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Notes on the nesting of three species of Megachilinae in the Dubai Desert Conservation Reserve, UAE

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Abstract

Some observations on the nesting of three species belonging to phylogenetically interesting lineages of Megachilinae are presented. Published knowledge of the nesting of these species, *Megachile* (*Maximegachile*) *maxillosa* Guérin-Méneville (Megachilini), *Megachile* (*Eurymella*) *patellimana* Spinola (Megachilini), and *Pseudoheriades grandiceps* Peters (currently assigned to the Osmiini), is fragmentary making the notes presented here a worthwhile addition. The brood cells of *M. maxillosa* and of *P. grandiceps,* constructed from a mixture of resin and sand, were positioned in pre-existing cavities, trap-nests, above ground. The cells of the former are equal in diameter to the boring and are constructed in linear series. Those of the latter are small ovoid and are grouped to form a cluster. *Megachile patellimana* was nesting in burrows in compacted sandy ground beneath a plant and in the banks of an irrigation furrow. At the former site a female was carrying a freshly cut leaf piece and at the latter another was carrying a cut length of narrow, tough, green plastic. The nest contained a group of identical lengths of plastic, clearly a substitute for leaves.

Keywords

Megachilinae, nests, sand, resin, leaves, plastic, trap-nests

Introduction

In 2015 a brief preliminary survey of the aculeate wasps and bees of the Dubai Desert Conservation Reserve in the United Arab Emirates was undertaken between 18 April and 4 May, at the end of spring, by Sarah Gess assisted by Peter Roosenschoon, Conservation Officer. The principal focus of the survey was flower visitation. The results of the flower visiting survey with accounts of the history, climate and vegetation of the DDCR and descriptions of the study sites have been published (Gess and Roosenschoon 2016).

Disappointingly little nesting activity was observed during this brief preliminary survey. However, notes were made on the nesting of some species. Included were three species of Megachilinae, *Megachile* (*Maximegachile*) *maxillosa* Guérin-Méneville (four nests), *Megachile* (*Eurymella*) *patellimana* Spinola (two nests) and *Pseudoheriades grandiceps* Peters (one nest). As these three species represent phylogenetically interesting lineages of the megachiline bees and as the published knowledge of the nesting of these species is fragmentary these notes offer a useful addition.

Methods

As flower visiting was being targeted most of the sampling was undertaken using hand nets. At all sites plants in flower were sampled for flower visitors. In addition wasps and bees perching on plants, resting on the ground, cruising, nesting and visiting water were collected.

Bundles of trap-nests (Figs 3, 5) of the Krombein design (boring in wood closed at inner end, open above, covered by a taped on clear Perspex (acrylic sheet) strip for viewing, above which covered by a wooden strip held in place by two elastic garters) were positioned horizontally in trees showing holes suggesting the presence of galleries resulting from boring by large carpenter bees, *Xylocopa* spp. (Apidae: Xylocopinae), or the larvae of longhorned beetles (Cerambycidae) (Figs 1a, 1b, 2). The trap-nests had cavities of length 155 mm and bore 5.5 mm, 9.5 mm or 12.7 mm. Each bundle was made up of six trap-nests, with two of each bore.

The positions selected for the trap-nests were: A branch of a the small tree *Calotropis procera* (Aiton) W.T. Aiton (Apocynaceae: Asclepiadoideae) (Fig. 3) at Tawi Ruwayyan (24.8968°N 55.6635°E) (Fig. 4), mainly a level drip irrigated area with a strong growth of low shrubby perennials, principally *Heliotropium kotschyi* (Bge.) Gurke (Boraginaceae), *Dipterygium glaucum* Decne. (Capparaceae), *Fagonia indica* Burm. *f.* (Zygophyllacae) and *Cyperus conglomeratus* Rotth. (Cyperaceae), beyond which on the surrounding dunes are scattered larger shrubs, *Leptadenia pyrotechnica* (Forssk.) Decne. (Apocynaceae: Asclepiadoideae) and *Salvadora persica* L. (Salvadoraceae), a clump of ghaf trees, *Prosopis cineraria* (L.) Druce. (Fabaceae: Mimosoideae), tamarix, *Tamarix aphylla* (L.) Karst. (Tamaricaceae), and the *Calotropis procera* tree; The trunk of a date palm (Fig. 5) at the Camel Farm (24.8030°N, 55.6503°E) (Fig. 6), a small grove of date palms, *Phoenix dactylifera* L. (Arecaceae), watered by irrigation

