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The use by wasps, bees and spiders of shells of *Trigonephrus* Pilsb. (Mollusca: Gasteropoda: Dorcasiidae) in desertic winter-rainfall areas in southern Africa

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The use of snail shells in desertic areas in the winter-rainfall region of southern Africa was investigated. Principal users are: spiders constructing silk-bag nests; megachilid-bees, species of *Wainia (Wainia)* (Osmiini), *Hoplitis (Anthocopa)* (Osmiini) and *Afranthidium (Oranthidium)* (Anthidiini), and a eumenine-wasp constructing nests within empty shells utilizing nesting materials brought in; and two masarine-wasps, *Quartinia* spp., excavating nesting burrows stabilized with self-generated silk in sand-filled shells. Species of *Allocoelia* (Chrysididae), *Tricholabiodes* (Mutillidae) and *Apolysis* (Bombyliidae) were reared from *Quartinia* nests. Notable is the use of sand-filled shells as stable nest sites in wind-swept deserts.

Keywords: snail-shell users; desert-life strategy; self-generated silk; Megachilidae; Masarinae; Chrysididae; Mutillidae; Bombyliidae

Introduction

Sun-bleached shells of *Trigonephrus* of the family Dorcasiidae (Mollusca: Gasteropoda: Pulmonata), endemic to southern Africa, are a common sight in the sandy, sparsely vegetated areas of western Namaqualand and south-western Namibia. Travelling through these areas on a hot, dry day it seems almost unbelievable that snails would be able to make a living here. However, the ability to live under these conditions is not unique. There are snails in other arid areas of the world that have adapted to withstand extreme heat and seasonal shortages of water and food (Evenari, 1985 citing the studies of Yom-Tov, 1971; Schmidt-Nielsen *et al.*, 1971; Shachak *et al.*, 1975).

Trigonephrus avoid heat stress and desiccation by retreating beneath the ground surface (Pallett, 1995). They are active only when humidity is high and the surroundings are moist, chiefly in winter or when there is a heavy fog. Under these conditions they emerge from beneath the ground surface to feed on plant matter. They breed most actively after the first good winter rains, when perennial plants put out new growth and annuals germinate ensuring a good food supply.

The present paper examines the use as shelters and nest sites of the shells of these snails, both when empty and when filled with sand. It is based on an investigation which was stimulated by the interesting discovery by Robert Gess, when assisting the authors

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in the field in September 1996, that *Quartinia* spp. (Masarinae) were excavating nesting burrows in compacted sand held within shells. Some aspects of this study were briefly reported in a conference poster paper (Gess & Gess, 1997*b*).

Study area and sampling sites

The study area lies within the winter-rainfall region of the Karoo Biome, that is within the area designated Succulent Karoo by Rutherford & Westfall (1986). The snails are characteristic of sandy areas, that is the areas of wind-blown sand immediately north and south of the Orange River; the sandy coastal plain, designated Strandveld, Veld Type 34, by Acocks (1975); and the isolated sandy area to the north of Vanrhynsdorp seen by Acocks as an isolated pocket of Strandveld. The Strandveld is predominantly open drought resistant scrub composed of woody, semi-succulent or succulent low-growing shrubs. In the areas of wind-blown sand to the north and south of the Orange River shrubby species are few and far between beyond the drainage channels and rocky slopes.

