JHR 50: 1–24 (2016)
doi: 10.3897/JHR.50.6870
http://jhr.pensoft.net

RESEARCH ARTICLE

JOURNAL OF Hymenoptera RESEARCH
A peer-reviewed open-access journal
The International Society of Hymenopterists

Contribution to the bionomics of the pollen wasp *Quartinia canariensis* Blüthgen, 1958 (Hymenoptera, Vespidae, Masarinae) in Fuerteventura (Canary Islands, Spain)

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Academic editor: *Jack Neff* | Received 12 April 2016 | Accepted 4 June 2016 | Published 27 June 2016

http://zoobank.org/BE03CE00-9AF9-4A1D-8737-DA7529469730

Citation: 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. doi: 10.3897/JHR.50.6870

Abstract

Quartinia canariensis was recorded from three semidesertic sand habitats in Fuerteventura. All localities were sparsely covered by halophytic vegetation and characterized by large patches of flowering plants of *Frankenia laevis* (Frankeniaceae). Males and females were exclusively observed to visit flowers of *Frankenia laevis*. During flower visits the imagines often switched between nectar and pollen uptake. Pollen was consumed directly from the anthers or pollen uptake was indirect with pollen grains gathering on the frons being brushed towards the mouthparts with the fore legs. During nectar uptake the wasps protruded their long proboscis into the nectariferous pockets between the claws of the petals of the *Frankenia* flowers. Brood cell provisions consisted mainly of pollen from *Frankenia* but to a small amount also from *Polycarpaea* (Caryophyllaceae) suggesting that *Quartinia canariensis* is polylectic with strong preference. Males regularly stood on the ground in the vicinity of *Frankenia* plants and frequently performed patrol flights along the flowers. Flower visiting females avoided contact with the males and mainly offered resistance against the insertion of the male genitalia. The behavioural sequence during copulation of a species of *Quartinia* is described for the first time. The nest was a multicellular sub-vertical burrow surmounted by a short turret. The burrow was excavated by the female in friable sandy soil. The walls of the nest were stabilized by silk produced by the nest building female and applied with the mouthparts. Inconsistencies concerning the host-parasite-relationship between *Quartinia canariensis* and *Chrysis atrocomitata* established by Gusenleitner 1990 are discussed.

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Keywords
Palaearctic, flower associations, mating behaviour, nest construction, silk spinning, *Chrysis umbofascialis*

Introduction

The genus *Quartinia* is a monophyletic subtaxon of the Masarinae (Carpenter 1993, Krenn et al. 2002). It has a disjunct distribution with an Afrotropical and a Palaearctic range. Within the Masarinae *Quartinia* is the genus with the highest species diversity (Richards 1962), with 101 described species occurring in the Afrotropical region (Gess and Gess 2010, Gess 2011a, 2011b) and 42 species in the Palaearctic (Carpenter 2001, 2003, Gusenleitner 2010a, 2010b, 2012a, 2012b, Schmid-Egger 2015). *Quartinia* species are on average the smallest of the pollen wasps, ranging from ± 2–7 mm in length (Gess 2007, Gess and Gess 2010) with 80 % of the species measuring less than 5 mm (n = 80 species; female body length taken from Richards 1962). Information about flower visiting, nesting, sleeping and sheltering, mating and associated organisms is mainly available for some Afrotropical species of *Quartinia* that have been studied in detail by Gess (2007, 2008, 2009, 2011a, 2011b), Gess and Gess (1992), Gess (1996) and Gess and Gess (1989, 2003, 2006, 2008, 2010). In contrast, knowledge about the bionomics of the Palaearctic species of *Quartinia* is still very limited and mainly restricted to a small number of occasional flower visiting records relating to ten species published by Morice (1900), Benoist (1929), Bequaert (1940), Popov (1948), Gusenleitner (1973, 1990) and Carpenter (2003). A systematic survey of the flower associations of various aculeate Hymenoptera including three *Quartinia*-species was conducted by Hohmann et al. (1993) for the Canary Islands. Many of the Palaearctic species seem to be associated with members of the Asteraceae, but there are also records from another eight plant families and five species of *Quartinia* were not or rarely recorded from Asteraceae. The degree of specialisation of any Palaearctic *Quartinia* species with regard to its pollen source is unknown.

Quartinia canariensis was described in 1958 by Blüthgen from three females collected by H. Lindberg from Fuerteventura during the Finnish Canary-Expedition. Further material from the Canary Islands, which had been collected by K.M. Guichard between 1964 and 1966, led to the description of the previously unknown male of *Q. canariensis* by Richards (1969) yet again recorded from Fuerteventura. Up to now the species has been found at 23 localities exclusively situated in Fuerteventura and Lanzarote (Gusenleitner 1990, Hohmann et al. 1993), suggesting that it is probably endemic to these two islands of the Canaries. Two closely allied *Quartinia* species occur on neighbouring islands, with *Quartinia guichardi* Richards, 1969 being restricted to Gran Canaria and *Quartinia tenerifina* Richards, 1969 inhabiting Tenerife and La Gomera (Richards 1969, Hohmann et al. 1993).

Published information about the bionomics of *Quartinia canariensis* is very fragmentary. There are several records of males and females having been observed visiting flowers

of *Frankenia laevis* L. (Frankeniaceae) (Gusenleitner 1990, Hohmann et al. 1993), but there are also single flower visiting records from plants belonging to the Asteraceae, Boraginaceae, Caryophyllaceae and Fabaceae (Hohmann et al. 1993). Gusenleitner (1990) established *Q. canariensis* as a host of what he called "*Chrysis atracomitata* LINS." (Chrysididae) without giving any details (for inconsistencies and nomenclatural inaccuracies relating to this host record see below).

In the present study data concerning flower associations, flower visiting behaviour, nesting and mating of *Quartinia canariensis* are recorded for the first time, as an example for a *Quartinia* species from the Palaearctic. A comparison is made with published data on the bionomics of the Afrotropical species of the genus.

Material and methods

Investigations were carried out from 29 March to 5 April 2015 in the vicinity of Costa Calma in Fuerteventura (Canary Islands, Spain). Geographic coordinates (WGS 84) were measured using a Garmin GPS 12. *Quartinia canariensis* was studied at three localities [**I** Montaña Pelada, 2 km SW Costa Calma, eastward exposed slope W of a Barranco SW of the road to Los Gorriones, 28°08.325'N 14°14.999'W, 55 m a.s.l.; **II** SW Costa Calma between "Playa Esmeralda" and "Playa Paraíso" 28°08.677'N 14°14.368'W, 60 m a.s.l.; **III** Istmo de la Pared, 0.5 km NW Costa Calma 28°10.202'N 14°14.396'W, 90 m a.s.l.]. Most observations were made at locality I.

