

Flower associations and nesting of the pollen wasp *Quartinia major* Kohl, 1898 (Hymenoptera, Vespidae, Masarinae) in Morocco

Volker Mauss¹, Andreas Müller², Rainer Prosi³

1 Staatliches Museum für Naturkunde, Abt. Entomologie, Rosenstein 1, D-70191 Stuttgart, Germany

2 ETH Zürich, Institute of Agricultural Sciences, Biocommunication and Entomology, Schmelzbergstraße 9/LFO, CH-8092 Zürich, Switzerland **3** Lerchenstraße 81, D-74564 Crailsheim, Germany

Corresponding author: Volker Mauss (volker.mauss@gmx.de)

Academic editor: J. Neff | Received 9 December 2017 | Accepted 4 January 2018 | Published 26 February 2018

<http://zoobank.org/426192A5-7E3A-46CD-9CDF-48A8FBD63AC5>

Citation: Mauss V, Müller A, Prosi R (2018) Flower associations and nesting of the pollen wasp *Quartinia major* Kohl, 1898 (Hymenoptera, Vespidae, Masarinae) in Morocco. Journal of Hymenoptera Research 62: 15–31. <https://doi.org/10.3897/jhr.62.22879>

Abstract

Females of *Quartinia major* Kohl were observed to visit flowers of *Pulicaria mauritanica* Batt., *Cladanthus arabicus* (L.) Cass. and *Asteriscus graveolens* (Forssk.) Less., (all Asteroideae Asteraceae) at two localities in southern Morocco. Pollen in the provisions of two brood cells was more than 99% *Aster*-type (Asteroideae), indicating broad oligolecty. During pollen uptake from *P. mauritanica*, the females of *Q. major* employed a hitherto undescribed harvesting technique: They used their mouthparts to squeeze pollen from the corolla tubes of early male phase disc florets. Pollen was ingested immediately after it had been extracted. The nest was a multicellular subterranean burrow excavated in friable soil and surmounted by a turret. The nest walls were stabilized with self-generated silk.

Keywords

Palaeartic, Asteroideae, flower visiting behaviour, pollen uptake, oligolecty, nest construction, silk

Introduction

The pollen wasp genus *Quartinia* is comprised of more than 140 species, occurring either in the Afrotropical or the Palaearctic region (Carpenter 2001, 2003, Gess and Gess 2010, Gess 2011a, 2011b, Gusenleitner 2010a, 2010b, 2012a, 2012b, Schmid-Egger 2015). The members of *Quartinia* are small in comparison with other taxa of the Masarinae, ranging from $\pm 2\text{--}7$ mm in length (Richards 1962, Gess 2007, Gess and Gess 2010). Knowledge of the bionomics of the Palaearctic species of *Quartinia* is still very limited and mainly restricted to flower visitation records for fourteen species published by Kohl (1898), Morice (1900), Saunders (1905), Benoist (1929), Bequaert (1940), Popov (1948), Gusenleitner (1973, 1990), Hohmann et al. (1993), and Carpenter (2003). Recently Mauss and Müller (2016) and Mauss and Mauss (2016) investigated in more detail flower visiting, nesting and mating behaviour of two allied *Quartinia* species endemic to the Canary Islands. Both species were found to be polylectic, using pollen from at least two different plant families with very different flower architecture. In contrast, most of the other Palaearctic *Quartinia* species have been recorded from only Asteraceae, suggesting oligolecty, though the actual degree of their pollen specialisation is still unknown. In the same way, Popov (1948) classified *Quartinia shestakovi* Kostylev and two undescribed taxa of *Quartinia* as oligolectic as they were observed to exclusively visit Chenopodiaceae.

Quartinia major was described by Kohl in 1898 based on four specimens collected by Otto Schmiedeknecht in Oran. Since then it has been recorded from several localities in Algeria and Morocco (Richards 1962, Carpenter 2001). The imagines have been observed to visit only flowers of various Asteraceae belonging to the subfamily Asteroideae, namely *Calendula* sp. (Kohl 1998), *Pallenis maritima* (L.) Greuter (Saunders 1905 as *Asteriscus maritimus* Moench) and *Coleostephus myconis* (L.) Rchb. f. (Bequaert 1940 as *Chrysanthemum myconis* L.). Further information about the bionomics of the species was until now lacking.

In the following study data concerning flower associations, flower visiting behaviour and nesting of *Quartinia major* are presented for the first time. A comparison is made with published bionomic characters of other species of the genus.

Material and methods

Investigations were carried out on four days between 13 and 17 April 2017 at two localities in the Anti Atlas in southern Morocco [I Ruderal road side 0.6 km NW Tizourgane, 20 km N Tafraout, 29°53.416'N, 09°00.399'W, 1240 m a.s.l.; II Wadi 2.75 km SW Ifrane Atlas Saghir, 29°12.178'N, 09°30.323'W, 750 m a.s.l.]. Geographic coordinates (WGS 84) were measured using a Garmin GPS 12. Most observations were made at locality I. Dry specimens of *Quartinia major* from both localities were identified using the key by Richards (1962) and compared with the holotype at the Natural History Museum Vienna.

For all documentation of observations the local time (= Greenwich Mean Time) was used. Observations were made with a close-up binocular (Pentax Papilio 8.5×21) and documented by using a Canon EOS 70D camera with a 180 mm macro lens and a 25 mm extension tube (scale more than 1:1, resolution 20 mega pixel) and macro flash-lights. The behaviour at flowers was also recorded and analysed by short video movies taken with a Canon EOS 70D camera with a 100 mm macro lens.