Figures 1–6. 1a, b Branches of *Calotropis procera*: **a** opening to boring **b** cut longitudinally to show a boring with at its base nest cells of a leaf cutting megachilid bee **2** Boring openings in the leaf bases of *Phoenix dactylifera* **3** *C. procera* tree outside the drip irrigation area at Tawi Ruwyyan with a bundle of trap-nests suspended from a branch **4** Tawi Ruwayyan, looking from the *C. procera* tree towards the drip irrigation area **5** Trap-nest bundle on trunk of *Phoenix dactylifera* in the date palm grove at the Camel Farm **6** Date palm grove at the Camel Farm.

furrows where the banks of the furrows, cavities in palm tree stumps and insect borings in palm leaf bases offer nesting sites for wasps and bees.

The trap nests were set out on 20 April 2105. Construction of nests within these trap-nests was monitored up until the end of April by SKG and PAR. After SKG's departure PAR continued to observe the nests and, after each was completed, took in the trap-nest and taped a vial over the open end to receive the imagines when they emerged. After the emergence of the imagines the Perspex sheets were removed and the opened trap-nests and the imagines were sent to SKG to be housed in the Albany Museum.

Results

Megachile (*Maximegachile*) *maxillosa*

Taxonomy. In their phylogenetic analysis of the tribe Megachilini Trunz et al. (2016) found that the subgenus *Maximegachilae* with the subgenus *Neglectella* formed a monophyletic group representing an isolated lineage.

Distribution. Senegal, Namibia, Botswana, South Africa, Zimbabwe, Malawi, Kenya, Sudan, Ethiopia, Saudi Arabia, Yemen and the DDCR (Gess and Roosenschoon 2016).

Flower visiting. There are no records for flower visiting by *Megachile maxillosa* in the DDCR (Gess and Roosenschoon 2016) nor as far as could be established are there any flower visiting records for this bee from elsewhere in the UAE. However, it has been commonly collected visiting flowers in the semi-arid to arid areas of South Africa and Namibia (Gess and Gess 2003) where it was collected from flowers of Acanthaceae, Apocynaceae (Asclepiadoideae), Asteraceae, Brassicaceae, Fabaceae (Caesalpinoideae, Mimosoideae and Papilionoideae), Pedaliaceae and Polygalaceae, although in Namibia it was most commonly visiting Papilionoideae, most notably species of *Crotalaria*. No distinction was made between pollen collection and nectar uptake. Though clearly polyphagous, a preference for Fabaceae is suggested, possibly indicating some degree of specialization.

Nesting. The only published mention of the nesting of the subgenus *Maximegachile* appears to be a comment by Kronenberg and Hefetz (1984, page 178) stating that "*Megachile maxillosa* nests in canes apparently without any further lining".

Four nests of *Megachile maxillosa* were constructed in trap-nests. Two of these trap-nests, both of 12.7 mm bore were part of the bundle suspended from the branch of the *Calotropis procera* tree at Tawi Ruwayyan and two of 9.5 mm bore were part of the bundle attached near the base of a date palm at the Camel Farm.

The walls of the cells, the cell closures and the nest closure were constructed from a mixture of sand and resin. The average length of the cells is 26.4 mm (sample of 12 cells). In three of the nests the first cell was initiated in contact with the inner end of the boring and in the fourth, one of the two from the Camel Farm, the first cell was initiated 25 mm from the inner end beyond a nest of *Pseudoheriades grandiceps* (Fig. 7, trap-nest 3).