For all documentations of observations the local time (= Greenwich Mean Time + 1h) was used. Sunrise was approximately at 7h45, sun's zenith at 14h00 and sunset at 20h15. Time intervals were measured using a digital stop-watch. Observations were made with a close-up binocular (Pentax Papilio 8.5x21) 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. In addition, in the course of one investigation interval during nest observations, the system was combined with a close-up lens (4 dioptre).

Specimens of all plant species flowering at locality I were collected and preserved dried. The material was placed in the herbarium of the Staatliches Museum für Naturkunde Stuttgart (Herbarium STU). The plant taxa were identified following Hohenester and Welss (1993). Flower preferences of imagines were studied by counting the number of sightings (= first observations) of flower visiting individuals while walking randomly across the area at localities I and III (total investigation time 9.5 h). Flower visiting behaviour of *Q. canariensis* at *Frankenia laevis* was investigated at various patches of this plant at locality I for 7 h in total. In addition, various other flowers were randomly scrutinized for visitors in a parallel study on *Hoplitis zandeni* (Teunissen and van Achterberg 1992) (Müller and Mauss in press). Pollen samples from five 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 genus level with the aid of a reference collection consisting of pollen samples of 500 mainly Mediterranean plant species and pollen samples from the collected plants. For characterizing different degrees of host-plant association among pollen wasp species, the categories defined by Müller and Kuhlmann 2008 (based on Cane and Sipes 2006) were used.

Activity and behaviour of the female of nest No.1 were observed on 6 days in the morning and in the afternoon for 18.75 h in total always including the onset and ending of the diurnal activity period. The nest was excavated on 5 April using a combination of two reading glasses that provided a sufficient magnification. In the field, nest dimensions were measured using a strip of millimetre paper (accuracy 1 mm). The cells with their content were separately stored in Eppendorf vials in a freezer until they were finally investigated under a Wild M3 stereomicroscope (maximum magnification times 60) on 6 August 2015. Micro-photos were taken with a Leica IC 80 HD camera mounted on a Leica MS 5 stereomicroscope (magnification times 80).

Results

Habitat

Quartinia canariensis inhabited semidesertic areas on sandy ground sparsely covered by halophytic vegetation with scattered shrubs of *Salsola divaricata* Masson ex Link in Buch (Amaranthaceae), *Launaea arborescens* (Batt.) Murb. (Asteraceae) and *Zygophyllum fontanesii* Webb & Berthel. (Zygophyllaceae) (Fig. 1). All localities were characterized by large patches of flowering plants of *Frankenia laevis*. Altogether at least 14 plant species were in flower at the study sites [Asteraceae: *Reichardia tingitana* (L.) Roth., *Asteraceae spec.*; Boraginaceae: *Heliotropium erosum* Lehm.; Caryophyllaceae: *Polycarpaea divaricata* (Aiton) Poir. ex Steud.; Cistaceae: *Helianthemum canariense* (Jacq.) Pers.; Convolvulaceae: *Cuscuta planiflora* Ten.; Fabaceae: *Astragalus hamosus* L., *Lotus glaucus* Sol., *L. glinoides* Delile, *L. lancerottensis* Webb and Berth., *Ononis natrix* L.; Frankeniaceae: *Frankenia laevis* L.; Resedaceae: *Reseda lancerotae* Webb and Berth. ex Delile; Scrophulariaceae: *Kickxia sagittata* (Poir.) Rothm]. Noteworthy abiotic factors were the nearly continuous, fresh and often cool northerly wind that led to a permanent sand movement and the only moderate air temperatures that rose only slightly above 20 °C during the diurnal flight period of *Q. canariensis*. A single nest (nest No. 1) was located at locality I on a slope exposed towards the south-east with an inclination of 10°. The nesting site was a sparsely covered area situated in the centre of a patch of 21 small to medium-sized *Frankenia* plants 1.2 m to the SSW of a *Salsola* shrub (Fig. 4). The nest was 2 cm away from a little dry stem of an annual plant jutting obliquely above the entrance. The soil was sandy and friable but relatively stable. Although a vast number of empty and sand filled snail shells was inspected, no nests of *Quartinia canariensis* were found in the shells.



Figures 1–5. 1 Habitat of *Quartinia canariensis* at locality III Istmo de la Pared, 0.5 km northwest of Costa Calma, Fuerteventura **2** Female of *Quartinia canariensis* resting on the ground near plant of *Frankenia* **3** Male of *Quartinia canariensis* standing on the ground close to *Frankenia* dwarf shrub **4** Nesting site at locality I Montaña Pelada. **5** Male resting in partly sand filled shell of the snail *Theba geminata*.

Flower associations

During random searching for flower visitation by *Q. canariensis* 15 sightings of flower visiting females, 2 sightings of flower visiting males as well as the sighting of 1 individual of unidentified sex of *Q. canariensis* were exclusively recorded at *Frankenia laevis*. Likewise, sightings of 41 females, 5 males and 7 individuals of unidentified sex were recorded during point observations at flowers of *F. laevis*. Visits to flowers of other plant species were not observed. In addition, males and females of *Quartinia canariensis* were often observed standing on the ground close to *Frankenia* plants (Figs 2, 3).

