusively of oligoleges, i.e., species which use pollen from a small set of related floral hosts (Linsley 1958; Stage 1966; Eickwort and Ginsberg 1980; Cane et al. 1996; Minckley et al. 2013). A recent partial phylogeny is available for *Perdita* (Danforth 1996) and preliminary ones are available for *Hesperapis* (Stage 1966; Michez et al. 2009).

At present, the incidence of *Perdita* species that transport moist, dry, or glazed pollen loads is unknown. Although many are thought to transport a pollen mass that has been continuously moistened with nectar as it is packed onto the hind tibia (Timberlake 1954; Thorp 1979; Michener 2007; Neff 2008), the genus is large (>630 species, Portman et al. 2016) and the transport modes of only seven species have been studied in detail. Of these, six are moist transporters and one transports glazed pollen (Online Resource 1: Table SI). Species that “glaze” their pollen loads are thought to be confined to one monophyletic section of seven subgenera (Danforth 1996; Timberlake 1954; Michener 2007). The pollen transport mode of most *Hesperapis* (~40 species, Cane et al. 1996) species is also poorly known; only three, all moist-transporters, have been investigated in depth (Online Resource 1: Table SI).

At least two salient factors may influence pollen transport mode: host plant choice, scopal hair morphology and distribution, or an interaction of the two. Thorp (1979) proposed that moist pollen transport would be particularly advantageous to generalist pollen foraging species because moistening facilitates the agglutination of pollen of diverse shapes and sizes (see also Vaissière and Vinson 1994). Paradoxically, however, many of the species that transport moistened pollen are oligolectic (Thorp 1979). In addition, there are many examples of host plant pollen being collected by different bee species that employ contrasting transport modes (e.g., Hurd and Linsley 1975, *Larrea* specialists; Hurd et al. 1980, *Helianthus*

specialists). Since both dry and moist transport are exhibited by diverse generalist and specialist pollen foragers on the same host, it suggests that additional factors such as scopal hair characteristics or evolutionary limitations might be germane.

It has been previously suggested that the structure, density, and distribution of the scopae correspond to pollen properties. The scopal hairs associated with dry transport often reflect the size and ornamentation of the pollen specialized on (Linsley 1958; Thorp 1979). Examples include long simple hairs on bees specialized on Onagraceae (Michener 1944; Linsley et al. 1963; Thorp 1969, 1979); hair brushes of long, simple, curved hairs on bees specialized on Cucurbitaceae (Hurd and Linsley 1964); and dense, finely plumose, or branched scopal hairs on bees specialized on small, spiny Asteraceae pollen (Linsley 1958; Linsley and MacSwain 1958; Moldenke 1979). Alternatively, other studies suggest that the simple scopal hairs of moist transporters are adaptable to holding many pollen types (Roberts and Vallespir 1978; Thorp 1979, 2000; Michener 2007). In *Perdita*, there are clear differences in the structure of the scopal hairs between species that transport moist or glazed pollen; species that transport glazed pollen typically have longer, denser, and more structurally complex scopal hairs (Timberlake 1954; Danforth 1996).

Our objectives here are threefold: (1) expand our knowledge of the distribution of dry, moist, and glazed pollen transport in *Perdita* and *Hesperapis*, (2) determine if pollen transport mode is associated with specialization on particular floral hosts or pollen types, and (3) uncover associations between scopal hair types and pollen transport mode. We then use extant though inchoate phylogenies to derive systematic hypotheses which address the origin and evolution of pollen transport.

2. METHODS

Specimens in the genera *Perdita* and *Hesperapis* were examined from the USDA Pollinating Insect Research Unit (PIRU) collection in Logan, UT and the Entomology Research Museum, University of California, Riverside, CA using a Leica M125 or MZ12 stereomicroscope with a

Techniquip ProLine 80 LED ring light. A subset of specimens was further examined using a Quanta FEG 650 Scanning Electron Microscope to confirm or refine findings on the distribution and morphology of scopal hairs and pollen grains.