Specimens of all plant species that were visited by pollen wasps were collected and preserved dried. The material was placed in the herbarium of the State Museum of Natural History in Stuttgart (Herbarium STU). The plant taxa were identified following Fennane et al. (1999, 2007); the nomenclature follows the African Plant Database (version 3.4.0). Flower preferences of imagines were studied by counting the number of sightings (= first observations) of flower visiting individuals at the flowering plant species independent of the number of flowers or plants visited by an individual during a single observed foraging incident. Sightings of flower visiting individuals were either counted while walking randomly along flowering plants across the area at locality I (random transect, total investigation time 120 min) or during unsystematic, random observations at localities I and II (total investigation time 360 min). Flower visiting behaviour of *Quartinia major* at *Pulicaria mauritanica* Batt. was observed at various patches of the plant at locality I (point observation, total investigation time 90 min). In addition, various other flowers were randomly scrutinized for visitors in a parallel study on bees (Müller et al. in prep.). Pollen samples from two brood cell provisions from a single nest were prepared using the method outlined by Westrich and Schmidt (1986). The different pollen types were identified under a light microscope at magnifications of times 400 or 1000 and determined to the subfamily level taking genus types into account. For characterizing the degree of host-plant association, the categories defined by Müller and Kuhlmann 2008 (based on Cane and Sipes 2006) were used.

Nests were marked in the field with little ice-cream national flags and named after the country code of the flag used. Female behaviour at the nest was only observed at nest CH for approximately 180 min in total from the discovery of the nest at 12h50 on 14 April until 11h20 on April 15 when the female was collected. The nest GB was already abandoned on its discovery on 13 April. Both nests were excavated on 15 April using a combination of two reading glasses that provided a sufficient magnification. In the field, nest dimensions were measured using a calliper rule (accuracy 0.01 mm). The cells along with their contents were separately stored in small vials in a freezer until they were investigated under a Wild M3 stereomicroscope (maximum magnification times 60) on 7 August 2017.

Results

Habitat

At locality I *Quartinia major* was found on a richly flowering ruderal area along a roadside and on the adjacent broad embankment which changed onto a weakly grazed

stony hillside covered with widely spaced trees, namely *Argania spinosa* (L.) Skeels (Sapotaceae) (Fig. 1). The climate is arid with a mean annual precipitation of 235 mm and a mean annual temperature of 16.6 °C (data from Tafraout, AM ONLINE Project). The vegetation type could be categorized as degraded *Argania spinosa* scrub forest and bushland (sensu White 1983) comprised of at least 13 flowering plants from 9 families, including *Pulicaria mauritanica* and *Cladanthus arabicus* (L.) Cass. from Asteraceae.

At locality II *Quartinia major* inhabited a dry riverbed with adjacent plains and slopes (Fig. 2). The climate is arid with a mean annual precipitation of 170 mm and a mean annual temperature of 17.3 °C (data from Ifrane Atlas-Saghir, AM ONLINE Project). The ground surface was densely strewn with many stones of variable size and sparsely covered with several species of richly flowering dwarf shrubs as well as chamaephytes and therophytes, including *Cladanthus arabicus* and *Asteriscus graveolens* (Forssk.) Less. The vegetation type was Succulent sub-Mediterranean scrubland (sensu White 1983).

Flower associations

At locality I the females of *Quartinia major* were observed to visit only flowers of *Pulicaria mauritanica* and *Cladanthus arabicus*, which were the only plants in flower belonging to the Asteroideae (Table 1). During the random transect investigation 87 % of the sightings were recorded at *P. mauritanica* and 13 % at *C. arabicus* (n= 31 sightings). At locality II females of *Q. major* were recorded exclusively at flowers of *Asteriscus graveolens* (Table 1).

During a flower visit a female of *Quartinia major* would stand on the capitula (»heads«) of the composites with her longitudinal body axis orientated in a more or less radial manner, her head facing outwards (Fig. 3). In this radial position she moved sideways from disc floret to disc floret in a circle around the central axis of the inflorescence (Fig. 3). For nectar uptake a female moved her head downwards and protruded her proboscis into the corolla tube of a disc floret (Figs 9, 10). After a moment she raised her head again, removed and retracted her proboscis from the disc floret, moved her body slightly sideways, starting the whole process again, by inserting her proboscis into the next disc floret.

Pollen collection was observed only at flowers of *Pulicaria mauritanica*. During pollen uptake a female rapidly moved her head and mesosoma characteristically downward and horizontally forward, clasping the base of the corolla tube of a disc floret that had just started flowering with her mandibles. The female would then move her head and mesosoma forward-upwards, thereby pressing pollen out of the corolla tube with her mouthparts (Figs 12, 13a). On several occasions her fore tarsi came into contact with the corolla tube closely below her mandibles in addition. The extruded pollen mass was quickly ingested with the mouthparts, aided by movements of the fore tarsi (Fig. 13b). Pollen would also gradually accumulate on the surface of the head and the mesosoma during nectar or pollen uptake. This was removed from time to time by very fast alternating forward grooming movements of the fore legs (Fig. 14) and eventually brought between the mouthparts where the pollen grains were ingested (Fig. 11).



Figures 1–2. Habitat of *Quartinia major*. **1** Locality I, ruderal road side 20 km to the north of Tafraout, with yellow flowering dwarf shrubs of *Pulicaria mauritanica*. Two nests were found close to the little white flag in the foreground on the left **2** Locality II, wadi 2.75 km to the south-west of Ifrane Atlas Saghir, with yellow flowering plants of *Asteriscus graveolens* that were visited by females of *Q. major*.

Table 1. Sightings of flower visiting females of *Quartinia major* at the flowers of various plant taxa at two localities in Morocco. Sightings were made during random transect investigations, point observations and unsystematically recording.