Figure 7. Trap-nests 1–4 as at 25 May 2016 after *Megachile maxillosa* imagines had emerged from all of the cells. Trap-nest 3 shows the remains of the nest of *Pseudoheriades grandiceps* that preceded the nest of *M. maxillosa.*

In completed nests the opening of the boring had been sealed with a 3 mm thick plug of sand and resin in consistency similar to that of the cell walls and closures. The empty space, the vestibular cell, between the last cell and the closure varied from 12 to 40 mm. In one of the nests the vestibular cell had been divided into two and in another three compartments (Fig. 7, trap-nests 3 and 1).

Nesting progress. At Tawi Ruwayyan on 23 April a female *Megachile maxillosa* was provisioning a newly constructed cell in one of the trap-nests (trap-nest 1). By 27 April this nest consisted of two completed and sealed provisioned cells. After the second cell had been completed a leaf-cutting megachilid had usurped the nest (Fig. 9) and *M. maxillosa* had initiated cell construction in the neighbouring trap-nest (trap-nest 2) (Fig. 8). By the following day the walls of this cell had been completed and provisioning was in progress (Fig. 10). When taken in later during May the nest in trap-nest 2 had four completed cells and that in trap-nest 1 three completed cells, a large sub-divided vestibular cell and an outer seal, indicating that the usurper had been ousted (Fig. 7, trap nest 1).

At the Camel Farm on 23 April *Megachile maxillosa* was provisioning a cell in trap-nest 4 (Fig. 11). By 28 April she had constructed, provisioned and sealed two cells and was busy constructing a third cell (Fig. 12). When inspected on 30 April there were 4 cells, all provisioned and closed. During May *M. maxillosa* had constructed, provisioned and sealed three cells in the neighbouring trap-nest 3 beyond a nest of *Pseudoheriades grandiceps* (Fig. 13). An empty vestibular cell had then been constructed subdividing the vestibular area between the last cell and the opening of the trap-nest, which had been sealed (Fig. 14).

Figures 8–15. 8 Trap-nest 2 of trap-nest bundle at Tawi Ruwayyan on 27 April 2015, showing *Megachile maxillosa* initiating a cell **9** Trap-nest 1 of trap-nest bundle at Tawi Ruwayyan on 27 April 2015, showing two closed cells of *M. maxillosa* followed by leaf pieces, presumed to be those of a leaf cutting *Megachile* sp. **10** Trap-nest 2 of trap-nest bundle at Tawi Ruwayyan on 28 April 2015, showing first cell being provisioned by the builder, *M. maxillosa* **11** Trap-nest 4 of trap-nest bundle at the Camel Farm on 27 April, showing one open cell being provisioned by *M. maxillosa* **12** Trap-nest 4 of trap-nest bundle at the Camel Farm on 28 April 2016, showing two closed provisioned cells with *M. maxillosa* initiating a third cell **13** Trap nest 3 of trap-nest bundle at the Camel Farm showing nest of *Pseudoheriades grandiceps* at inner end followed by three-celled nest of *M. maxillosa* **14** Trap-nest 4 of trap-nest bundle at the Camel Farm showing final seal of nest of *M. maxillosa* **15** *M. maxillosa* female imago (actual length approx. 22 mm) with open cocoon.

When PAR inspected the nests in early April 2016 no imagines had emerged but by 11 May five females and four males had emerged (Figs 7, 15).

Provision. The provision was a bright yellow, moist mixture of pollen and nectar (Figs 9–12).

The identity of the pollen was not established. In order not to damage the nests the Perspex sheets were not removed until after the imagines had emerged.

Cocoon. The cocoons were brown, smooth and papery on the inside and lightly covered with silk spinnings on the outside. Each cocoon occupied the inner two thirds of a cell, the outer third being closely packed with fecal pellets.