Pollen transport mode was classified into three groups: moist (Figure 1a, b, entire pollen load moistened), dry (Figure 2c, d, no moistening detected), or glazed (Figure 1c, d, an initial layer of dry pollen covered by a layer of moistened pollen). In bees that transport glazed pollen, we estimated the proportion of the pollen load on the tibia and basitarsus that was dry. Some species were represented only by specimens with partially filled dry pollen loads, making it impossible to distinguish between dry and glazed transport. These specimens were classified as transporting initially dry pollen.

We categorized scopal hair type by the location of hairs on different areas of the hind legs, hair length, hair morphology, and the presence of pollen in those hairs. Although hair density and length are continuous rather than discrete characters, we were able to confidently place them into discrete categories. Hair density was estimated based on the space between scopal hairs and was classified into three groups: sparse, medium, or dense, based on whether the integument was clearly visible, partially obscured, or fully obscured, respectively. Hair length was classified as short, medium, or long based on whether the hairs were less than $2\times$ the maximum width of the hind tibia, between 2 and $3\times$, or greater than $3\times$, respectively. We also classified the associated pollen-transporting hairs on the anterior face of the hind tibia as either simple, branched, wavy, or corkscrew-shaped (Figure 3).

We used two steps to determine whether pollen in the scopae was moist or dry: a pollen load was deemed moist-packed if it was compact and extended beyond the scopal hairs. To further confirm the moist-packed designation, an insect pin was used to poke the pollen mass. Moistened pollen in museum specimens hardens into an impervious mass that resists “poking,” whereas dry pollen offers no resistance and is readily penetrated. Because pollen in the scopae can be wetted passively when bees are collected in pan traps, malaise traps, or when bees regurgitate nectar in kill jars,

we did not survey specimens with signs of wetting on other parts of the body such as matted hairs.

We surveyed a representative subset of species from every subgenus and major species group of the target genera (Online Resource 2: Table SII). Multiple specimens of each species from varying collection locations and times were surveyed whenever possible (Online Resource 1: Table SI). An attempt was made to survey species that collectively specialize on a wide range of floral hosts. Particular attention was paid to bee groups thought to contain species that transport dry or glazed pollen; these groups had all available species surveyed. Records for four species not represented in the PIRU collection by specimens with pollen were compiled from the literature (Online Resource 1: Table SI).

Floral specialization of *Perdita* and *Hesperapis* species was compiled from various published sources and visitation records in the PIRU database (US NPID 2016; Online Resource, Table SI). Lastly, scopal pollen of representative specimens was compared to pollen on slides prepared from previous studies in Clark County, NV, and Colorado (Tepedino et al. 1999; Griswold et al. 2006). Morphological terminology and taxonomic classification of *Perdita* follow Michener (2007), and taxonomic classification of *Hesperapis* follows Michez et al. (2007) and includes the unnamed species from Stage (1966) and Michener (1981).

3. RESULTS

The vast majority of both *Perdita* and *Hesperapis* species surveyed are oligolectic, specializing on floral hosts in one of 21 and 9 plant families, respectively (Table I). Most species in both genera transported pollen that had been uniformly moistened with nectar (94 of 136 species of *Perdita*; 11 of 17 species of *Hesperapis*). Dry or glazed pollen transport only occurred in species of both genera that specialized on Asteraceae or Onagraceae pollen.