Plant taxon	Sightings ♀
Asteraceae	
<i>Pulicaria mauritanica</i> Batt.	92
<i>Cladanthus arabicus</i> (L.) Cass.	6
<i>Asteriscus graveolens</i> (Forssk.) Less.	6
other plant taxa	
more than 10 flowering species from 8 families	0

Female brood care

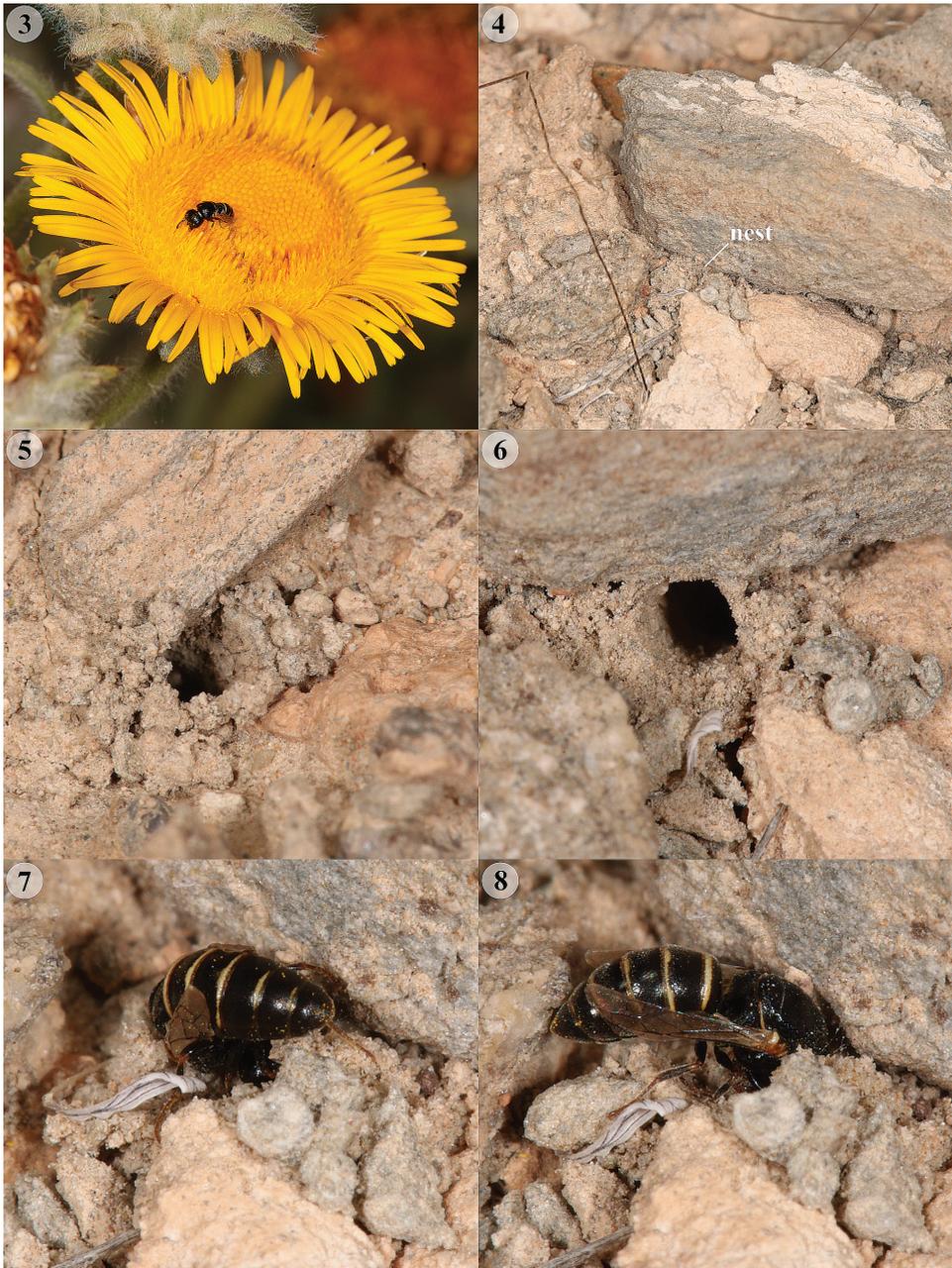
Nest site: Two nests were situated in horizontal ground on a terrace at the upper edge of the embankment (Fig. 1). The ground consisted of gravel mixed with friable soil sparsely covered by plants including *Pulicaria mauritanica* and in a distance of about 20 m also *Cladanthus arabicus*. The distance between the nests was 43 cm, the distance from the nest to the next plant of *P. mauritanica* measured 65 cm in nest CH and 28 cm in nest GB.

Nest structure: The nest consisted of a subterranean burrow with the entrance surmounted by a short oblique turret with an outer diameter of about 4.5 mm (Figs 5, 6). The inner diameter of the turret measured 2.0 mm at its base, which corresponded to the diameter of the shaft, but measured towards the opening was slightly greater in nest CH. The height of the turret varied between 1–2 mm. Both nests had the entrance to one side of a little stone (Figs 4, 15). The burrow of nest GB consisted of a sub-vertical shaft ending blindly at a depth of 10 mm just above a little underground stone (Fig. 15). In nest CH the shaft continued in a slope of about 20 degrees beneath the adjacent little stone, where it turned downwards more sharply and continued at about 75 degrees to the surface till it reached a depth of 20 mm, where it turned again into a more horizontal direction for 3–4 mm. Then the shaft turned obliquely downwards again and continued into an open brood cell with the opening orientated obliquely upwards (Fig. 15, cell No. 1). A second cell was situated at a distance of 18 mm from the shaft (Fig. 15, cell No. 2). The depth of the cells below the ground was 20 mm and 24 mm respectively (Table 2).