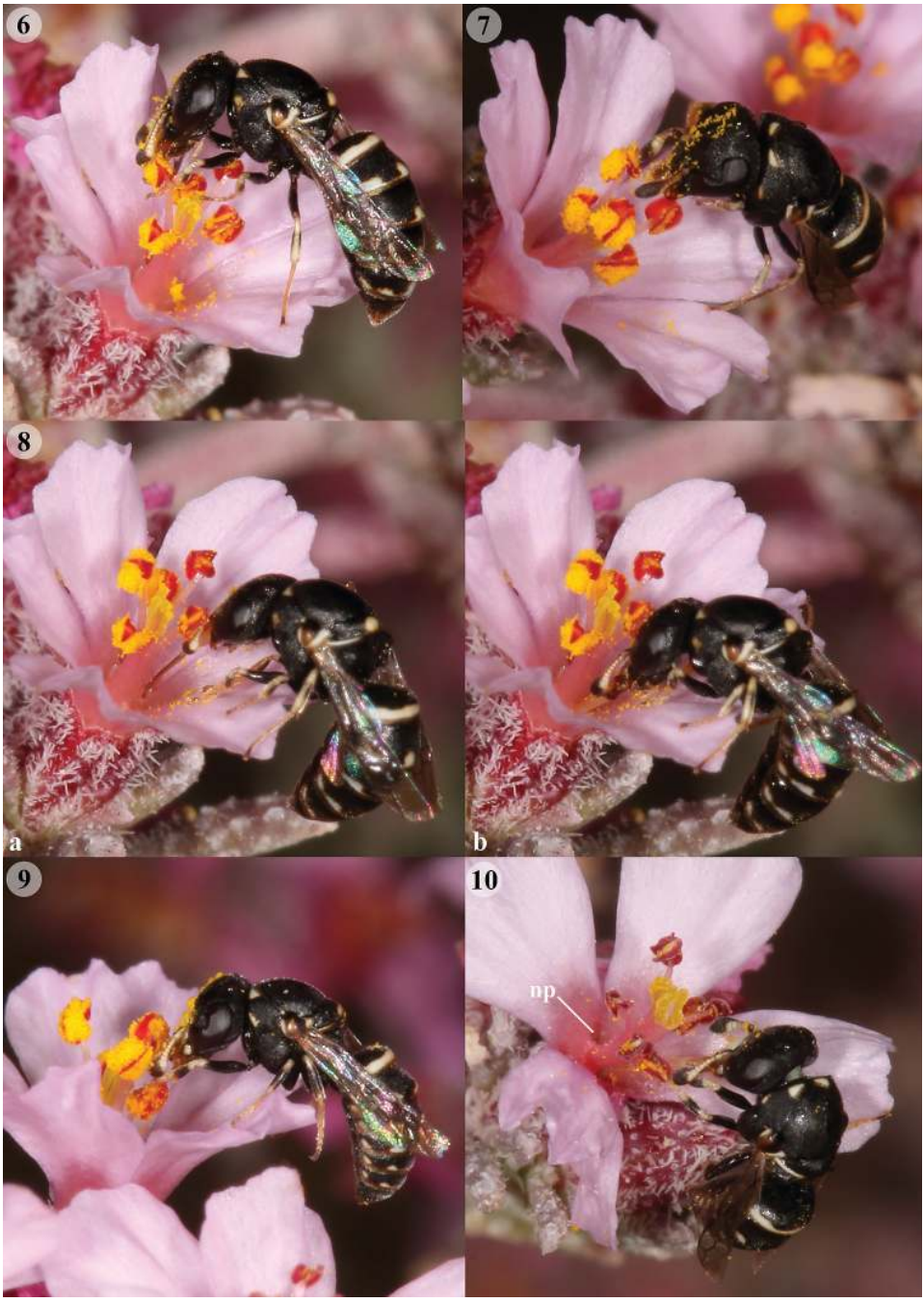
During pollen uptake at flowers of *Frankenia laevis* the females of *Quartinia canariensis* stood on the petals and occasionally also on parts of the androecium or gynoecium with their hind and mid legs, while the head was orientated towards the anthers (Fig. 6). Pollen was directly removed from the anthers through manipulation with the mandibles, and probably also the maxillae, and ingested (Fig. 6). This was repeatedly accompanied by brushing movements of the fore tarsi from the anthers towards the mouthparts (Fig. 9). In addition, the females performed indirect pollen uptake, when pollen accumulated on their frons as a result of contacts with the anthers during nectar uptake (Fig. 8b). In this case, the females remained for a short while on the margin of the corolla brushing pollen grains from the frons to the mouthparts by alternating movements of their fore legs (Fig. 7). To reach the nectar the females protruded their long proboscis down into the corolla tube (Fig. 8a) and moved their head deep down between the stamina and the wall of the corolla (Fig. 8b) indicating that the tip of the proboscis was probably pushed into the nectariferous pockets between the claws of the petals (Fig. 10). These nectariferous pockets are formed by the prominent and inwards projecting nectar scales on the adaxial sides of two adjacent claws each dividing the floral tube into five chambers (Brochmann et al. 1995, Kubitzki 2003, Fig. 10). During a visit to a particular flower the females often switched from pollen gathering to nectar uptake, or vice versa, or nectar uptake took place between two longer phases of pollen feeding.

The behaviour of the males during pollen gathering (Fig. 9) and nectar uptake (Fig. 10) from flowers of *Frankenia laevis* was similar to that of the females.

The pollen composition of the brood cell provisions of *Quartinia canariensis* is summarized in Table 1.

Mating

Males of *Quartinia canariensis* frequently stood on the ground close to flowering patches of *Frankenia laevis* (Fig. 3). They repeatedly took off from the ground and patrolled along the *Frankenia* plants in a rather rapid irregular flight closely above the flowers with several abrupt changes in direction before they alighted on the ground again. Whilst on the ground the males adopted a characteristic posture with their antennae raised and spread at an angle of approximately 45° to the longitudinal axis and their wings longitu-



Figures 6–10. Flower visiting behaviour of *Quartinia canariensis* at flowers of *Frankenia laevis*: **6** Female feeding on pollen directly from the anthers **7** Female brushing pollen from her frons with alternating movements of her fore legs **8** Nectar uptake by female: **a** Proboscis protruded into corolla **b** Head and proboscis pushed deeper down into corolla tube **9** Male feeding on pollen directly from the anthers **10** Male with protruded proboscis taking up nectar (np = nectariferous pocket).

Table 1. Details of the brood cells of nest No.1 of *Quartinia canariensis* investigated on 5 April, 2015 at locality I.

Cell No.	Orientation to the north (°)	Depth below ground surface (mm)	Condition	Content	Pollen composition
1	250	20	?	pollen loaf [egg or larva probably artificially lost, as cell had been damaged during excavation]	*Frankenia* >99%
2	340	20	?	egg at distal end of cell beyond pollen loaf	*Frankenia* 95%, *Polycarpaea* 5%
3	70/250	20	sealed	large larva, pollen loaf	*Frankenia* >99%
4	110/290	15	sealed	small larva, pollen loaf	*Frankenia* 80%, *Polycarpaea* 20%
5	70/250	23	sealed	large larva, small remnants of pollen loaf	*Frankenia* >99%

dinally folded (Fig. 3). Flower visiting females of *Q. canariensis* left the *Frankenia* plants immediately whenever they recognized the arrival of a patrolling male.

The behavioural sequence during copulation was subdivided into three phases: 1. initiation, 2. insertion, 3. separation. Initiation always started by a flying male pouncing on a female that was visiting flowers or resting on the ground. The male always alighted on the back of the female and managed to hold on and to orientate his longitudinal axis parallel to hers. Finally, the head of the male was situated above the mesonotum of the female, level with her tegulae. His antennae were orientated straight anterior-downwards. The fore legs of the male were placed on the female's tegulae or on adjacent parts of her mesonotum or metanotum and his mid and hind legs were wrapped around her wings and her metasoma (Figs 11, 15a). In this stage of the initiation the female offered successful resistance in 30 out of 31 observed copulation attempts. Characteristic behaviours of female resistance were raising of the fore, mid or hind legs above the body (Figs 11b–c, 13) and bending of the metasoma in an anterior-ventral direction to preclude the male from inserting his genitalia (Figs 11b, 12, 13). Antagonistic interactions between the male and the female were observed to continue for up to 121 s (median 28 s; n = 16). During this time, periods in which the male was just calmly holding on to the back of the female (Fig. 11a, c) alternated several times with periods of intensive "grappling", during which the male protruded his genitalia accompanied by vigorous wing vibrations (Fig. 12) and the pair often fell to one side (Figs 11b, 13). When initiation did not release insertion behaviour, both individuals finally detached from each other and flew off. The behavioural sequence of the single complete copulation observed is summarized in Table 2 and Fig. 15a–f.