3.1. Glazed or dry pollen transport

Forty-two species of *Perdita* transported either glazed or dry pollen: 24 glazed, 15 dry at least

Fig. 3 Optical and SEM examples of the different hair types. **a** and **b** Simple hairs on moist-transporting *Perdita koebelei* Timberlake. **c** and **d** Branched hairs on *P. asteris* Cockerell. **e** and **f** Wavy hairs on *P. lingualis* Cockerell and *P. albovittata* Cockerell, respectively. **g** and **h** Corkscrew-shaped hairs on *P. moabensis* Timberlake. All SEM scale bars = 50 μ m

initially, and 3 dry (Table I; Online Resource 1: Table SI). Thirty-eight of those 42 species specialize on Asteraceae hosts with the proportion of dry pollen ranging from 25 to 80%. Bees that glaze their pollen loads do not entirely cap the basal layer of dry pollen; instead, moistened pollen is always added at a similar location on the anterior face of the hind tibia and only partially covers the dry pollen (e.g., Figure 1c, d). Of the four species specialized on Onagraceae hosts, three transported dry pollen loads and one transported pollen dry at least initially.

The distribution of glazed and dry pollen transport follows a clear phylogenetic pattern. Although *Perdita* species in at least 11 subgenera and species groups are specialized on Asteraceae pollen (Online Resource 2: Table SII), the species that transport glazed pollen fall into a single monophyletic group of seven subgenera (Online

Resource 2: Fig. S2; Timberlake 1954; Danforth 1996). In contrast, the 18 surveyed species that transported entirely moist Asteraceae pollen are scattered across at least four unrelated subgenera and species groups: subgenus *Pygoperdita* (2) and the species groups *Octomaculata* (9), *Ventralis* (2), and *Zonalis* (5) within subgenus *Perdita* s. s. (Online Resource 2, Table SII). All of the *Perdita* species specialized on Onagraceae are in the single monophyletic subgenus *Xerophasma* (Griswold and Miller 2010).

No *Hesperapis* transported entirely dry pollen: of six species that transported glazed pollen, five specialized on hosts in Asteraceae and one on an Onagraceae host (Table I; Online Resource 1: Table SI). The proportion of dry pollen in glazed loads ranged from 10 to 25% for Asteraceae specialists and 50% for the lone Onagraceae specialist. As with *Perdita*, moist pollen was added by

Table 1. The number of *Perdita* and *Hesperapis* species examined, categorized by host plant family and mode of pollen transport

Host plant family	Transport mode									
	<i>Perdita</i>					<i>Hesperapis</i>				
	M	G	D	DI	SUM	M	G	D	DI	SUM
Amaranthaceae	1				1					
Aquifoliaceae	1				1					
Asparagaceae	1				1					
Asteraceae	18	24		14	56	1	5			6
Boraginaceae	7				7					
Brassicaceae	3				3					
Cleomaceae	2				2					
Euphorbiaceae	7				7					
Fabaceae	11				11	1				1
Fabaceae and/or Zygophyllaceae	1				1	1				1
Hydrophyllaceae						1				1
Lamiaceae	2				2					
Liliaceae	3				3					
Loasaceae	4				4	2				2
Malvaceae	4				4	1				1
Onagraceae			3	1	4		1			1
Papaveraceae	4				4					
Polemoniaceae	3				3	2				2
Polygonaceae	4				4					
Rosaceae	3				3	1				1
Salicaceae	2				2					
Solanaceae	6				6					
Unknown	2				2					
Zygophyllaceae	5				5	1				1
Total	94	24	3	15	136	11	6			17

M moist, *G* glazed, *D* dry, *DI* dry initially

Hesperapis females atop dry pollen only on the anterior face of the hind tibia and did not evenly cap the dry pollen in the scopa.

3.2. Hair types

Pollen transport mode is associated with particular hair types in both *Perdita* and *Hesperapis* (Online Resource 2: Table SII; Figure 3). Ninety-three of 94 *Perdita* species that transport moistened pollen have simple scopal hairs. The exception is

one species in the Sphaeralceae Group which transports Fabaceae pollen on minutely branched hairs. Otherwise, the hairs of the moist-transporting *Perdita* species are remarkably uniform, despite transporting pollen of 20 diverse plant families (Online Resource 2: Table SII). Similarly, all 11 species of *Hesperapis* that transport moistened pollen have simple scopal hairs that appear to act as generalized anchors for masses of agglutinated pollen; these species specialize on collecting pollen from nine disparate plant families.