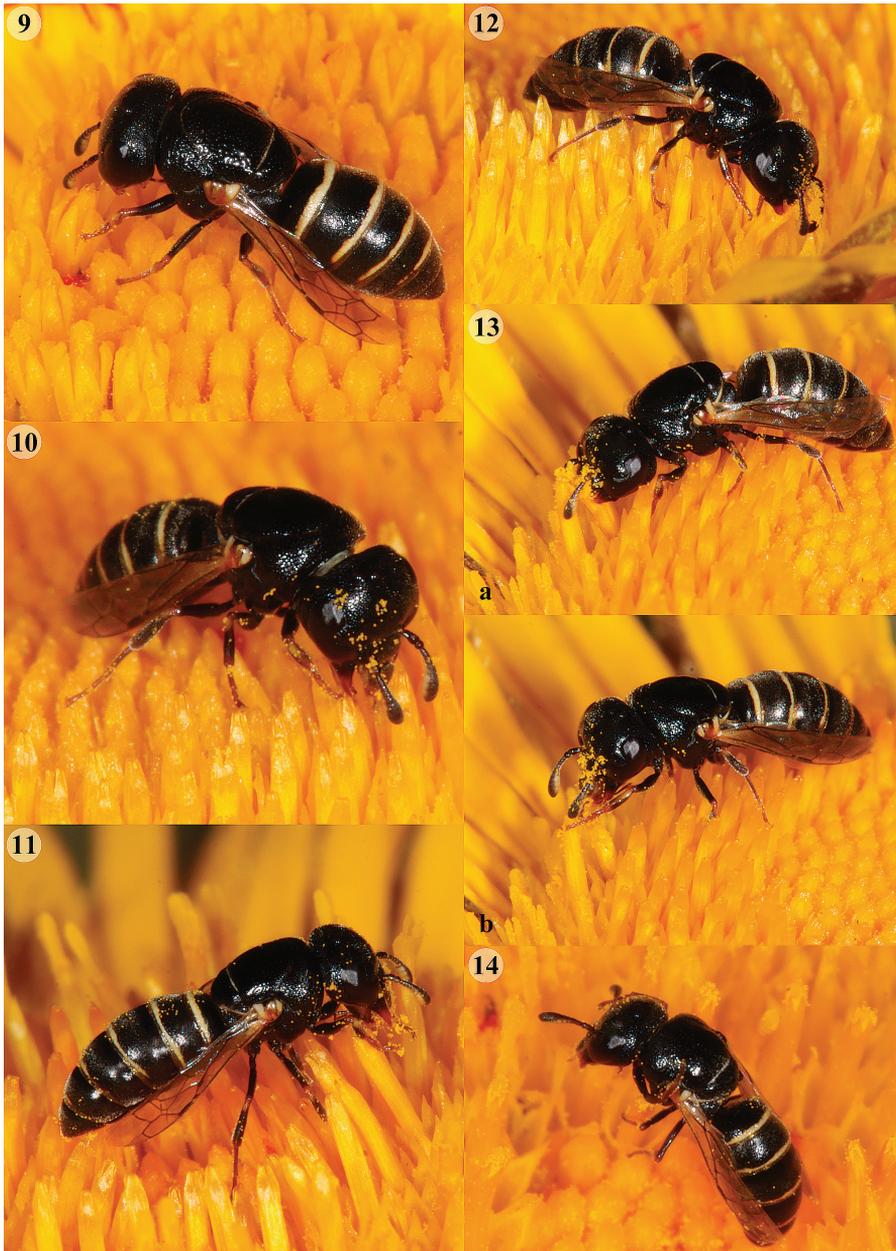
The delicate, non-rigid walls of the turret, the shaft and the brood cells consisted of little particles of the friable soil bonded together with a continuous lining of silk¹. The silken lining of the shaft continued into the lining of the terminal cell.

Brood cell content: The content of the brood cells is summarized in Table 2. The provision consisted of an orange-yellow, moistly shining, rather sticky pollen loaf. The loaf was well separated from the cell wall and had a papillate surface. The provision

¹ The term silk is used in a generic sense in accordance with Gess and Gess 1992, while the chemical constitution of the »silk« filaments is unknown.



Figures 3–8. **3** Female of *Quartinia major* visiting disc florets on a capitulum of *Pulicaria mauritanica*. The proterandric disc florets open from the outer ones inwards. The mouthparts of the female are situated in the zone where disc florets are in an early male phase of anthesis **4** Location of nest CH of *Q. major* at locality I **5** Nest entrance of nest GB (viewed at an angle) **6** Nest entrance of nest CH (viewed from above) **7** Female of nest CH partly backed out of the turret moving slightly around her longitudinal axis with her mouthparts orientated towards the inner surface of the turret wall **8** Female of nest CH backing out of the nest carrying a load of soil particles with her mouthparts (visible between fore and mid femur).



Figures 9–14. Flower visiting behaviour of females of *Quartinia major*. **9** Nectar uptake from disc florets on capitulum of *Asteriscus graveolens* **10** Female with protruded proboscis taking up nectar from disc florets of *Pulicaria mauritanica* **11** Ingestion with the mouthparts of pollen grains that had accumulated on the fore legs **12** Female pressing pollen out of the corolla tube of a disc floret of *P. mauritanica* with her mouthparts, while the pollen grains accumulate above the corolla in front of her head surrounded by her antennae **13** Pollen uptake from disc floret of *P. mauritanica* **a** Female pressing pollen out of the corolla tube **b** female immediately afterwards ingesting pollen supported by her fore legs **14** Female brushing pollen from her exoskeleton with rapid alternating movements of her fore legs.

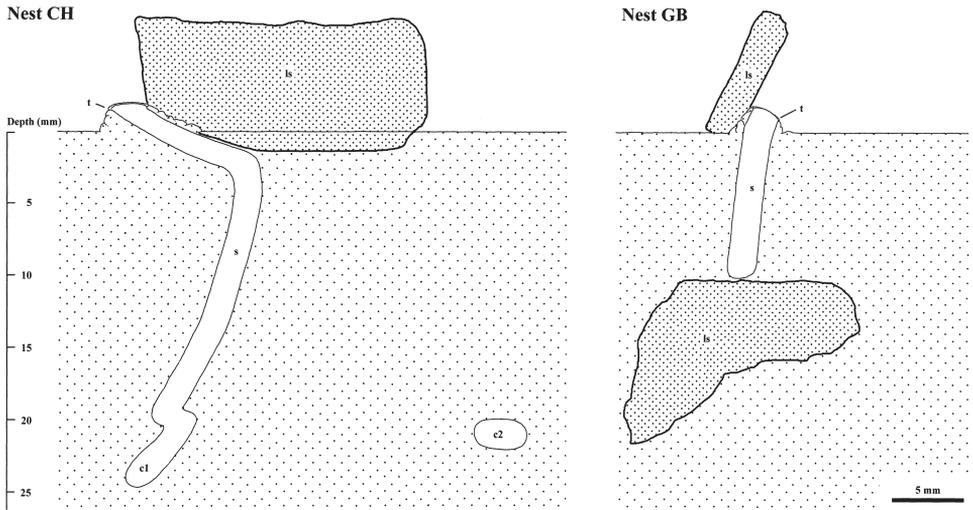


Figure 15. Schematic vertical cross sections of the nest architecture and brood cell arrangement of nest CH and nest GB of *Quartinia major* investigated on 15 April, 2017 at locality I (c = brood cell with cell number, ls = little stone, s = main shaft, t = turret).