Male-male interactions were only rarely observed: Twice a patrolling male was observed approaching and pouncing on a male that was on the ground. On both occasions this led to a short interaction before both males flew off. Furthermore, there



Figures 11–14. Initiation phase of copulation of *Quartinia canariensis*: **11a** Calm position of a male on the back of a female after mounting **b** Male trying to accomplish insertion of his genitalia while the female raises her fore legs and bends her metasoma anterior-ventrad. **c** Female raising hind leg against the male **12** Male vibrating vigorously with his wings during "grappling" between the partners while the female is bending her metasoma strongly anterior-ventrad **13** Female is raising her mid and hind legs against the male and bending her metasoma anterior-ventrad **14** Second male holding on to mounting male of a pair after alighting on his back.



Figure 15. Behavioural sequence of a complete copulation of *Quartinia canariensis* on a flower of *Frankenia laevis* (for details see Table 2).

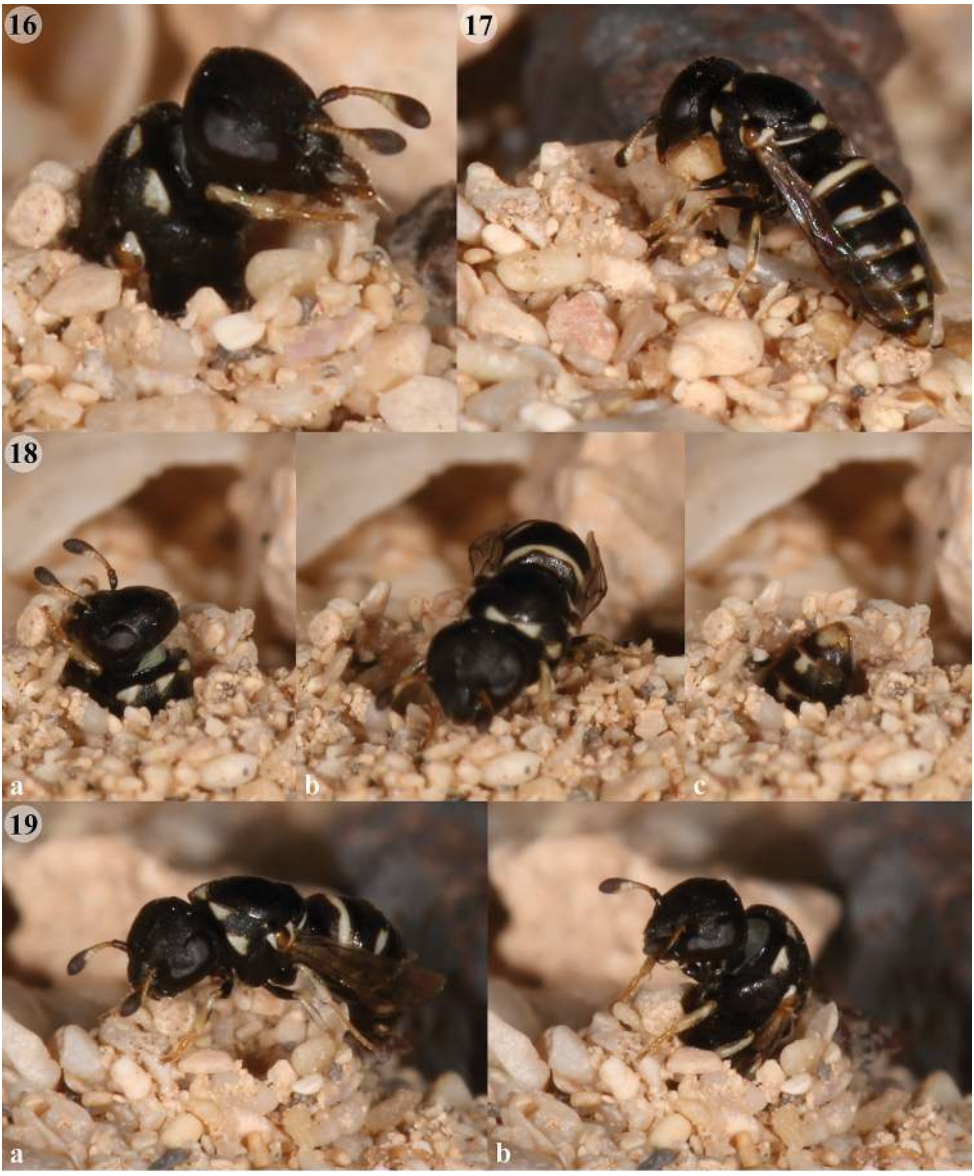
are two observations of a second male alighting on a male that had already mounted a female and was holding on to her back (Fig. 14). In both cases the second male left the pair shortly thereafter and the first male remained on the female.

Table 2. Behavioural sequence of the copulation of *Quartinia canariensis* (reconstructed from a series of 16 photos).