In both *Perdita* and *Hesperapis*, glazed transport of Asteraceae pollen is associated with denser and longer hairs compared to those that transport moistened pollen (Online Resources: Tables SII, SI). *Perdita* species that transport glazed Asteraceae pollen are also more likely to have diverse scopal hair types, including simple, branched, wavy, or corkscrew-shaped (Figure 3); the most common scopal hair type is wavy (24 species, 3 subgenera), followed by branched (10 species, 2 subgenera), corkscrew-shaped (3 species, 2 subgenera), and simple (1 species) (Table SII). A 2×2 contingency table analysis (Maxwell 1961) of hair type (simple vs. elaborate) by transport mode (moist vs. glazed or dry) for *Perdita* was highly significant ($X^2 = 109.2$, $df = 1$, $P < 0.0001$): moist and simple hairs are highly associated as are elaborate hairs and glazed or dry transport (Online Resource 2: Table SIII). The *Hesperapis* species that transport glazed Asteraceae pollen have either branched (4 species) or simple (1 species) hairs (Table SII).

In both *Perdita* and *Hesperapis*, dry or glazed transport of Onagraceae pollen is associated with simple scopal hairs, although they are sometimes longer and denser than the scopal hairs of species that transport moistened pollen. Of the four surveyed *Perdita* species which are Onagraceae specialists, two have scopal hairs whose type, length, and spacing are similar to moist-transporting *Perdita* species (Figure 2a), although the other two species have longer and denser scopal hairs (Figure 2b).

3.3. Hair distribution

The distribution of pollen-transporting hairs on a bee's hind legs also differs between moist and dry or glazed pollen collectors, with scopal hairs of species that transport moist pollen tending to cover a smaller surface area than species that transport dry or glazed pollen. For example, the scopal hairs of *Perdita* that transport moist pollen are located only on the anterior face of the hind tibia and basitarsus. In contrast, all *Perdita* examined that transport dry or glazed Asteraceae pollen have pollen-transporting hairs that also cover the lateral and posterior face of the hind tibia, the anterior side of the hind femur, and the anterior

face of the hind trochanter (Figure S1_B). The morphology of the scopal hairs on the posterior face of the tibia matches the hairs on the anterior face, but the hairs on the femur and trochanter are always branched, regardless of the hair type on the tibia. Similar to *Perdita*, all four *Hesperapis* species that transport glazed Asteraceae pollen have scopal hairs on the posterior face of the hind tibia, and three also have branched hairs on the femur and trochanter of the hind legs. However, the hairs on the femur and trochanter of those *Hesperapis* are relatively sparse and short compared to *Perdita* and appear to transport only a dusting of pollen, if any. In both *Perdita* and *Hesperapis* species that transport glazed pollen, the expanded scopal hairs on the trochanter, femur, and posterior face of the hind tibia always transport entirely dry pollen; they are never capped with moistened pollen like the scopal hairs on the anterior face of the tibia.

The differences in the distribution of the scopal hairs of bees that collect dry or glazed Onagraceae pollen are relatively minimal compared to those that transport moist pollen. All of the *Perdita* species that transport dry Onagraceae pollen have an expanded distribution of scopal hairs only on the posterior face of the hind tibia. Similarly, the one species of *Hesperapis* that transported moist-capped Onagraceae pollen has simple and sparse scopal hairs on the posterior face of the hind tibia, though they are shorter than the hairs on the anterior face.

4. DISCUSSION

The distantly related bee genera *Perdita* (Andrenidae) and *Hesperapis* (Melittidae) (Cardinal and Danforth 2013; Hedtke et al. 2013) display convergent (Arendt and Reznick 2008) evolutionary patterns of pollen transport. In both genera, most species examined transport completely moistened pollen loads and a minority transport either glazed or dry pollen loads. Those that transport glazed or dry pollen specialize only on floral hosts in the families Asteraceae and Onagraceae, even though *Perdita* and *Hesperapis* contain species that specialize on 21 and 9 plant families, respectively (Table I).