Table 2. Details of the brood cells of nest CH of *Quartinia major* investigated on 15 April, 2017 at locality I.

Cell No.	Orientation to the north (°)	Depth below ground surface (mm)	Condition	Content	Pollen composition
1	330	24	open	pollen loaf, egg	Asteraceae Asteroideae, <i>Aster</i> -type: >99% Cichorioideae, <i>Taraxacum</i> -type: single grains
2	?	20	sealed	pollen loaf [egg or larva probably artificially lost, as cell had been damaged during excavation]	Asteraceae Asteroideae, <i>Aster</i> -type: >99% Asteroideae, <i>Anthemis</i> -type: single grains Cichorioideae, <i>Taraxacum</i> -type: single grains

consisted nearly exclusively of pollen of the *Aster*-type of Asteroideae, while pollen of the *Anthemis*-type of Asteroideae and from flowers of Cichorioideae was present only in single grains.

Behaviour at the nest: The female always entered the nest head first and left the nest backwards. At the beginning of a short period of nest building behaviour the female appeared a few times backwards in the nest entrance and remained for a few seconds with her head and parts of her mesosoma inside of the turret moving slightly around her longitudinal axis with her mouthparts orientated towards the inner surface of the turret wall (Fig. 7) before she moved downwards again into the nest shaft. After that the female backed out of the shaft and performed a typical orientation flight with

several ever-widening arcs until she was approximately 50 cm away from the nest entrance, returned straight forward to the nest and re-entered it head first. After a short time she reappeared and backed a bit further out of the turret carrying a load of small soil particles with her mouthparts (Fig. 8). Then she stopped, probably discharged the load and moved rapidly forwards and re-entered the nest head first again. She repeated this process a few times.

On her last return to the nest in the afternoon at 15h57, the female entered the nest directly head first and remained in the nest until the end of the observation period at 16h27. In the morning the female appeared backwards in the nest shaft at 10h09, 18 min after the onset of the nest observation period, backed out of the entrance immediately afterwards and remained for 7 s on the nest with her head above the turret before she flew off. During the following section of the observation period the female was absent from the nest three times probably performing provisioning flights, as indicated by the condition of brood cell No. 1 of the nest that was in the provisioning phase (Table 2). These potential provisioning flights lasted between 13 min and 18 min (median 16 min, $n = 3$).

Activity

The median diurnal activity of the females at flowers lasted for 6.6 h ($n = 2$) with the first activity recorded at 9h55 and the last at 16h36. Males were not observed at any time during the observation period.

Discussion

Flower associations

At both study sites the females of *Quartinia major* were observed to visit only flowers of three different species from three genera of Asteroideae, a subfamily of the Asteraceae. This is in congruence with the flower visiting records published by Kohl (1898), Saunders (1905) and Bequaert (1940) that are also all for members of the Asteroideae. Moreover, the brood cell provisions contained nearly exclusively pollen from flowers of Asteroideae. These findings suggest that *Q. major* is broad oligolectic (sensu Müller and Kuhlmann 2008) with regard to its pollen source, using exclusively pollen of Asteroideae for brood cell provisioning but from more than one genus of Asteroideae. Association with Asteraceae seems to be widespread within *Quartinia* as 79 % of 14 Palaearctic species (Benoist 1929, Bequaert 1940, Carpenter 2003, Gusenleitner 1973, Gusenleitner 1990, Hohmann et al 1993, Morice 1900, Popov 1948, Saunders 1905) and 55 % of 42 Afrotropical species (summarized by Gess and Gess 2010) for which flower-visiting records are available have been recorded from this plant family. In the Palaearctic eight species have been exclusively recorded from Asteraceae. However, *Q. major* is the first Palaearctic species for which oligolecty has been demonstrated by pollen analysis from brood cell provisions. In

the Afrotropical region ten species were exclusively recorded from Asteraceae (cf. Gess and Gess 2010), indicating specialization on this plant family as the single pollen source, even though the oligolectic use of pollen of Asteraceae for brood cell provisioning has been demonstrated solely for *Quartinia vagepunctata* von Schulthess (Gess and Gess 1992).

At locality I the brood cell provisions contained nearly exclusively pollen of the *Aster*-type suggesting that pollen was actively collected only from *Pulicaria mauritanica*. This is also supported by the fact that pollen uptake by females of *Quartinia major* was observed only at this plant. In contrast pollen from *Cladanthus arabicus*, which is of the *Anthemis*-type, was probably only included in the provisions as a result of passive contamination either due to pollen grains adhering to the exoskeleton of the female wasp during nectar visits to *C. arabicus* or due to pollen transfer from disc florets of *C. arabicus* to the capitula of *P. mauritanica* by other flower visitors. A preference for flowers of *P. mauritanica* over flowers of *C. arabicus* by *Q. major* females is also suggested by the results of the random transect walks since more than 85 % of the females were recorded from *Pulicaria*. However, since both investigated brood cells originated from the same nest, the presumed preference for taxa having pollen of the *Aster*-type over taxa possessing pollen of the *Anthemis*-type should be confirmed with larger sample sizes.