Associated insects. A bombyliid larva was found in nest 1, suggesting that it had been responsible for the failed cell.

Megachile (*Eurymella*) *patellimana*

Taxonomy. In Gess and Gess (2003) and in Gess and Roosenschoon (2016) *Megachile patellimana* is given as belonging to the subgenus *Eutricharaea,* following Michener (2007) who did not consider the subgenus *Eurymella* Pasteels (1965) to be distinct from the subgenus *Eutricharaea*. Michener's opinion was generally accepted (e.g. Eardley et al. 2010, Eardley 2013). However, in their analysis Trunz et al. (2016) revisit the status of *Eurymella* and recognize it as a valid subgenus distinct from *Eutricharaea.* Their opinion has been accepted and in the present contribution *Eurymella* is recognized as being distinct from *Eutricharaea* given that both groups appear distantly related in the phylogeny of Trunz et al.

The female of *Megachile patellimana*, like most species of *Eurymella,* has robust mandibles with particularly large and acute teeth, as also seen in the subgenus *Creightonella*. In *Eutricharaea*, in contrast, the female mandibles are mostly less robust and the teeth smaller.

Distribution. Widely distributed in western Palaearctic, particularly in the Mediterranean, Asia Minor, Egypt and UAE, also south-western Africa, Sudan, Niger and Mozambique (Gess and Roosenschoon 2016).

Flower visiting. In the DDCR *Megachile patellimana* has been recorded from flowers of Apocynaceae: Asclepiadoideae, *Leptadenia pyrotechnica*; Asteraceae: *Centaurea pseudosinaica* Czerep.; Boraginaceae: *Heliotropium kotschyi*; Brassicaceae: *Farsetia linearis* Decne ex Boiss.; Fabaceae: Mimosoideae: *Prosopis cineraria* ; Fabaceae: Papilionoideae: *Crotalaria aegyptiaca* Benth.; Zygophyllaceae: *Tribulus maropterus* Boiss. (Gess and Roosenschoon 2016).

In Namibia this species has been recorded from flowers of *Crotalaria podocarpa* DC (Papilionoideae) (Gess and Gess 2003).

Nesting. The only published mention of the nesting of *Megachile patellimana* appears to be the statement in Alfken (1934, page 148) that "Als echte Blattschneiderbiene ist auch *M. patellimana* M. Spin. beobachet worden" [*M. patellimana* has also been observed as a true leaf-cutting species]. The nesting situation does not seem to have been recorded.

The only other observations on nesting by a species of the subgenus *Eurymella* seem to be those for *Megachile bucephala* (Fabricius) (as *M. semifulva* Friese, recently placed in synonymy with *M. bucephala* (Eardley, 2013); this synonymy requires confirmation given that Pasteels (1965: 127) mentions that there are sculptural differences

Figure 16. *Megachile patellimana:* female (actual length approx. 16 mm) with a leaf piece (green and fresh when collected) and female (actual length approx. 16 mm) with cut lengths of plastic, one from female and the rest from her nesting burrow.

between *M. semifulva* and *M. bucephala* (C. Praz, pers. comm.)). These observations "Nests in ground 6-7 inched vertical; lined with blade of certain grass, selected them before biting; measures it by running up and down. The pieces varied in length from 3-4 inches. St. W. Warley, 29.X.1916" quoted by Pasteels (1965: page 127) are from manuscript copies in the Natal and Durban museums.

It therefore seems worth recording the fragmentary observations on the nesting of *Megachile patellimana* in the DDCR where it was observed to be nesting at Tawi Manana in burrows excavated in compacted sand beneath *Heliotropium kotschyi* plants and at the Camel Farm in burrows excavated in the compacted sand banks of an irrigation furrow. It was not clear whether the burrows had been originated by *M. patellimana* or were pre-existing.