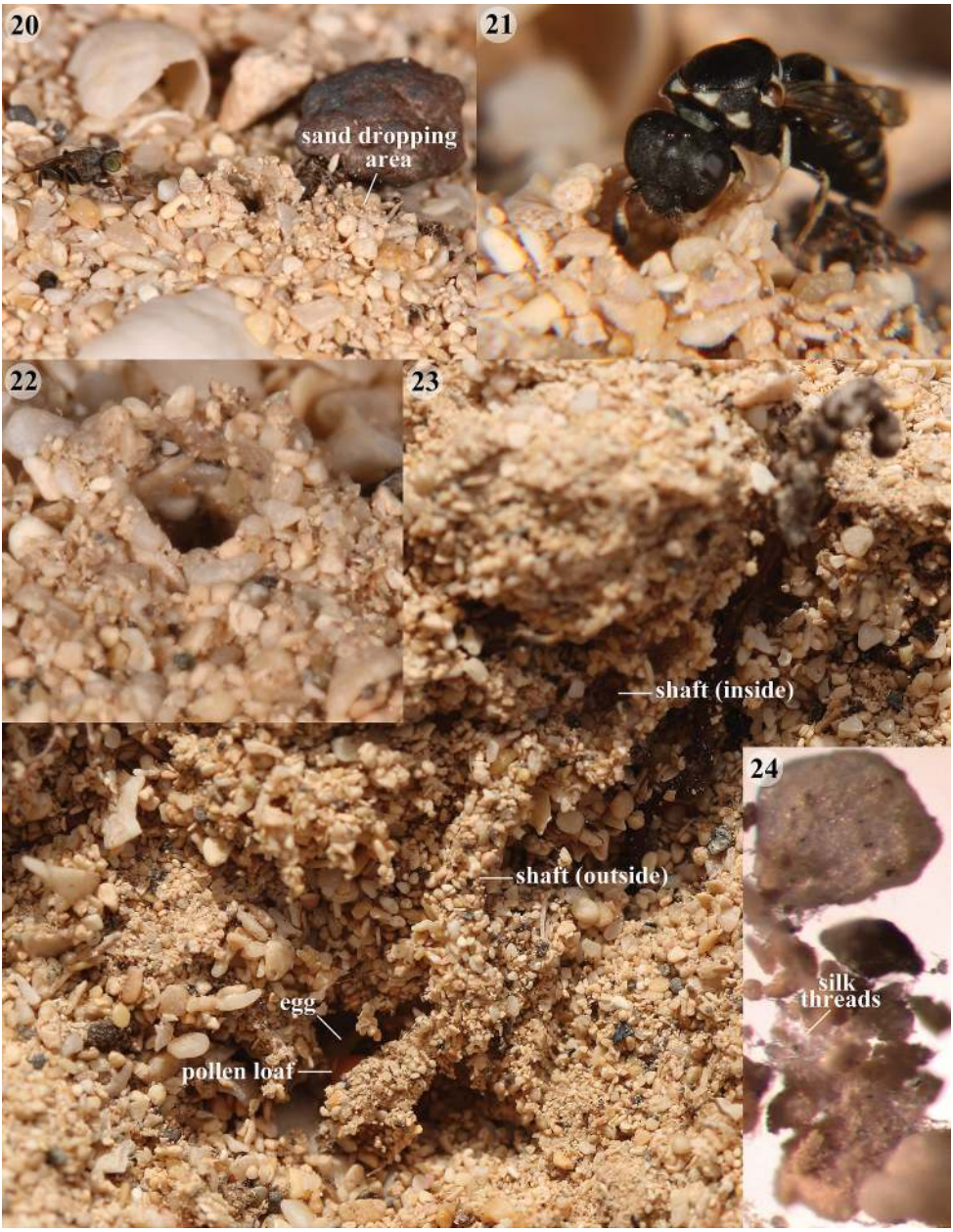
Time (s)	Behaviour	Figure
0	*Initiation*: ♂ pounced on ♀ on *Frankenia* flower. ♂ alighted on back of ♀; body axis of ♂ parallel to hers; head of ♂ situated above mesonotum of ♀ level with her tegulae; ♂ directed antennae straight anterior-downwards, so that ventral side of distal end of antennal club came into contact with posterior parts of pronotum and anterior parts of mesonotum of ♀; fore legs of ♂ placed laterally on scutellum and wing base of ♀, mid and hind legs of ♂ wrapped around wings and metasoma of ♀. ♀ remained passive, with antennae orientated 45° to longitudinal axis.	15a
32	♂ moved slightly backwards and shifted antennae laterally-outwards (transverse to body axis); metasoma of ♂ was turned to the right side of ♀ and was curved anterio-ventrad; ♂ genital protruded. ♀ shifted antennae laterally-outwards and opened genital chamber.	15b
37	*Insertion*: ♂ moved antennae to a position 45° to longitudinal axis and inserted his genital in genital chamber of ♀.	15c
43	♂ changed his position on ♀ very rapidly. After that, body of ♂ curved around posterior end of ♀ metasoma, only connected to ♀ by genitalia. Head of ♂ protruded and erect, mandibles spread, antennae stretched straight forward; ♂ fore legs stretched forward, mid and hind legs bent but raised without contact to body of ♀. Wings of ♀ drooping obliquely downwards.	15d
52	Head of ♂ directed downwards, mandibles of ♂ open, touching posterior margin of metasomal tergum III of ♀, antennae of ♂ directed obliquely downwards; fore, mid and hind legs of ♂ pressed against distal end of ♀ metasoma.	15e
58	Head of ♂ protruded and erect, mandibles spread, antennae stretched straight forward; ♂ fore legs stretched forward, mid and hind legs bent but raised without contact with body of ♀.	as in 15d
79	Head of ♂ directed downwards, mandibles of ♂ open touching posterior margin of metasomal tergum III of ♀, antennae of ♂ directed obliquely downwards; fore, mid and hind legs of ♂ attached to distal end of ♀ metasoma.	as in 15 e
93	Head of ♂ protruded and erect, mandibles spread, antennae stretched straight forward; ♂ fore legs stretched forward, mid and hind legs bent but raised without contact with body of ♀.	as in 15d
144	Head of ♂ directed downwards, mandibles of ♂ open, touching posterior margin of metasomal tergum III of ♀, antennae of ♂ directed obliquely downwards; fore, mid and hind legs of ♂ pressed against distal end of ♀ metasoma.	as in 15e
152	*Separation*: ♂ genital removed from ♀ genital chamber. ♀ shifted antennae to a position 45° to longitudinal axis and moved slowly forward. ♂ dismounted ♀ postero-laterally. ♂ and ♀ flew off.	15f

Female brood care

Nest structure: The nest consisted of a subterranean burrow. The entrance was surmounted by a short cylindrical turret measuring about 2.5 mm in diameter and 1.5 mm in height (Figs 20, 22). The inner diameter of the turret opening was somewhat more than 1 mm wide, the same as that of burrow. On the first days of observation, when the female was excavating the nest, the wall of the turret was lower on the side orientated towards the adjacent sand dropping area (Figs 20, 22). Later on, this gap in the turret wall was closed (Fig. 21). The burrow consisted of a sub-vertical to oblique shaft that ran down in curves to a depth of 20 mm, where it terminated into a cell (Fig. 25, cell No. 2). A second cell was situated close to the end of the shaft (Fig. 25,



Figures 16–19. Behaviour of the nest owning female of *Quartinia canariensis* at nest No. 1: **16** Female "lining" of the turret rim with the mouthparts (mandible spread, labrum erected, part of maxilla visible) at the onset of activity in the morning **17** Female backing out of the shaft during nest excavation, carrying a large sand grain behind the mandibles **18** Female turning around outside of the nest prior to the start of flight activity in the morning: **a** Female "lining" the turret wall from the inside **b** Female turning quickly around after she has left the turret head first **c** Tip of the metasoma of the female is visible in the nest entrance after re-entering the nest head first **19** Female turning around outside of the nest at the end of activity in the afternoon: **a** Female situated above the turret after she has backed out of the nest and moved forward again **b** Female re-entering the nest backwards.