The distinct technique of *Quartinia major* females during pollen uptake from disc florets of *Pulicaria mauritanica* has not been reported before for any other pollen wasp or bee species. Other *Quartinia* species ingest pollen either directly from the anthers or they brush pollen with their fore legs from the anthers or the body surface towards the mouth where it is ingested (Gess 1996, Gess and Gess 2010, Mauss and Müller 2016, Mauss and Mauss 2016). Squeezing out pollen from the corolla of disc florets in the early male phase with the mouthparts probably enables the females of *Q. major* to remove the pollen efficiently before it becomes available for other flower visitors. In this context it is of note that during cell provisioning, probable combined pollen and nectar collection flights of the female of *Q. major* from nest CH lasted for only 16 min in the median which is at the lower end of the range observed for some other pollen wasp species (17.3 min in *Celonites abbreviatus* (Villers), Bellmann 1984; 41.9 min in *Celonites fischeri* Spinola, Mauss and Müller 2014; 31.5 min in *Pseudomasaris phaceliae* Rohwer, Neff and Hook 2007; 31.3 min in *Pseudomasaris edwardsii* (Cresson) Torchio 1970). The comparatively short duration of the potential provisioning flights of *Q. major* may be associated with the derived technique of pollen uptake in this species. This is supported by the fact that *C. abbreviatus*, that also performs comparatively short provisioning trips (cf. Bellmann 1984), also uses a highly derived method for pollen uptake (Schremmer 1959, Bellmann 1984, Müller 1996, Mauss 2006).

Female brood care

Quartinia major was found nesting in friable soil close to its main forage plant. This is similar to the nesting situation in *Quartinia canariensis* Blüthgen (Mauss and Müller 2016), the Afrotropical *Quartinia vagepunctata* (Gess and Gess 1992), nesting in a metre

square area clear of plants that was surrounded by the forage plants, and *Quartinia poecila* von Schulthess (Gess and Gess 2010), nesting on the mound formed around the forage plant, a situation suspected by Gess and Gess (2010) to be common to some other Afrotropical species of *Quartinia*. Each nest of *Q. major* had its entrance to one side of a little stone, slightly embedded in the substrate, offering some protection to and a somewhat stable substrate for the burrow descending beneath it and which is identical with the nest location next to a stone or an earth clod, recorded for *Q. vagepunctata* (Gess and Gess 1992) whereas the nests of other species were found on bare ground (Gess 2009, Gess and Gess 2010, Mauss and Müller 2016) and those of seven species in sand-filled snail shells (Gess and Gess 1999, Gess and Gess 2008).

The walls of the burrow and the newly provisioned cells of *Quartinia major* were non-rigid soil particle and silk structures with a silk lining, the silk being produced by the nest building female. This character occurs in all *Quartinia* species for which nesting is known (Gess and Gess 1992, 1999, Gess and Gess 2010, Mauss and Müller 2016) and is unique among the Masarinae (Gess and Gess 1992, Mauss 2007). Therefore it can be regarded as an outstanding apomorphic trait of *Quartinia* that enabled the members of the stem-line of *Quartinia* to inhabit ecosystems with friable, sandy soil (Mauss and Müller 2016).

A short more or less vertical turret surmounting the nest entrance as in *Quartinia major* is also present in nests of *Q. canariensis* (Mauss and Müller 2016) and most Afrotropical *Quartinia* species (Gess and Gess 2010). The existence of a turret at the nest entrance is probably a plesiomorphic trait of *Quartinia* adopted from the ground pattern of the Masarinae (Mauss 2007). A probably derived turret form exists in *Q. vagepunctata* that builds a horizontal, bag-like turret (Gess and Gess 1992).

As in *Quartinia canariensis* (Mauss and Müller 2016) there is no evidence that females of *Q. major* are able to turn inside the nest, as the focally observed female always entered the nest head first and reappeared backwards. This was also the case in the earliest observed appearance in the morning and on the last return to the nest in the evening. Therefore females of *Q. major* probably spend the night in the burrow head downwards. This is in contrast to the behaviour of females of *Q. canariensis* that spend the night inside the nest with their head orientated upwards towards the nest entrance, so that they appear head first in the morning (Mauss and Müller 2016). This is the result of a characteristic behaviour of the females of *Q. canariensis* that reappear backwards in the nest entrance after the last return to the nest in the afternoon, back out a few steps from the nest entrance, move forward on top of the turret and re-enter the nest metasoma first with the dorsal side orientated downwards (Mauss and Müller 2016). This distinct behaviour seems to be absent in *Q. major*.

The nest of *Quartinia major* consisted of a subterranean burrow terminated by a cell, which is principally similar to the nest architecture of *Q. vagepunctata* (Gess and Gess 1992) and *Q. canariensis* (Mauss and Müller 2016). The depths of the brood cells of *Q. major* below the ground surface were also within the range of these species measuring 20–24 mm in *Q. major*, 25–30 mm in *Q. vagepunctata* (Gess and Gess 1992) and 15–23 mm in *Q. canariensis* (Mauss and Müller 2016). Like the nest of

Q. canariensis (Mauss and Müller 2016) the nest CH of *Q. major* is believed to have been multicellular and this was also suggested for nests of *Q. vagepunctata* (Gess and Gess 1992). Moreover, in all *Quartinia* species nesting in snail shells the nest is multicellular with up to 20 or even more cells (Gess and Gess 2010). The distant and isolated position of cell No. 2 in nest CH of *Q. major* is remarkable and resembles the situation in the nest of *Q. canariensis* (Mauss and Müller 2016). The isolated position of the sealed cell No. 2 demonstrates that it was excavated and provisioned by the female previous to the cell No. 1. As in the nest of *Q. canariensis* a connection from this isolated cell to the main shaft was no longer perceptible during nest excavation, indicating that it had been built at the end of a separate long secondary shaft that was either filled with soil by the female or that just collapsed after the brood cell had been sealed.

During nest excavation the female of *Quartinia major* backed out of the shaft carrying soil particles with her mouthparts, which is similar to the behaviour of *Q. canariensis* (Mauss and Müller 2016) and all other primarily ground nesting masarine wasps (cf. Gess 1996, Gess and Gess 2010, Mauss 2007). Therefore, these elements of the behaviour are probably plesiomorphic. As in other species of *Quartinia* (Gess and Gess 1992, Gess and Gess 2010, Mauss and Müller 2016) no observable liquid was used by *Q. major* during nest excavation.