At Tawi Manana a female was captured carrying a piece of cut green leaf (approx. length 10 mm and approx. width 5 mm) and at the Camel Farm a female was captured carrying into a burrow a piece of tough green plastic approximately 10 mm in length cut from a strip 2 mm wide and almost 1 mm in thickness (Fig. 16). Attempts to excavate the nests did not yield nest plans. In the nest of the female carrying plastic six more identical pieces of plastic (average length10 mm) were discovered grouped together in an apparent attempt to construct a cell. The cutting of the tough plastic would have been possible by using the large, robustly and acutely toothed mandibles.

The use of plastic by *Megahile patellimana*, though surprising, is supported by the observations of MacIvor and Moore (2013) who reported that *Megachile rotundata* Fabricius, which normally uses cut pieces of plant leaf, was found constructing brood cells out of cut pieces of polyethylene-based plastic bags. In addition to recording the use of plastic bags by *M. rotundata* MacIvor and Moore reported, even more surprisingly, that *Megachile campanulae* (Robertson), which uses plant and tree resins, was found to have made brood cells constructed out of a polyurethane-based exterior building sealant. In their discussion they suggested that "Although perhaps incidentally collected, the novel use of plastics in the nests of bees could reflect eco-

logically adaptive traits necessary for survival in an increasingly human-dominated environment".

It is clear that the flexible pieces cut from polyethylene bags by *Megachile rotundata* were successfully used to construct cells whereas it is seems unlikely that *Megahile patellimana* would have successfully constructed cells from the stiff, narrow strips of plastic that she was assembling within her nesting burrow.

Provision. As both the nesting females were captured carrying nesting materials their scopae were empty and as nesting was in an early stage no provision was obtained from the nests.

Pseudoheriades grandiceps

Taxonomy. The phylogenetic position of the genus *Pseudoheriades* is debated. In a molecular phylogeny of the Osmiini (Praz et al. 2008) this genus was allied with the genus *Afroheriades*. Both genera were not closely related to the Osmiini but formed an isolated lineage with currently uncertain phylogenetic affinities. In contrast, in cladistic analyses of morphological characters, these two genera appeared within the *Heriades*-group of the Osmiini although statistical support for this placement was low. Consequently, the phylogenetic placement of the *Pseudoheriades/Afroheriades* lineage within the megachiline phylogeny remains unsettled (see also Litman et al. 2011).

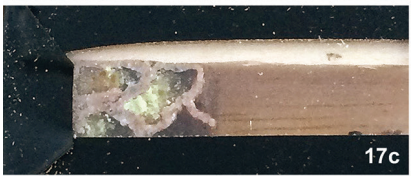
Distribution. Saudi Arabia, United Arab Emirates, Iran, Pakistan and India (Ungricht et al. 2008, Dathe 2009, Ascher and Pickering 2016)

Nesting. The only published information on nesting by *Pseudoheriades* appears to be a brief account of the nesting biology of *P. moricei* (Friese) (Krombein 1969; as *Heriades moricei* Friese) and notes on a nest of *P. grandiceps* (Rozen and Praz 2016).

Krombein described the construction of four nests of *Pseudoheriades moricei* in trap-nests positioned variously on a vine-covered summer-house, a trellis and the trunk of a casuarina tree in gardens at three sites in Egypt. The cells, of the same diameter as the borings, were in linear series. The partitions capping the cells, dividing vestibular cells, and the closure of the nest were of resin or resin mixed with tiny pebbles.

The nest of *Pseudoheriades grandiceps* described by Rozen and Praz is based on notes, nest fragments and cocoons pinned with adults from the UAE preserved at Logan, Utah. Their figures 64 and 65 show two adults, one a female pinned with a leaf covered nest cell and a male pinned with a petal covered nest cell from which they had emerged. It was recorded that cell partitions within the leaf covering and petal covering were constructed from resin. It was not clear whether the leaves and petals had been placed by the female *P. grandiceps* or whether, as suggested by Praz, the trap-nest had been previously occupied by a different megachilid. The use of a pre-existing cavity, and the use of resin are the only similarities with the nest from the DDCR.