Available evidence suggests that moist pollen transport is ancestral in both genera and that the most probable evolutionary pathway is from moist to glazed or moist to dry. This hypothesis is supported in *Perdita* by the near ubiquity of moist transport in the subfamily Panurginae (Rozen 1967; Michener 2007), of which *Perdita* is a member, and by Danforth's (1996) morphological phylogeny for *Perdita* which shows that glazed and/or dry pollen transport is limited to two derived clades (Online Resource 2: Fig. S2). In addition, subgenera that transport the highest proportion of dry pollen fall in the more derived clades (Danforth 1996). The hypothesis that moist transport is basal in *Hesperapis* is supported by Stage's (1966) inchoate morphological phylogeny as well as the seven species of *Hesperapis* included in the molecular phylogeny of Michez et al. (2009). Both phylogenies have the glazed and dry-transporting species limited to derived clades, with glazed transport of Asteraceae and dry transport of Onagraceae likely arising in separate derived clades in *Perdita*. Overall, the patterns in both genera suggest that they are responding to similar selective pressures.

Evidence also suggests that the evolution of glazed or dry transport in these genera was initiated by a host switch to either Asteraceae or Onagraceae pollen. Host switches to Onagraceae by single clades of *Perdita* (*Xerophasma*) and *Hesperapis* (*Panurgomia*) do not entail modifications of scopal hairs (Table SII). However, for both bee genera, host switches to Asteraceae are associated with modified scopal hairs. In *Perdita*, all but one member of the Asteraceae clade exhibits elaborate scopal hairs (corkscrew-shaped, wavy, or branched) that appear derived (Danforth 1996, Table SII, Figure 3). In contrast, moist transport of Asteraceae pollen occurs in four large, species-rich clades of *Perdita* (subgenus *Pygoperdita* and the *Octomaculata*, *Ventralis*, and *Zonalis* species groups within subgenus *Perdita s.s.*), all of which contain species that specialize on a wide variety of other plant taxa and have simple scopal hairs. The pattern is repeated in *Hesperapis*, with both simple and branched scopal hairs found in Asteraceae specialists, suggesting that more elaborate scopal hairs are recent adaptations for transporting glazed Asteraceae pollen.

The association of Asteraceae or Onagraceae pollen with glazed or dry pollen transport, and more elaborate scopal hairs may be due to the physical properties of the pollen grains, particularly those which may confer an alternative binding mode. Onagraceae pollen in particular has sticky viscin threads that attach the pollen grains together and to the scopal hairs of bees (Linsley 1958; Roberts and Vallespir 1978; Hesse 1981). A similar binding function may be provided by the copious pollenkitt and echinate projections of Asteraceae pollen. Pollen with copious pollenkitt, such as Asteraceae and Malvaceae, is more adhesive than other pollen types and readily attaches passively to foragers in large amounts (Allard 1910; Parker 1981; Buchmann and Shipman 1990; Neff and Simpson 1997; Thorp 2000; Goulson et al. 2005). Pollenkitt's adhesive properties may also be enhanced by pollen sculpturing because spiny or echinate pollen grains can promote adhesion to other pollen grains or other surfaces by increasing the available surface area with which pollenkitt may interact (Roberts and Vallespir 1978; Lin et al. 2013). Pollen spines may also enhance the electrostatic binding potential of pollen (Chaloner 1986; Hesse 2000). Overall, despite being unrelated and dissimilar in morphology, the viscin threads of Onagraceae pollen and the pollenkitt and spines of Asteraceae pollen both provide an alternative to using nectar to bind the pollen grains together and to the scopae.