Acknowledgements

Annette Rosenbauer kindly identified the collected plants. Dominique Zimmermann made it possible to study the type of *Quartinia major*. Jim Carpenter, Alexander Fateryyga and Jack Neff carefully revised the manuscript and made valuable suggestions. Moreover, Jack Neff was kind enough to improve our English.

References

- African Plant Database (2017) African Plant Database (version 3.4.0) – Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute, Pretoria. <http://www.ville-ge.ch/musinfo/bd/cjb/africa/> [retrieved October 2017]
- AM ONLINE Project (2017) AM ONLINE Project. <https://climate-data.org> [retrieved 2 October 2017]
- Bellmann H (1984) Beobachtungen zum Brutverhalten von *Celonites abbreviatus* Villers (Hymenoptera, Masaridae). *Zoologischer Anzeiger* 212: 321–328.
- Benoist R (1929) Les *Quartinia* (Hymen. Vespidae) de la région méditerranéenne. *Bulletin de la Société des Sciences Naturelles du Maroc* 9: 92–95.
- Bequaert J (1940) Notes on the distribution of *Pseudomasaris* and the food plants of Masariinae and Gayellinae (Hymenoptera Vespidae). *Bulletin of the Brooklyn Entomological Society* 35: 37–45.

- Cane JH, Sipes S (2006) Characterizing floral specialization by bees: analytical methods and a revised lexicon for oligolecty. In: Waser NM, Ollerton J (Eds) Plant-pollinator interactions from specialization to generalization. University of Chicago Press, Chicago, 99–122.
- Carpenter JM (2001) Checklist of species of the subfamily Masarinae (Hymenoptera: Vespidae). American Museum Novitates 3325: 1–40. [https://doi.org/10.1206/0003-0082\(2001\)325<0001:COOTS>2.0.CO;2](https://doi.org/10.1206/0003-0082(2001)325<0001:COOTS>2.0.CO;2)
- Carpenter JM (2003) A new species of pollen wasp from Egypt (Hymenoptera: Vespidae: Masarinae). Journal of the Kansas Entomological Society 76: 143–146.
- Fennane M, Ibn Tattou M, Mathez J, Ouyahya A, El Oualidi J (1999) Flore Pratique du Maroc: Manuel de Détermination des Plantes Vasculaires. Vol. 1 Pteridophyta, Gymnospermae, Angiospermae (Lauraceae – Neuradaceae). Travaux de l'Institut Scientifique Série Botanique 36: 1–560.
- Fennane M, Ibn Tattou M, Ouyahya A, El Oualidi J, Mathez J (2007) Flore Pratique du Maroc: Manuel de Détermination des Plantes Vasculaires. Vol. 2 Angiospermae (Leguminosae - Lentibulariaceae). Travaux de l'Institut Scientifique Série Botanique 38: 1–636.
- Gess FW (2007) The genus *Quartinia* Ed. André, 1884 (Hymenoptera: Vespidae: Masarinae) in Southern Africa. Part I. Descriptions of new species with complete venation. Journal of Hymenoptera Research 16: 211–233.
- Gess FW (2009) The genus *Quartinia* Ed. André, 1884 (Hymenoptera: Vespidae: Masarinae) in Southern Africa. Part III. New and little known species with incomplete venation. Journal of Hymenoptera Research 18: 244–281.
- Gess FW (2011a) The genus *Quartinia* Ed. André, 1884 (Hymenoptera: Vespidae: Masarinae) in Southern Africa. Part IV. New and little known species with complete venation. Journal of Hymenoptera Research 21: 1–39. <https://doi.org/10.3897/JHR.21.870>
- Gess FW (2011b) The genus *Quartinia* Ed. André, 1884 (Hymenoptera: Vespidae: Masarinae) in Southern Africa. Part V. New and little known species with incomplete venation. Journal of Hymenoptera Research 22: 29–43. <https://doi.org/10.3897/JHR.22.871>
- Gess FW, Gess SK (1992) Ethology of three Southern African ground nesting Masarinae, two *Celonites* species and a silk-spinning *Quartinia* species, with a discussion of nesting by the subfamily as a whole (Hymenoptera: Vespidae). Journal of Hymenoptera Research 1: 145–155.
- Gess FW, Gess SK (1999) The use by wasps, bees and spiders of shells of *Trigonephrus* Pilsb. (Mollusca: Gasteropoda: Dorcasiidae) in desertic winter-rainfall areas in southern Africa. Journal of Arid Environments 43: 143–153. <https://doi.org/10.1006/jare.1999.0549>
- Gess SK (1996) The pollen wasps – Ecology and natural history of the Masarinae. Harvard University Press, Cambridge Massachusetts, 340 pp. <https://doi.org/10.4159/harvard.9780674281684>
- Gess SK, Gess FW (2008) Patterns of usage of snail shells for nesting by wasps (Vespidae: Masarinae and Eumeninae) and bees (Megachilidae: Megachilinae) in Southern Africa. Journal of Hymenoptera Research: 17: 86–109.
- Gess SK, Gess FW (2010) Pollen wasps and flowers in southern Africa. SANBI Biodiversity Series 18: 1–147. [South African National Biodiversity Institute, Pretoria]
- Gusenleitner J (1973) Über Masaridae aus dem nahen Osten (Vespoidea, Hymenoptera). Bolletino della Museo Civico di Storia Naturale di Venezia 24: 55–69.