The notes presented here on nesting by *Pseudoheriades grandiceps* in the DDCR provide the first detailed observations on nest structure for this species. The nest was constructed in a trap-nest of 9.5 mm bore, part of the bundle attached near the base of



Figures 17–19. 17a–c Cells of *Pseudoheriades grandiceps* in trap-nest 3 of trap-nest bundle at the Camel Farm **18** Nest of *P. grandiceps* after emergence of imagines, visible trapped between their natal nest and a nest of *Megachile maxillosa* which usurped trap-nest 3 **19** *P. grandiceps,* imago (actual approx.7mm) from nest.

the trunk of a date palm at the Camel Farm. It consisted of a cluster of cells constructed from a mixture of sand and resin. The cells free from the walls of the boring were ovoid, approximately 6 mm in length and at the widest point 3.5 mm in width with the wall approximately 1 mm in thickness. Those constructed against the Perspex cover were incompletely constructed, the Perspex forming part of the cell wall (Fig. 17a–c).

That no leaves or petals formed part of the nests of either *Pseudoheriades moricei* described by Krombein nor that of *P. grandiceps* described in the present contribution confirms the suggestion that the leaves and petals present in the nest of *P. grandiceps* nest described by Rozen and Praz were present in the trap nest before the female *P. grandiceps* started her nesting activities and that she had constructed her cells within the walls of cells of another megachilid that had previously occupied the cavity. Furthermore that the cells, composing the nest of *P. grandiceps* here described, were in a boring of larger diameter than the cells and that the cells were not constructed in linear series but were grouped to form a cluster suggests that *P. grandiceps* may be found to nest in cavities other than straight borings.

Nesting progress. The first cell had been constructed by 27 April and by 2 May five cells had been constructed. Sometime later the boring was usurped for nesting by *Megachile maxillosa* (Fig. 13). When the nest was inspected in early April 2016 no imagines had emerged but by May imagines had emerged from all of the cells (Figs 18, 19).

Provision. The identity of the pollen used in provisioning was not established. In order not to damage the cells the Perspex sheet was not removed until after the imagines had emerged.

Associates. Three specimens of *Zonitoschema iranica* Kasab, 1959 (Meloidae) from Ras al-Khaymah in the United Arab Emirates were recorded as having been reared from a nest of *Pseudoheriades grandiceps* (Batelka and Bologna 2014).

Discussion

The large genus *Megachile* (*sensu* Trunz et al. 2016) has commonly been divided into two series based on nesting biology: the leafcutter subgenera (Michener's group 1) and the dauber subgenera (Michener's group 2), sometimes recognized as a distinct genus, *Chalicodoma*. Michener (2007) also placed the subgenus *Creightonella* into a third group (Michener's group 3). Trunz et al. (2016) have recently suggested that the dauber bees (*Chalicodoma sensu lato*) formed a paraphyletic group from which the leafcutter arose, a result also found in cladistic analyses of morphological characters (Gonzalez 2008). Phylogenetic relationships between the various lineages of the dauber bees remained unresolved. The genus-group name *Chalicodoma* was first proposed for the group allied to *M. parietina* Geoffroy, a species building hard, exposed nests made of mud (Lepeletier 1840), but it appears that numerous lineages of Michener's group 2 use resin to build their nests, such as the subgenera *Callomegachile* and *Chelostomoides* (Michener 2007). Those species of *Megachile* (*Callomegachile*), the nesting of which was known to Michener, construct cells from resin mixed with wood fibers or together with layers of leaf pieces or mud in pre-existing cavities, however, *M. chrysorrhea* Gerstäcker constructs its cells entirely from resin, the walls being thin and almost cellophane-like and *M. rufiventris* Guérin-Menéville (as *M.* (*Callomegachile*) *aridissima* Cockerell) apparently lines its cells with resin (Gess and Gess 2014). In the subgenus *Pseudomegachile* some species construct their cells entirely of mud (Gess and Gess 2014) and others, for example *Megachile ericetorum* Lepeletier, use resin to line the inside of the mud walls (Westrich 1989). The present observations on the nesting biology of *M. maxillosa* give the first account for this species and for the subgenus *Maximegachile* of the use of resin and sand in cell wall construction and for sealing the nesting gallery. In the phylogeny of Trunz et al. (2016), the subgenus *Maximegachile* formed an isolated lineage not closely related to *Callomegachile* but forming a monophyletic group with the subgenus *Negelectella*. Michener (1968) gives a brief account of the nesting biology of an unknown species of *Neglectella*. Interestingly, like *M. maxillosa,* it uses resin and sand in cell wall construction within a pre-existing cavity. Taken together, these findings suggest that resin, possibly used in combination with mud, may be the ancestral building material in the genus *Megachile* and in the tribe Megachilini.