Figures 20–24. Nest No. 1 of *Quartinia canariensis*: **20** Close vicinity of the nest with a small fly (Diptera, Cyclorrhapha, Fam. indet.) probably inspecting the nest entrance **21** Female re-entering nest head first after backing out of the shaft prior to onset of flight activity in the morning **22** Nest entrance with dull whitish inner silken lining **23** Excavated burrow on 5 April, 2015 with turret removed and the shaft opened in the upper part to show the inner wall. The content of the opened brood cell No.2 is visible at the lower end of the shaft **24** Silk threads on and between sand grains from the wall of the nest.

cell No. 1). Another three cells were located at distances of up to 25 mm in a northerly direction from the shaft with no traceable connection to it (Fig. 25). The median depth of the cells below the ground was 20 mm (n = 5; Table 1). The inner dimensions of the brood cells measured approximately 3 mm in length and a little more than 1 mm in width.

The walls of the turret, the shaft and the brood cells consisted of sand grains (Figs 22, 23) bonded together with a dense, continuous lining of silk on the inside (Figs 22, 24). 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 1. The provision consisted of an orange, more or less spherical loaf constituted of a mixture of pollen and a liquid, probably nectar, (Fig. 23) with a relatively firm surface adhering only weakly to the cell wall.

Behaviour at the nest: During nest excavation the female backed out of the shaft carrying a load of small sand grains or a single larger particle with her mouthparts (Fig. 17). The sand particles were positioned behind her mandibles and held with the aid of the elongated labial palpi. She moved a few steps backwards from the turret opening towards the sand dropping area where she stopped and discharged the sand particles curving her body downwards for a short moment. Then she moved rapidly forwards and re-entered the nest head first again. The female repeated the whole sequence of sand-load formation and sand dropping many times without interruption. The longest observed continuous phase of nest excavation lasted from 14h43 until 16h02. During these 79 min the female backed out the shaft 138 times. The time spent in the nest until the female reappeared with a new sand-load varied from 6.4 s to 123.3 s (median 17.4 s; n = 61). The sand-loads always appeared to be dry. The female always used the same sand dropping area, although she slightly modified the direction of her body axis when she was moving backwards resulting in the formation of a conical heap of excavated sand (Fig. 20). The sand dropping area was situated directly down slope as well as to the lee side of the nest entrance.

In the morning, at the start of diurnal activity, the female always appeared head first in the nest entrance continually treating the inner surface of the shaft and the turret with the mouthparts. These were moved slowly in close contact over the surface (Figs 16, 18a) while the female rotated gradually around her body axis. Throughout this process of "lining" the mandibles were moderately spread and the labrum was erected. Moreover, moistly shining, protruded parts of the epi- and hypopharynx were visible as well as distal parts of the maxillae performing some movements. At the margin of the turret the "lining"-behaviour led to the fixation of loose sand grains to the silken lining. After 3 to 7 min (median 6 min; n = 5) of "lining" the female left the turret head first, turned around and immediately re-entered the nest head first again (Figs 18a–c, 21). In the following 15 to 56 min (median 35 min; n = 4) the tip of the metasoma occasionally became visible in the nest entrance (Fig. 18c), indicating that the female was moving up and down inside the shaft. Finally, the female backed out of the nest entrance and remained for a short moment on the ground with her head above the turret before she flew off at last. On two occasions, after leaving the nest, she

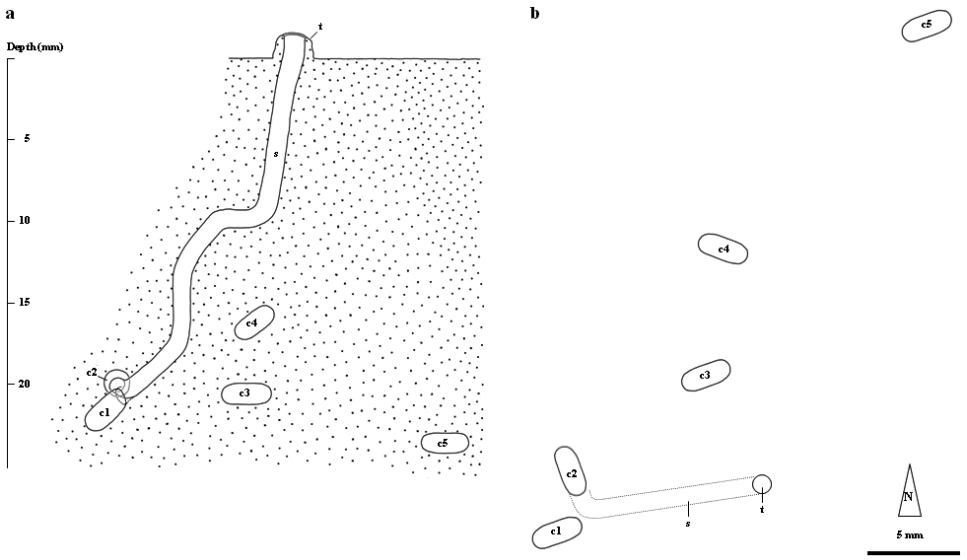


Figure 25. Nest architecture and brood cell arrangement of Nest No. 1 of *Quartinia canariensis* on 5 April, 2015: **a** schematic vertical cross section **b** schematic horizontal section (c = brood cell with cell number, s = main shaft, t = turret).

performed up to three arcs of a typical orientation flight. On two days it was observed at the end of the activity period that the female backed out of the shaft and then moved rapidly forwards again above the turret (Fig. 19a), where she curved her metasoma into the nest entrance (Fig. 19b) and moved backwards deep into the burrow with her head directed towards the nest entrance. The whole behavioural sequence took less than 2 s.

Activity, sleeping and sheltering

The diurnal activity of the female from nest No. 1 lasted for 4.8 to 6.0 h (median 5.6 h; n = 5) starting in the morning from 10h17 to 11h24 (median 10h53; n = 5) and finishing in the afternoon from 15h48 to 17h32 (median 16h22; n = 5). The female always spent the night within her burrow. The activity of males and females at flowers of *Frankenia* declined noticeably early in the afternoon and was mainly over around 15h00. On a single occasion at the end of the diurnal flight period, a male was observed to enter head first into an empty snail shell of *Theba geminata* (Mousson). The shell was approximately 10 cm away from a flowering patch of *Frankenia*. Within the shell the male first performed some movements then he rolled up his metasoma and remained motionless in a resting position (Fig. 5). However, after nine minutes the male became active again and reappeared, but this could have resulted from his being disturbed by the placing of a glass vial over the snail shell to prevent the male to escape unidentified.

Associated organisms

On a single occasion a small fly (Diptera, Cyclorrhapha, family indet.) was resting on the ground close to the turret, probably inspecting the nest entrance (Fig. 20). Other potential nest parasites were not observed.