- Gusenleitner J (1990) Kurze Mitteilung über Faltenwespen der Insel Lanzarote (Canarische Inseln) (Hymenoptera, Vespoidea, Eumenidae und Masaridae). Linzer biologische Beiträge 22: 561–564.
- Gusenleitner J (2010a) Order Hymenoptera, family Vespidae. Arthropod fauna of the UAE 3: 422–467.
- Gusenleitner J (2010b) Bemerkenswertes über Faltenwespen X (Hymenoptera: Vespidae: Eumeninae, Masarinae). Linzer Biologische Beiträge 42: 1347–1352.
- Gusenleitner J (2012a) Vespidae aus dem Oman und der Union der Arabischen Emirate (Hymenoptera: Vespidae: Eumeninae, Masarinae). Linzer Biologische Beiträge 44: 307–312.
- Gusenleitner J (2012b) Neue Masarinae aus der paläarktischen Region (Hymenoptera: Vespidae: Masarinae). Linzer Biologische Beiträge 44: 319–326.
- Hohmann H, La Roche F, Ortega G, Barquin J (1993) Bienen, Wespen und Ameisen der Kanarischen Inseln (Insecta: Hymenoptera: Aculeata). Veröffentlichungen aus dem Übersee-Museum Bremen Naturwissenschaften (vormals Reihe A) 12: 14–712.
- Kohl FF (1898) Über neue Hymenopteren. Termeszetráji Füzetek 21: 363. [pl. XV figs. 8, 21]
- Mauss V (2006) Observations on flower association and mating behaviour of the pollen wasp species *Celonites abbreviatus* (Villers, 1789) in Greece (Hymenoptera: Vespidae, Masarinae). Journal of Hymenoptera Research 15: 266–269. <https://doi.org/10.3897/jhr.31.4235>
- Mauss V (2007) Evolution verschiedener Lebensformtypen innerhalb basaler Teilgruppen der Faltenwespen (Hymenoptera, Vespidae). Denisia 20: 701–722.
- Mauss V, Mauss H (2016) Field observations of the behaviour of the pollen wasp *Quartinia tenrifina* Richards, 1969 (Hymenoptera, Vespidae, Masarinae) at flowers in Tenerife (Canary Islands, Spain). Linzer biologische Beiträge 48: 1327–1332.
- Mauss V, Müller A (2016) Contribution to the bionomics of the pollen wasp *Quartinia canariensis* Blüthgen, 1958 (Hymenoptera, Vespidae, Masarinae) in Fuerteventura (Canary Islands, Spain). Journal of Hymenoptera Research 50: 1–24. <https://doi.org/10.3897/JHR.50.6870>
- Morice FD (1900) An Excursion to Egypt, Palestine, Asia Minor, etc., in search of Aculeate Hymenoptera. Entomologist's Monthly Magazine 36: 164–172.
- Müller A (1996) Convergent evolution of morphological specializations in Central European bee and honey wasp species as an adaptation to the uptake of pollen from nototribic flowers (Hymenoptera, Apoidea and Masaridae). Biological Journal of the Linnean Society 57: 235–252. <https://doi.org/10.1111/j.1095-8312.1996.tb00311.x>
- Müller A, Kuhlmann M (2008) Pollen hosts of western Palaearctic bees of the genus *Colletes* (Colletidae) - the Asteraceae paradox. Biological Journal of the Linnean Society 95: 719–733. <https://doi.org/10.1111/j.1095-8312.2008.01113.x>
- Neff JL, Hook AW (2007) Multivoltinism and usage of multiple nest substrates in a West Texas sand dune population of *Pseudomasaris phaceliae* Rohwer (Hymenoptera: Vespidae: Masarinae). Journal of Hymenoptera Research 16: 266–276.
- Popov VB (1948) Oligotropism of species of the genus *Quartinia* Grib. (Hymenoptera, Vespoidea). Zoologicheskii Zhurnal 27: 317–328. [7 figs; In Russian]
- Richards OW (1962) A revisional study of the masarid wasps (Hymenoptera, Vespoidea). British Museum (Natural History), London, 294 pp.

- Saunders E (1905) Hymenoptera Aculeata collected in Algeria by the Rev. Alfred Edwin Eaton, M.A., F.E.S. and the Rev. Francis David Morice, M.A., F.E.S. Part II. Diploptera. Transactions of the Entomological Society of London, 399–417.
- Schmid-Egger C (2015) Order Hymenoptera, family Vespidae Subfamily Masarinae. Arthropod fauna of the UAE 6: 1–9.
- Schremmer F (1959) Der bisher unbekannte Pollensammelapparat der Honigwespe *Celoni-tes abbreviatus* Vill. (Vespidae, Masarinae). Zeitschrift für Morphologie und Ökologie der Tiere 48: 424–438. <https://doi.org/10.1007/BF00408580>
- Torchio PF (1970) The ethology of the wasp *Pseudomasaris edwardsii* (Cresson), and a description of its immature forms. Contributions in Science Natural History Museum of Los Angeles County 202: 1–32.
- Westrich P, Schmidt K (1986) Methoden und Anwendungsgebiete der Pollenanalyse bei Wildbienen (Hymenoptera, Apoidea). Linzer biologische Beiträge 18: 341–360.
- White F (1983) The vegetation of Africa. UNESCO, Paris, 356 pp.

Supplementary material 1

***Quartinia major* female nectar uptake from disc flowers on capitulum of *Pulicaria mauritanica* (Asteraceae, Asteroideae) I**

Authors: Volker Mauss, Andreas Müller, Rainer Prosi

Data type: Video file

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.62.22879.suppl1>

Supplementary material 2

***Quartinia major* female nectar uptake from disc flowers on capitulum of *Pulicaria mauritanica* (Asteraceae, Asteroideae) II**

Authors: Volker Mauss, Andreas Müller, Rainer Prosi

Data type: Video file

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.62.22879.suppl2>

Supplementary material 3

***Quartinia major* female indirect pollen uptake from the exoskeleton with brushing movements of the fore legs on capitulum of *Pulicaria mauritanica* (Asteraceae, Asteroideae)**

Authors: Volker Mauss, Andreas Müller, Rainer Prosi

Data type: Video file

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.62.22879.suppl3>

Supplementary material 4

***Quartinia major* female pressing pollen out of the corolla tube of the disc flowers of *Pulicaria mauritanica* (Asteraceae, Asteroidea) with her mouthparts**

Authors: Volker Mauss, Andreas Müller, Rainer Prosi

Data type: Video file

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/jhr.62.22879.suppl4>