Although pollen types with spines and copious pollenkitt are effective at attaching to pollinators and to each other, they apparently resist being packed together with nectar by bees. Spines seem to both increase the amount of nectar required to pack individual grains together and decrease the size and stability of the final pollen mass (Vaissière and Vinson 1994). In most instances, moist-transporting bees have difficulty packing, or even reject, pollen types with large spines and copious pollenkitt (Linsley 1960; Stephen et al. 1969; Raine and Chittka 2007; Lunau et al. 2015). In some cases, removing the pollenkitt or bending the spines increases the ability of bees to pack moistened pollen (Lunau et al. 2015). The hypothesis that pollen is kept partially dry primarily for transport purposes is supported by the fact that glazed-transporting *Perdita* whose nesting

biology has been studied (*P. albipennis*, *P. boharti*, *P. coreopsidis*, *P. graenicheri*) still shape the pollen provisions into uniformly moistened spheres but do so in the nest (Danforth 1989; Norden et al. 1992; Parker 1981).

The association of Asteraceae pollen with dry or glazed pollen transport on elaborate scopal hairs is also found in other bee groups. The subfamily Panurginae, which includes *Perdita*, contains multiple genera with some species that transport dry or glazed asteraceous pollen (Rozen 1989; Michener 2007). Examples include the genus *Panurgus*, whose members transport dry Asteraceae pollen on wavy scopal hairs (Münster-Swendsen 1970; Rozen 1971), as well as some species of *Protandrena* and *Pseudopanurgus*, which transport dry or glazed Asteraceae pollen on branched scopal hairs (Rozen 1967; Danforth 1996). Many apid bees that transport dry pollen on elaborate scopal hairs are strongly associated with Asteraceae pollen collection (e.g., *Melissodes*, *Svastra*), especially compared to related groups that transport moistened pollen such as *Eucera* and *Centris* (Moldenke and Neff 1974; *Eucera*: Timberlake 1969; *Centris*: Aguiar et al. 2003; Roubik and Villanueva-Gutiérrez 2009). Specialization on Onagraceae pollen is also commonly associated with bee genera that transport dry pollen such as *Andrena*, *Melissodes*, *Sphcodogastra*, *Megachile*, and *Diadasia* (Thorpe 1979).

Historically, internal or dry pollen transport has been thought to be the ancestral state in bees (Michener 1944; Jander 1976; Roberts and Vallespir 1978; Radchenko and Pesenko 1996; Michener 2007). However, our results best fit a hypothesis of *Perdita* and *Hesperapis* switching from moist to dry or glazed pollen transport due to the adhesive properties of pollen grains. This hypothesis is strengthened by the absence of apparent switches from dry to glazed or dry to moist and suggests a reconsideration of the evolutionary pathway of pollen transport in bees. For example, Melittidae, which is hypothesized to be the most basal bee family (Cardinal and Danforth 2013), contains multiple moist-transporting genera in addition to *Hesperapis*, including *Macropis*, *Melitta*, and *Rediviva* (Malyshev 1936; Cane et al. 1983; Whitehead et al. 1984; Michener

2007; Nilsson and Alves-dos-Santos 2009). The major exception, the genus *Dasypoda*, transports dry pollen on plumose scopal hairs and contains many Asteraceae specialists (Celary 2002; Michener 2007; Michez et al. 2008). The results of our initial investigations suggest that the question of the ancestral state of pollen transport and its evolutionary trajectory be reopened; only additional systematic and behavioral studies will settle this issue.

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Authors' contribution ZP came up with the initial idea for the project. ZP and VT designed the project. ZP gathered the data. ZP and VT wrote the manuscript

Evolution convergente du mode de transport du pollen chez deux genres d'abeilles vaguement apparentés (Hymenoptera: Andrenidae and Melittidae)

Apoidea / *Hesperapis* / *Perdita* / brosse à pollen

Konvergente Evolution einer Pollentransportform in zwei entfernt verwandten Bienengattungen (Hymenoptera: Andrenidae und Melittidae)

Apoidea / *Hesperapis* / *Perdita* / Scopa

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