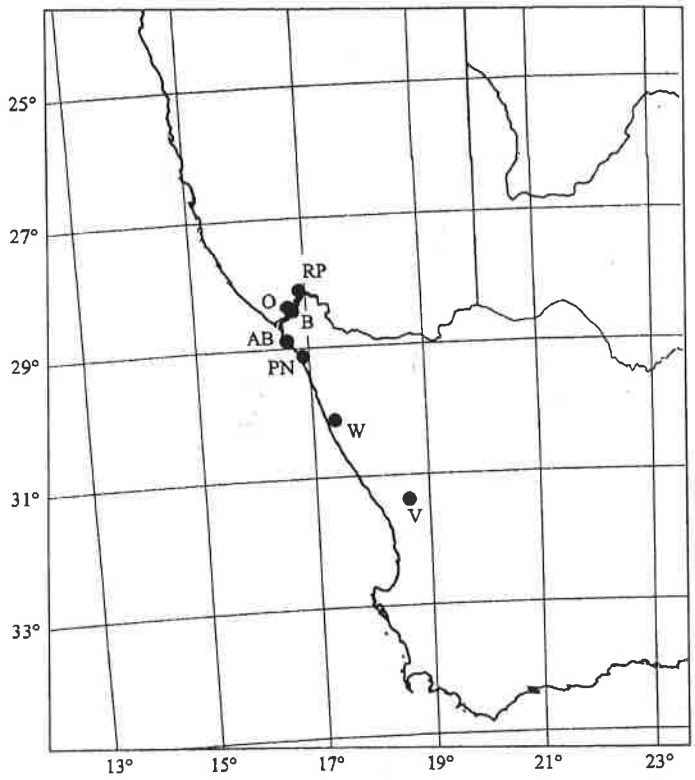


Figure 1. Map of south-western southern Africa showing location of sampling sites: RP = site 12·8 km south of Rosh Pinah; O = sites north of the Orange River, east of Oranjemund; B = sites south of the Orange River, south-west of Brandkaros; AB = sites south of Alexander Bay flanking the road to Port Nolloth; PN = site east of Port Nolloth; W = sites west of Wallekraal; V = site north of Vanrhynsdorp.

In all areas ephemeral annuals follow the winter rains; their abundance being determined by the timing and amount of rain. Overall, plants of the families Asteraceae, Aizoaceae and Zygophyllaceae predominate.

Sampling sites (Fig. 1):

- A sandy, sparsely vegetated slope 12·8 km south of Rosh Pinah, 28°03'S 16°51'E, in the desertic mountainous area immediately north of the Orange River (11 September 1996) (Fig. 2(a));
- Two sandy, sparsely vegetated sites immediately north of the Orange River, east of Oranjemund, 28 30'S 16 36'E and 28°26'S 16°42'E (22 September 1997 and 25 September 1997);
- Two sites in sandy slacks between sparsely vegetated rocky hills southwest of Brandkaros immediately south of the Orange River, 28°29'S 16°40'E (13 September 1996, 15 September 1996 and 17 September 1996) (Fig. 2(b));
- Two Strandveld sites to the south of Alexander Bay flanking the road to Port Nolloth, 28 47'S 16 38'E and 28 50'S 16 40'E (27 September 1997 and 19 September 1996) (Fig. 2(c));
- A Strandveld site east of Port Nolloth, 29°16'S 16°55'E (27 September 1997);
- Two Strandveld sites west of Wallekraal, 30°22'S 17°27'E (8 October 1997);
- A site in the isolated area of Strandveld, north of Vanrhynsdorp, 31°30'S 18°43'E (20 September 1996).

Shells

As live *Trigonephrus* were not obtained at any of the sites it could not be established with certainty which species were present. However, samples of their heliciform shells collected from all sites were measured (six measurements for each shell) following the method of Connolly (1938: text Fig. 1). Using the measurements, comparisons were made with Connolly's descriptions. In some instances tentative determinations were possible. Tentative determinations together with the first two measurements (major diameter and altitude) are given for each site. All the shells have a major diameter slightly less than the altitude. As the present interest in the shells is their function as useable cavities, their volumes are also given. Volume was measured by pouring water from a graduated cylinder into the shells, making sure that no airlock was created.

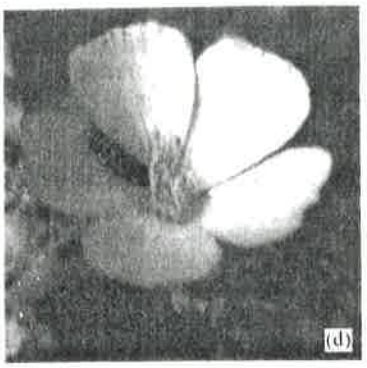
The shells can be divided into four groups:

- Shells from 12·8 km south of Rosh Pinah: major diameter 28–30 mm, altitude 32–34 mm, volume 6·5–7·0 ml, very heavy, some sub-fossil, ?*T. haughtoni* Connolly;
- Shells from 28 km east of Oranjemund and from east of Alexander Bay to Brandkaros: major diameter 24–29 mm, altitude 27–33mm, volume 6·0–6·5 ml, relatively thin shelled, species indetermined;
- Shells from Alexander Bay to Port Nolloth and from west of Wallekraal: major diameter 38–40 mm, altitude 40–44 mm, volume 14–17 ml, coarse, ?*T. porphyrostoma* (Melvill and Ponsonby)
- Shells from north of Vanrhynsdorp: major diameter 36 mm, altitude 36 + mm, estimated volume 12 ml, ?*T. heliocaustus* Connolly.

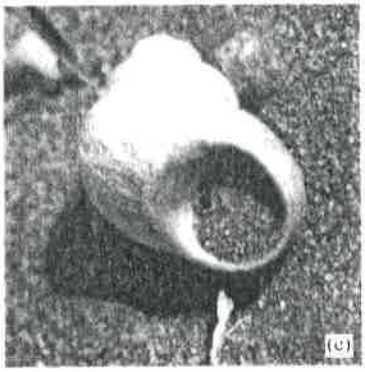
Methods

The investigation was not conducted as a pre-planned project and as a consequence, sample sizes were not fixed. As a rule samples were taken on cold or damp days or as


(a)


(d)


(b)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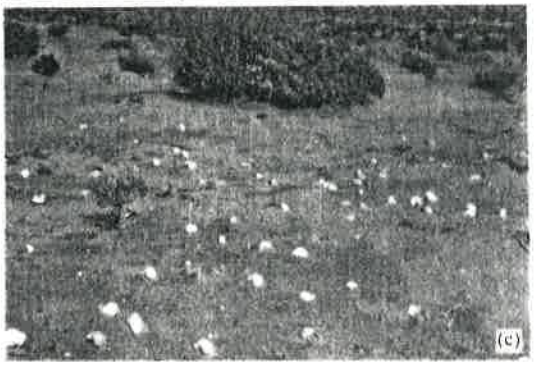
(e)


(f)


(g)

insect activity for the day was in decline, increasing the possiblity of finding occupiers of shells 'at home'.

At all 11 sites random samples of *Trigonephrus* shells lying on the sand surface, most with their openings at least partially exposed, were collected into plastic bags and taken back to the field laboratory where they were broken open and the contents recorded.

Voucher specimens of *Trigonephrus* shells, nests in shells, and the insect and spider users of the shells have been deposited in the Albany Museum, Grahamstown.

Results

The shell occupants can be grouped into five main categories:

- Temporary lodgers which use the shells only for sleeping and sheltering. These make no modifications and bring nothing into the shells.
- Residents, various spiders which 'fit out' the shells with ample silk spinnings.
- Nesters in pre-existing cavities which use the empty shells as ready-made burrows in which to construct cells for rearing their young. These, wasps and bees, bring in various building materials which they collect outside the snail shells.
- Burrow excavating nesters, pollen wasps, which dig their burrows in sand-filled shells and construct their cells from sand and self-generated silk. These bring in no building materials from outside the shells.
- Associates in the nests of the third and fourth category shell users.

Temporary lodgers

Nesters in pre-existing cavities and burrow excavating nesters were found sheltering in the snail shells even when they were not actively nesting. However, a *Bembecinus* sp. of the *Rhopalocerus* species group (Hymenoptera: Sphecidae: Nyssoninae) was the only species which was found sheltering in, but not nesting in, the shells. Only 2 out of 452 shells were found to have been used in this way. One shell from one of the Brandkaros sites contained 2 females and 1 male and from a site 60 km north of Port Nolloth one shell contained 1 male.

Considering the weather conditions and time of day that samples were taken, the low incidence of the presence of 'temporary lodgers' is surprising.

Residents

The only arthropods in this category were spiders which construct sac-like nests within the shells. Nests in shells were found at Alexander Bay and Port Nolloth (9% of 43 shells), at the Wallekraal sites (15% of 137 shells) and north of Vanrhynsdorp (21% of 34 shells).