Discussion

Flower associations

At all sites the only flowers that were observed to be visited by females and males of *Quartinia canariensis* were those of *Frankenia laevis*, indicating a close association with this plant that was used as a source of pollen and nectar. This is in congruence with the study by Gusenleitner (1990) in the neighbouring island Lanzarote, where members of the species were also recorded solely on flowers of or in close proximity to *Frankenia laevis*. However, the brood cell provisions of *Q. canariensis* consisted not only of pollen from *Frankenia* but also of small but substantial amounts of pollen from *Polycarpaea* that can not be explained by contamination. Therefore *Q. canariensis* is at least eclectic oligolectic, using at least pollen from two plant genera belonging to two different families that is Frankeniaceae and Caryophyllaceae. That *Q. canariensis* even may be polylectic with strong preference is supported by the results of Hohmann et al. (1993), who found the wasps mainly on flowers of *Frankenia laevis*, but recorded a specimen from *Polycarpaea* as well. Moreover, Hohmann et al. (1993) added single records from plants belonging to the families Asteraceae, Boraginaceae and Fabaceae. Such a broad spectrum of visited plant families and different flower types is unusual within the Masarinae for which various degrees of oligolecty (sensu Müller and Kuhlmann 2008) are more common (cf Gess 1996, Gess and Gess 2010). However, within the genus *Quartinia* the proportion of polylectic s.l. species seems to be comparatively high, as in Afrotropical *Quartinia* approximately 30% of the sufficiently examined species were recorded from more than two plant families (calculated from data by Gess and Gess 2010; n = 33). However, it is not known from how many of the plant families visited pollen is harvested.

During their visits to flowers of *Frankenia laevis* males and females of *Quartinia canariensis* usually came into contact with the anthers and stigmas of the flowers and there were often pollen grains on the exoskeleton of the wasps. Moreover, they showed a high flower fidelity to this plant. Therefore *Quartinia canariensis* probably acts as a pollinator of *Frankenia laevis*.

Mating

Males of *Quartinia canariensis* searched for females at flowers of *Frankenia laevis*, which was the main pollen source of the females. This is in congruence with mate searching in

Afrotropical species of *Quartinia* in which the males also frequently search for females at floral resources (Gess and Gess 1992, Gess and Gess 2010). However, the males of the Afrotropical *Quartinia* species commonly wait for females in flowers or rest on the ground in the vicinity of forage plants from where they rise up in response to the arrival of females, which they mount and copulate with on flowers (Gess and Gess 2010). In slight contrast, males of *Quartinia canariensis* were only observed to stand on the ground in the vicinity of the plants and not on the flowers (which is also reported for *Q. vagepunctata* by Gess and Gess 1992) and they frequently performed patrol flights along the flowers independent of the presence of females. Moreover, at least the initiation phase of the copulation in *Q. canariensis* took place both on flowers and on the ground as well as. Males of *Q. canariensis* were not observed at the nesting site whereas they were present in the nesting area of the Afrotropical *Q. vagepunctata* (Gess and Gess 1992). This might be explained by the formation of nesting aggregations in the latter species (Gess and Gess 1992) which makes it more predictable for the males to find potential mates in the vicinity of nests.

Females of *Quartinia canariensis* avoided contact with patrolling males at flowers and offered long lasting and predominantly successful resistance against insertion by males during the initiation phase. Since the females obviously bear considerable costs to withstand the male mating efforts, it can be assumed that insertion of the male genitalia is associated with high costs for the females of *Quartinia canariensis*, at least during the investigated period of the flight season. The nature of these costs is still unknown.

The copulation of a *Quartinia* species has not been described before in detail. Compared to photos of mating pairs of Afrotropical species of *Quartinia* in Gess and Gess (2010: 55) it seems that the position of the male on the female during the initiation phase is mainly similar in these taxa. The insertion phase has only been documented in *Quartinia femorata* (Gess and Gess 2010: 55). In this species the position of the male during the insertion seems to differ from *Q. canariensis* in that the male of *Q. femorata* is positioned less far posterior on the female with his head well above the posterior end of her mesosoma and the distal parts of his fore legs placed over the base of her wings. This is quite similar to the position in two species of the genus *Celonites* (Mauss 2006, Mauss and Müller 2014) the supposed sister group of *Quartinia* (Carpenter 1993, Krenn et al. 2002). In *Quartinia canariensis* the insertion phase lasted approximately 120 s. This is about ten times longer than the length of the insertion phase in members of the closely allied genera *Celonites* (Mauss 2006, Mauss and Müller 2014) and *Pseudomasaris* (Longair 1987). The significance and probable function of different insertion lengths is uncertain and should be investigated in detail.

Female brood care

Quartinia canariensis was found nesting in friable sandy soil close to its main forage plant. This is very similar to the nest situation recorded for two Afrotropical species, *Quartinia vagepunctata* (Gess and Gess 1992), nesting inland, and *Quartinia poecila*

(Gess 2009, Gess and Gess 2010), nesting on coastal dunes, from the Afrotropical region. In contrast utilization of sand-filled empty snail shells for nesting, as occurs facultatively or obligatorily in eight other Afrotropical species of *Quartinia* that also inhabit coastal and associated desert dune areas (Gess and Gess 1999, Gess and Gess 2008, 2010), seems to be absent in *Q. canariensis*.

As in all other Afrotropical *Quartinia* species for which nesting is known (Gess and Gess 1992, 1999, Gess and Gess 2010), the walls of the burrow and the cells of *Q. canariensis* were composed of non-rigid sand and silk structures with a silk lining. The silk was produced by the nest building female that apparently issued the material from the oral region and applied it with modified components of the mouthparts to the inner surface of the walls. Stabilization of the walls of the burrow by silk is unique among the Masarinae (Gess and Gess 1992, Mauss 2007), and can be regarded as an outstanding apomorphic trait of *Quartinia*. It probably had been the key adaptation for ground nesting in friable sandy soil that enabled the members of the stem-line of *Quartinia* to inhabit sand ecosystems. Within the evolution of the Masarinae the ability to exist in such sand habitats probably constituted a new adaptive zone for *Quartinia* and may at least partly explain the higher species diversity in *Quartinia* in relation to other genera of pollen wasps.