Furthermore, resin appears to be an important nesting material broadly in the Megachilinae. In addition to its use in the Megachilini, resin is used by members of

three of the four nest-building groups of the tribe Anthidiini (Litman et al. 2016), in the *Heriades* group of the tribe Osmiini (Praz et al. 2008; Rozen and Praz 2016), and by the genus *Pseudoheriades* of the isolated *Pseudoheriades/Afroheriades* lineage. Resin is particularly suitable as a nest-building material because it is waterproof (Litman et al. 2011) and antifungal (Messner 1985). In addition, it has been suggested by Eltz et al. (2015) that an overlooked property of plant secretions included in megachilid nests may be the deterrence of parasitoids.

Conclusion

It is clear that further studies on the nesting biology of additional species of Megachilidae will add to a fuller understanding of their phylogeny.

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References

Alfken JD (1934) Beitrag zur Kenntnis der *Megachile*-Arten von Aegypten (Hymenoptera: Apoidea). Bulletin de la Société Royale Entomologique d'Egypte 18: 146–163.

Ascher J, Pickering J (2016) Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species [Draft 46, 20 November 2016]

Batelka J, Bologna AA (2014) A review of the Saharo-Sindian species of the genus *Zonitoschema* (Coleoptera: Meloidae), with descriptions of new species from Tunisia, Yemen and Socotra Island. Acta Entomologica Musei Nationalis Prague 54: 241–268.

Dathe H (2009) Order Hymenoptera, superfamily Apoidea. In: van Harten A (Ed.) Arthropod fauna of the UAE, vol. 2. Dar Al Ummah Printing, Publishing & Advertising, AbuDhabi, 335–432.

Eardley C (2013) A taxonomic revision of the southern African leaf-cutter bees, *Megachile* Latreille *sensu stricto* and *Heriadopsis* Cockerell (Hymenoptera: Apoidea: Megachilidae). Zootaxa 3601(1): 1–134. https://doi.org/10.11646/zootaxa.3601.1.1

Eardley C, Kuhlmann M, Pauly A (2010) The Bee Genera and Subgenera of sub-Saharan Africa. Abc Taxa volume 7: 1–138.

Eltz T, Küttner J, Lunau K, Tollrian R (2015) Plant secretions prevent wasp parasitism in nests of wool-carder bees, with implications for the diversification of nesting materials in Megachilidae. Frontiers in Ecology and Evolution 2(86): 1–7. https://doi.org/10.3389/fevo.2014.00086

Gess SK, Gess FW (2003) A catalogue of flower visiting records for aculeate wasps and bees in the semi-arid to arid areas of southern Africa. Albany Museum, Grahamstown, 529 pp.

Gess SK, Gess FW (2006) Survey of flower visiting by solitary aculeate wasps and bees in the semi-arid to arid areas of southern Africa. Annals of the Eastern Cape Museums 5: 1–51.

Gess SK, Gess, FW (2014) Wasps and bees in southern Africa SANBI Biodiversity Series 24. South African National Biodiversity Institute, Pretoria, 320 pp.