Adult female spiders with young were obtained from nests from the site 60 km north of Port Nolloth and from the Wallekraal sites. Those from the former site are

Figure 2. (a) Looking towards Orange River, site south of Rosh Pinah; (b) from a hilltop above Brandkaros sites, *Sarcocaulon* (Geraniaceae) in foreground; (c) *Trigonephrus* shells south of Orange River near Alexander Bay; (d) female of the smaller species of *Quartinia* (Masarinae) imbibing nectar from *Grielum* (Rosaceae) (×2·2); (e) sand-filled *Trigonephrus* shell occupied by *Quartinia*, showing nest entrance (×1); (f) and (g) shells of *Trigonephrus* showing cells of *Quartinia* swept clean of surrounding sand, (f) × 1·6, (g) × 1·5).

Clubionidae (probably *Cheiracanthium simplicitarse* Simon) and those from the latter Salticidae (probably *Thyenula ogdeni* (Peckham & Peckham)), ant mimics, looking superficially like the Karoo Ant, *Camponotus fulvopilosus* (De Geer).

Nesters in pre-existing cavities

At all sites shells had been used as pre-existing nesting burrows by megachiline bees (Megachilidae) and in addition, at the Brandkaros sites, some shells had been used by a eumenine.

The bees concerned were *Wainia (Wainia)* sp. A (undescribed) (Osmiini), *Hoplitis (Anthocopa)* sp. (Osmiini) and *Afranthidium (Oranthidium)* sp. (Anthidiini).

Wainia (Wainia) sp. A was found nesting in shells north of the Orange River from east of Oranjemund (3·5% of 86 shells) (but not at the site south of Rosh Pinah), south of the Orange River, south-west of Brandkaros (16% of 106 shells), between Alexander Bay and Port Nolloth (5% of 43 shells), west of Wallekraal (48% of 137 shells) and north of Vanrhynsdorp (2% of 41 shells).

Wainia Tkalcu is an eastern Hemisphere genus with two sub-genera *Wainiella* recorded from Africa and *Wainia* from Africa to southern India and the Philippines. Little seems to have been recorded concerning their biology, however, *Wainia (Wainia) elizabethae* is also known to nest in snail shells. It was found by Ed Callan nesting in shells of *Tropidophora ligata* Müll. on coastal sand-dunes on the Eastern Cape Coast (as *Osmia* in Gess & Gess, 1988 and *Hoplitis* sp. in Gess & Gess, 1997*a*).

The nests of *Wainia (Wainia)* sp. A almost entirely fill the shell cavity. The cells are arranged in series around the spiral, the pollen and nectar provision is firm and fills the cells. Pollen from the provision of four nests from Wallekraal and one nest from 60 km north of Port Nolloth was deep yellow. Examined microscopically it was found to be heavily sculptured and spiny. Pollen grains from all the Wallekraal nests were 0·025 mm in diameter, and those from the nest from Port Nolloth were larger, all 0·04 mm in diameter.

The cells are separated from each other by a seal made from several layers of petal pieces. The final seal is multi-layered, very robust and hard. The inner layers are of petals only and the outer seal is of cemented sand and plant matter, approximately 5 mm in thickness. The nature of the bonding substance was not ascertained. In cells with fully-fed larvae the provision had all been consumed and the larva was encased in a parchment-like cocoon.

Hoplitis (Anthocopa) was found nesting in shells only from the sites north and south of the Orange River, that is, south of Rosh Pinah (5% of 21 shells), east of Oranjemund (5% of 86 shells) and southwest of Brandkaros (5% of 106 shells). Shells contained up to seven cells.

The walls of the cells of *H. (Anthocopa)* were entirely constructed from petal pieces from a deep pink flowered species of *Sarcocaulon* (Geraniaceae) that grows on the rocky slopes in close proximity to the sandy areas where the *Trigonephrus* shells were found (Fig. 2(b)). The cells were 10 mm in length and 5–6 mm in width. Pollen was obtained from a cell south-west of Brandkaros. This was examined microscopically and was found to be all of one kind, 0·08 mm in diameter, with a reticulate surface, and to match that of the deep pink flowered *Sarcocaulon*.