The short vertical turret surmounting the nest entrance of *Quartinia canariensis* is of the same form as in the Afrotropical *Quartinia* species (Gess and Gess 2010), exception being *Q. vagepunctata* that builds a horizontal, bag-like turret (Gess and Gess 1992), which is probably derived. The existence of a turret at the nest entrance is probably a plesiomorphic trait of *Quartinia* adopted from the ground pattern of the Masarini (Mauss 2007). It is of note that the focally observed female of *Quartinia canariensis* stabilized and repaired the turret walls from the inside of the turret while she was in the nest shaft with her head facing outwards. This situation is very unusual and it remains to be shown whether the turret is actually built and not only repaired in this position. In all other ground nesting pollen wasps in which the construction of the turret has been observed, i.e. *Priscomasaris namibiensis* (Gess 2001), several species of *Ceramius* (Gess and Gess 1980, Mauss et al. 2003, 2010), *Jugurtia* (Gess and Gess 1980, Gess and Gess 2010) and *Masarina* (Gess and Gess 1988a, Gess et al. 1997) as well as *Trimeria howardi* (Mechi 1999), the female is situated outside of the nest during turret building, standing on the ground or holding on to the outside of the walls of the growing turret with the mid and hind legs, simultaneously putting her head and her fore legs into the turret opening and curving her metasoma around the margin on the outside while she is adding mud with her mouthparts from the inside to the rim of the turret.

The nest of *Quartinia canariensis* consisted of a subterranean burrow terminated by a cell, which is principally similar to the nest architecture of *Quartinia vagepunctata* (Gess and Gess 1992). However, a minor difference between the nests of these species may exist in the depth of the cells varying between 15–23 mm in *Q. canariensis* and 25–30 mm in *Q. vagepunctata* (Gess and Gess 1992). Moreover, the nest of *Q. canariensis* was multicellular while all investigated nests of *Q. vagepunctata* contained only a single brood cell (Gess and Gess 1992). However, in one nest an additional blind

ending lateral shaft existed suggesting that *Q. vagepunctata* probably also constructs more than one cell per nest (Gess and Gess 1992). In all *Quartinia* species nesting in snail shells the burrow is multicellular with up to 20 or even more cells (Gess and Gess 2010). The distant and isolated position of the cells No. 3, 4 and 5 in the nest of *Quartinia canariensis* is remarkable. The developmental stages of the offspring in these cells clearly indicate that the cells had been excavated and provisioned by the female previous to the cells No. 1 and 2. Since the connection to the main shaft was not perceptible any more during nest excavation, it remains to be shown whether these cells were built either along a single earlier long lateral branch of the main shaft or at the end of three separate secondary shafts. Isolated brood cells at some distance from the main shaft have only been reported to occur in the subterranean burrows of the members of the species group 8 of *Ceramius* (summarized in Gess 1996) and of *Metaparagia angulata* (Gess et al. 1995). In these taxa each cell is probably built at the end of a relatively long separate secondary shaft connecting the brood cell to the main shaft. After the cell has been sealed by the female the secondary shaft is filled with soil particles to the point where it left the main shaft from which it is then sealed off (summarized in Gess 1996).

The behaviour of a *Quartinia* species during nest excavation has been observed for the first time. The female of *Q. canariensis* backed out of the shaft carrying soil particles with her mouthparts, which is similar to the behaviour of all other primarily ground nesting Masarine wasps, i.e. *Priscomasaris* (Gess 2001), *Paragia* (Houston 1984), *Metaparagia* (Gess et al. 1995, Houston 1995), *Ceramius* (Gess and Gess 1980, 1986, 1988b, Gess and Gess 2010, Mauss 1996, Mauss and Müller 2000, Mauss et al. 2003, 2006, 2010), *Trimeria* (Mechi 1999), *Jugurtia* (Gess and Gess 1980, Gess 1996) and *Masarina* (Gess and Gess 1988a). Therefore, these elements of the behaviour are probably plesiomorphic. However, the nest excavating behaviour of *Quartinia canariensis* differs from the ground pattern of the Masarinae (cf. Mauss 2007), in that no observable liquid was used during nest excavation. Liquid is probably not required, since firstly the friable sandy soil can be removed by the mandibles without softening it, and secondly bonding of the loose sand particles within the burrow is achieved by self-generated silk. This makes excavation more rapid as the necessity for interrupting excavation to fetch liquid is eliminated. In contrast, the other primarily ground nesting pollen wasps regularly have to interrupt nest excavation sequences to collect water, or rarely nectar, which is required for softening the soil and pellet formation.

The position of the egg at the distal end of the brood cell beyond the pollen loaf indicates that egg deposition precedes pollen provisioning in *Quartinia canariensis*. This is a plesiomorphic behavioural trait adopted from the ground pattern of the Masarinae and even the Vespidae (Gess 1996, Mauss 2007).

Associated organisms

In 1990 Gusenleitner established "*Chrysis atracomitata* LINS." as a cleptoparasite of *Quartinia canariensis*. Obviously, this is a misspelling of the name *Chrysis atrocomitata*

Linsenmaier, 1993 and the spelling has already been corrected in this sense by Hohmann et al. (1993: 109). Unfortunately, Gusenleitner used the name as a nomen nudum three years before the description of *Chrysis atrocomitata* was finally published by Linsenmaier (1993). Apparently Linsenmaier changed his opinion about the identity of the *Chrysis* taxon collected by Gusenleitner from the island Lanzarote as he described it as a separate species named *Chrysis umbofascialis* Linsenmaier, 1993. In fact, *Chrysis atrocomitata* sensu Linsenmaier (1993) does not occur in Lanzarote at all (Hohmann et al. 1993, Linsenmaier 1993), and the proposed parasite-host relationship refers to *Chrysis umbofascialis*, which was overlooked by Hohmann et al. (1993). However, the existence of a parasite-host relationship between *Chrysis umbofascialis* and *Quartinia canariensis* was in all probability only supported by the simultaneous occurrence of both taxa in the same habitat in Lanzarote and their matching small size, as Gusenleitner did not observe any behavioural interactions between them (Gusenleitner, pers. comm.). In contradiction, the geographic distribution of both taxa does not match with a close relationship between them. *Chrysis umbofascialis* has not been recorded from Fuerteventura, although most records of *Quartinia canariensis* come from this island. It was found in Tenerife instead, where *Q. canariensis* is missing (Hohmann et al. 1993, Linsenmaier 1993). Therefore, the existence of a parasite-host relationship between *Chrysis umbofascialis* and *Quartinia canariensis* seems doubtful at the moment. In this context it is of note that we did not observe any chrysidid wasp at the focally observed nest of *Quartinia canariensis*.

Acknowledgements

Sarah Gess made very helpful comments on the manuscript and kindly corrected our English. Jim Carpenter and Robert Paxton reviewed and improved the manuscript. Annette Rosenbauer identified the collected plants. Ashley Kirk-Spriggs helped with the identification of the fly in Fig. 20. Rainer Prosi assisted us with taking microphotos of the silk threads. Hans-Jörg and Inge Mauss kindly provided their cottage. The required permits to conduct the field studies on Fuerteventura were granted by M.A.R. Martinez (Medio Ambiente Fuerteventura).

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