Gess SK, Roosenschoon PA (2016) A preliminary survey of flower visiting by aculeate wasps and bees in the Dubai Desert Conservation Reserve. Journal of Hymenoptera Research 52: 81–141. https://doi.org/10.3897/jhr.52.10034

Gonzalez VH, Griswold T, Praz CJ, Danforth BN (2012) Phylogeny of the bee family Megachilidae (Hymenoptera: Apoidea) based on adult morphology. Systematic Entomology 37: 261–286. https://doi.org/10.1111/j.1365-3113.2012.00620.x

Krombein KV (1969) Life history notes on some Egyptian solitary wasps and bees and their associates (Hymenoptera: Aculeata). Smithsonian Contributions to Zoology 19: 1–18. https://doi.org/10.5479/si.00810282.19

Kronenberg S, Hefetz A (1984) Role of labial glands in nesting behavior of *Chalicodoma sicula* (Hymenoptera; Megachilidae). Physiological Entomology 9: 175–179. https://doi.org/10.1111/j.1365-3032.1984.tb00696.x

Litman JR, Danforth BN, Eardley CD, Praz CJ (2011) Why do leafcutter bees cut leaves? New insights into the early evolution of bees. Proceedings of the Royal Society B 278: 3593–3600. https://doi.org/10.1098/rspb.2011.0365

Litman JR, Griswold T, Danforth BN (2016) Phylogenetic systematics and a revised generic classification of anthidiine bees (Hymenoptera: Megachilidae). Molecular Phylogenetics and Evolution 100: 183–198. https://doi.org/10.1016/j.ympev.2016.03.018

MacIvor JS, Moore AE (2013) Bees collect polyurethane and polyethylene plastics as novel nest materials. Ecosphere 4(12): 155. http://dx.doi.org/10.1890/ES13-00308.1

Messner AC (1985) Fresh dipterocarp resins gathered by megachild bees inhibit growth of pollen-associated fungi. Biotropica 17: 175–176.

Michener CD (1968) Nests of some African megachilid bees, with description of a new Hoplitis (Hymenoptera, Apoidea). Journal of the Entomological Society of Southern Africa 31: 337–359.

Michener CD (2007) The bee genera of the world. Second Edition. The John Hopkins University Press, Baltimore and London, 953 pp.

Pasteels JJ (1965) Révision des Megachilidae (Hymenoptera Apoidea) de L'Afrique Noire I. Les Genres Creightoniella, Chalichodoma et Megachile (s. str.). Musée Royal de L'Afrique Centrale , Tervuren, Belgique, Annales Serie in-8°, Sciences Zoologiques 137: 1–579.

Praz CJ, Müller A, Danforth BN, Griswold TL, Widmer A, Dorn S (2008) Phylogeny and biogeography of bees of the tribe Osmiini (Hymenoptera: Megachilidae). Molecular Phylogenetics and Evolution 49: 185–197. https://doi.org/10.1016/j.ympev.2008.07.005

Rozen J, Praz CJ (2016) Mature larvae and nesting biologies of bees currently assigned to the Osmiini (Hymenoptera: Megachilidae). American Museum Novitates 3864: 1–46. https://doi.org/10.1206/3864.1

Trunz V, Packer L, Arrigo N, Praz CJ (2016) Comprehensive phylogeny, biogeography and new classification of the diverse bee tribe Megachilini: Can we use DNA barcodes in phylogenies of large genera. Molecular Phylogenetics and Evolution 103: 245–259. https://doi.org/10.1016/j.ympev.2016.07.004

Ungricht S, Müller A, Dorns S (2008) A taxonomic catalogue of the Palaearctic bees of the tribe Osmiini (Hymenoptera; Apoidea: Megachilinae). Zootaxa 1865: 1–253.

Westrich P (1989) Die Wildbienen Baden-Wurttembergs: Spezieller Teil: Die Gattungen und arten. Eugene Ulmer, Stuttgart, 437–972.