The fully-fed larvae spin a hard, brown, ovoid silken cocoon 7·38 mm in length and 4·53 mm in width at the widest point (average of 3).

The sites from which *Hoplitis (Anthocopa)* was not recorded were all sandy sites not associated with rocky slopes, with an absence of *Sarcocaulon*.

Afranthidium (Oranthidium), probably *odonturum* (Cockerell), like *H. (Anthocopa)*, was found only in shells from north and south of the Orange River, east of Oranjemund (3% of 86 shells), east of Alexander Bay (1 out of 4 shells) and south-west of Brandkaros (5%

of 106 shells). The shells were used by these bees for sheltering as well as nesting, both males and females having been found in shells without nests. The cells are embedded in a mass of white, closely packed, cottonwool-like plant fibres.

At the Wallekraal sites 3 male and 2 female *Afranthidium (Afranthidium) hamaticauda* Pasteels were found in shells. Nests were not, however, discovered and it is therefore not known whether these bees use the shells for nesting. This bee has previously been recorded from the Wallekraal sites foraging on yellow flowers (Papilionaceae) (16 September 1992) and from east of Oranjemund foraging on pale yellow flowers of *Lebeckia parvifolia* (Schinz) Harms and deep pink flowers of *Indigofera longispina* Baker (both Papilionaceae) (26 September 1997).

One of these *Afranthidium* spp. may well be the bee referred to by Hesse (1944): 'The most remarkable site adopted by a certain *Anthidium*-bee in Namaqualand and Bushmanland for storing its bee-bread is the empty shells of the desert snail *Trigonephrus* ... '. Apparently there are no extant voucher specimens of Hesse's bees (Margie Cochrane, pers. comm.).

At the Brandkaros sites, nests of a eumenine (Vespidae: Eumeninae) were found in 5% of the 106 shells examined. The remains of a dead adult and desiccated prey, 29 lepidopteran larvae, were obtained from one of the nests. Unfortunately the condition of both the adult and the prey precluded further determination. Another nest contained a fully-fed eumenine larva in a white silken cocoon. The nests were all single celled, the upper part of the spiral forming the cell, and the closure was composed of small pebbles embedded in a matrix of sand and an unidentified bonding substance. In the cell containing a cocoon the inner surface of the seal had been coated with silk, presumably by the larva prior to cocoon spinning. It seems likely that this is the eumenine referred to by Hesse (1944) as 'a certain Eumenid-wasp inhabiting the very arid and sandy belt of the Namib desert... [which] makes its nest in empty snail shells'. Apparently there are no extant voucher specimens of Hesse's wasps (Margie Cochrane, pers. comm.).

Burrow excavating nesters

The empty snail shells lying on the sand surface in this wind-swept area mostly fill with sand. The sand within the shells forms a protected site for the excavation of burrows by two ground nesting *Quartinia* spp. (both undescribed) (Vespidae: Masarinae). *Quartinia* nests were found in shells at all sites, south of Rosh Pinah (71% of 21 shells), east of Oranjemund (30% of 86 shells), south-west of Brandkaros (57% of 106 shells), Alexander Bay to Port Nolloth (35% of 43 shells), east of Port Nolloth (22% of 18 shells), west of Wallekraal (20% of 137 shells) and north of Vanrhynsdorp (10% of 41 shells).

The burrows of these two species are stabilized by the spinning together of sand grains with self-generated silk as described for *Quartinia vagepunctata* Schulthess (Gess & Gess, 1992) nesting in open compacted sandy ground. The nests of the two present species consist of a multicellular burrow, with up to 20 or more cells. The burrow entrance is surmounted by a turret a few millimetres in height constructed from sand grains spun together with silk (Fig. 2(e)). The turrets are vertical or, less commonly, somewhat curved. In this they differ from those of *Q. vagepunctata*, which constructs a horizontal bag-like turret with the opening to the burrow at some distance from the closed end of the bag. However, they are similar to the turrets of an undescribed species of *Quartinioides* from Helskloof Pass, Richtersveld (unpublished fieldnotes, Gess & Gess, 1996). The shaft penetrates into the upper part of the spiral of the shell into which cells are closely packed (Fig. 2(f, g)). It is stabilized with silk and can be extracted as a tube.

The cells of the two species, though similar in general appearance, differ in size. Samples of cells from the Rosh Pinah nests and sites south of the Orange River were

measured. The cells of the larger species were 7–8 × 4–5·5 mm and those of the smaller species 6·5 × 3·5 mm. The presence of old evacuated cells and cells being actively provisioned together in single shells suggests re-use of shells or even of nests as practised by *Ceramius* and *Jugurtia* (Masarinae) (Gess, 1996).

The walls of newly constructed, not yet provisioned cells are delicate, non-rigid sand and silk structures with a silk lining. The inner end is rounded. Oviposition is into an empty cell. An egg of the larger species was obtained. It was translucent white, gently tapering to rounded ends, 1·8 mm in length, 0·6 mm at its widest point.

Provision from the cells of both species from Rosh Pinah was moist and bright yellow. The pollen was examined microscopically. It was found to be of mixed origin, some being round and spiny, 0·02 mm in diameter, apparently asteraceous in origin, some smooth and oval, 0·04 mm in diameter, appearing to match that of *Grielum* (Rosaceae) and, less commonly, some were triangular in shape, 0·05 mm in diameter. Mixed with the pollen were what had the appearance of oil droplets. At this site the smaller species of *Quartinia* was captured visiting flowers of four species of Asteraceae and of *Grielum* sp. (Fig. 2(d)).

The fully provisioned cell is sealed with silk with sand grains spun onto the outer surface. The sealed end of the cell can be distinguished from the rounded inner end of the cell as it is somewhat truncate. The fully-fed larva spins a substantial cocoon within the cell, in contact with the cell walls, such that the cell becomes quite hard and rigid.

At the Rosh Pinah site, lumps of calcrete had rolled down the slope and lay around on the sand surface together with the snail shells. Open cavities in these lumps had filled with sand and in some instances had been used for nesting by *Quartinia*. However, these nesting cavities were shallower and no more than four cells were found in nests in such cavities.

Associates

The only true parasite found associated with any of the bees was a species of Eupelminae (Chalcidoidea: Eupelmidae), 18 females and 11 males of which were reared from three cocoons of *H. (Anthocopa)* from shells from south-west of Brandkaros. These wasps appear to have been primary parasites of the fully-fed post-cocoon-spinning bee larvae or possibly prepupae or pupae. The wasps are highly dimorphic. The females are brachypterous, largely brown with a blue-metallic lustre in parts, whereas the males are fully winged, darker and with a blue-metallic lustre throughout.

One shell from the Wallekraal site, which had been used for nesting by *W. (Wainia)* sp. A, contained a single, dead *Trichodes aulicus* Kl. (Coleoptera: Cleridae). As *Trichodes* are known to develop as predators in the nests of bees where they feed on the larvae and prepupae (Krombein, 1967: 376) it is highly likely that this clerid was present in the nest of the bee for this purpose.

Five female *Tricholabiodes* sp. (Mutillidae: Sphaeropthalminae: Dasylabrini) were obtained from nests of *Quartinia*. Two were collected as adults, one from south-west of Brandkaros and one from east of Alexander Bay. Three were reared from *Quartinia* cells from the second site collected on 13 September 1996. Emergence took place on 4–5 March 1997.

Tricholabiodes is the only genus of nocturnal mutillids recorded from southern Africa (Bayliss & Brothers, 1996). It is restricted to arid and semi-arid regions. This is apparently the first host record (previously noted by Gess & Gess, 1997*b*). (Identification to species awaits the revision of the genus currently being undertaken by P.S. Bayliss & D.J. Brothers.)

An undescribed, markedly melanistic species of *Allocoelia* (Chrysididae: Chrysidinae: Allocoeliini) was found to be associated with the smaller of the *Quartinia* species. Up to

6 cocoons of *Allocoelia* sp. were found attached to the sides of the *Quartinia* cells in 6 of 20 nests, 3 in shells and 3 in cavities, at the site south of Rosh Pinah and in 1 nest east of Port Nolloth. Six adults were obtained from nests. One of these was extracted from its cocoon. Further specimens of this species only were collected from the ground within the vicinity of the shells, calcrete lumps and the *Quartinia* forage plants.

The *Allocoelia* cocoon, 3·67 mm in length and 2·5 mm in width, is pale brownish–ochre, constructed from fine silk spinnings. The fecal pellets, which are in no way compressed, adhere to the outside of the cocoon. One end of the cocoon is rounded and the other truncate. On emerging the adult cuts off the plate-like, truncate end of the cocoon.

Allocoelia is a southern African genus of which host associations, all masarines, are known for 7 species. The only other record of an association with a *Quartinia* species is that between *A. mocsaryi* (Brauns) and nests of *Q. vagepunctata* Schulthess (Gess, 1996).

In a shell from east of Oranjemund there was, together with *Quartinia* cells, a dead bombyliid with an empty shuck (subsequently lost). The *Quartinia* cells were placed in a tube sealed with cottonwool and later it was found that a bombyliid had emerged from one of the cells. Unfortunately it became entangled in the cottonwool and was unable to escape from its shuck. Its identity was nonetheless determined by David Greathead. In his detailed report Greathead (1999) states that the visible characters of the pupa and pharate adult accord with the conclusion that the specimen is an *Apolysis* sp. (Usiinae: Usiini) and furthermore that it is very likely that it is a specimen of *A. capicola* Hesse. This is, apparently, the only confirmed association between a bombyliid and a masarine. However, Naumann & Cardale (1987) in Australia observed an *Anthrax* sp. (Anthracinae: Anthracini) entering the nests of *Paragia (Paragia) decipiens* Shuckard.

Discussion

The use of empty snail shells by bees that do not excavate nesting burrows, but search out pre-existing burrows in which to construct their brood-cells, is widely known in the Northern Hemisphere: in the Nearctic 2 species of Osmiini, species of *Osmia* and *Ashmeadiella*; and in the Palaearctic 14 species of Osmiini (*Osmia* and *Hoplitis*), 3 in Britain, 5 in Central Europe, 3 in the Mediterranean, 4 in Eurasia and 1 in Japan, and for 1 species of Anthidiini, a species of *Rhodanthidium*, from the Mediterranean into Asia Minor (extracted from O'Toole & Raw, 1991 and Bellmann, 1995). It is practised not only in areas of sparse vegetation but also in well vegetated areas and is therefore not a strategy solely associated with wind-swept sandy areas such as the present study sites.

Amongst these bees, concealment, by burial and/or the use of plant material, of the shell containing the nest is a common practice. No attempts at burial or other forms of concealment had been made by any of the bees investigated in the present study.

Use of snail shells as pre-existing nesting cavities by wasps, though not surprising, appears not to have been recorded otherwise than for the eumenine of the present study. However, the present first-records of the use of stabilized sand held within shells as a substrate for burrow excavation is of particular interest. Whereas at the study sites pre-existing cavities for nesting are clearly in short supply, rocks and sizeable plants being confined to the inselbergs, there is an abundance of available exposed ground surface. This ground surface is unstable, however, being subject to winds which shift the sands. It is, therefore, unsuitable as a nesting substrate for small ground nesting wasps that excavate relatively shallow burrows. Amongst such wasps are pollen wasps of the genus *Quartinia*, generally less than 5 mm in length, which are found abundantly at the

study sites foraging on the flowers of low growing annuals, appearing, as do these plants, in response to rain. For these wasps, sand-filled *Trigonephrus* shells are safe nesting sites made even safer by the use of self-generated silk for stabilizing burrow and cell walls. These cells within the shells are not dislodged even when the shells are tumbled and some of the sand matrix lost. Thus, the use of sand-filled snail shells for nesting by ground nesters, unlike the use of empty snail shells by cavity nesters, does appear to represent a desert-life nesting strategy, the shells being islands of calm in wind-swept desert.

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