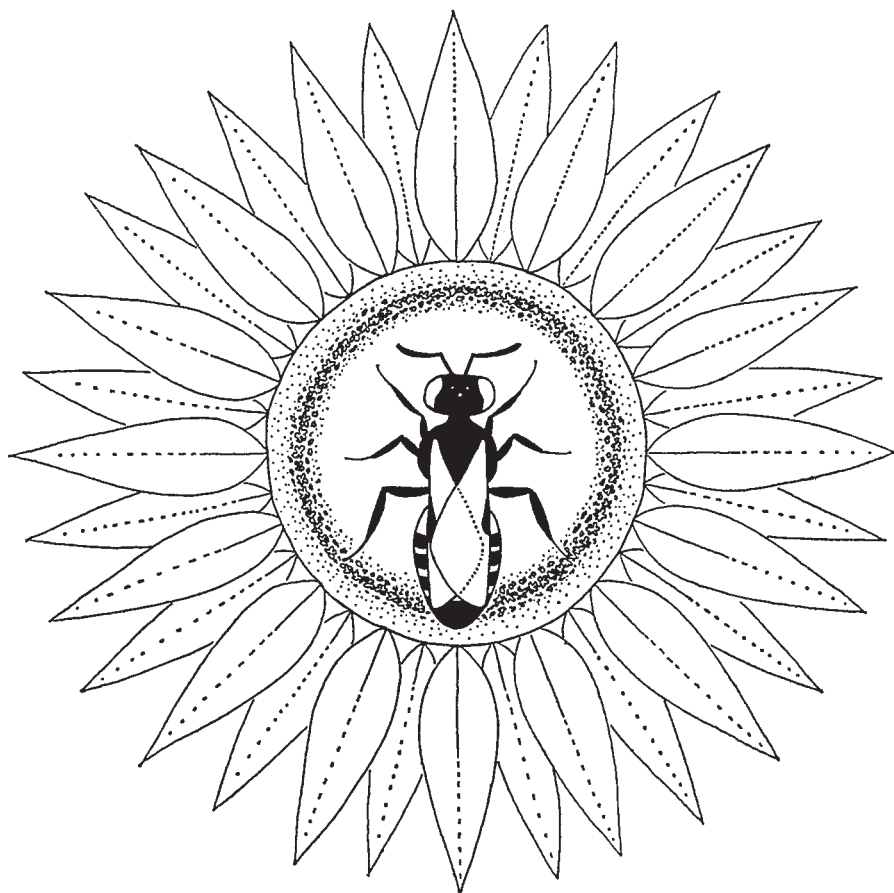


JKES

JOURNAL OF THE KANSAS ENTOMOLOGICAL SOCIETY
(CENTRAL STATES ENTOMOLOGICAL SOCIETY)



**Unexpected Polylecty in the Bee Genus *Meganomia*
(Hymenoptera: Apoidea: Melittidae)**

D. MICHEZ,^{1,*} C. D. EARDLEY,² K. TIMMERMANN,³ AND B. N. DANFORTH⁴

Unexpected Polylecty in the Bee Genus *Meganomia* (Hymenoptera: Apoidea: Melittidae)

D. MICHEZ,^{1,*} C. D. EARDLEY,² K. TIMMERMANN,³ AND B. N. DANFORTH⁴

ABSTRACT: The melittid bees represent an early branch of bee phylogeny. They are therefore of special interest in understanding the early evolution and diversification of bees. Most species have been observed to be oligolectic (i.e., highly specialized in their choice of host-plant species). However, knowledge of host-plant associations is not equivalent across all melittid groups. Dasypodainae and the Melittinae are relatively well-known, while the African Meganomiinae are poorly studied. Preliminary field records seem to indicate that at least some meganomiine species are oligolectic. Here we present the first palynological analysis of pollen loads and pollen preference in Meganomiinae. Our results indicate that *M. binghami* is clearly a polylectic species. More data are needed to draw conclusions on the foraging behaviour of the other Meganomiinae. Our results show that, while oligolecty is widespread among melittid bees, there are polylectic lineages as well.

KEY WORDS: Oligolecty, polylecty, host plant associations, palynology

Introduction

Melittidae is a small family of bees comprising 16 extant genera and approximately 200 described species (Michez *et al.*, 2009). Female melittid bees generally forage on pollen from a restricted number of host plants, and many species are believed to be oligolectic (*sensu* Cane and Sipes, 2006) (Michez *et al.*, 2008). They are strictly ground-nesting and occur in the temperate, semi-desert and Mediterranean regions of the Old World and the Nearctic Region (Michener, 1979). Three subfamilies are traditionally recognized: Dasypodainae, Meganomiinae and Melittinae (Michener, 2007). Some authors proposed to consider these three subfamilies as families but the results of phylogenetic studies have so far remained inconclusive (Alexander and Michener, 1995; Danforth *et al.*, 2006). Melittid bees are possibly the sister group of all other bees or a basal grade from which the other bee families arose (Fig. 1; Danforth *et al.*, 2006; Michener, 2007). The study of their biology and their systematics is therefore of great interest in understanding the origin and the early evolution of bees.

Meganomiinae is the least speciose subfamily among the three melittid subfamilies (Michener, 2007; Michez *et al.*, 2009). Taxonomic affinities of Meganomiinae were unclear until Stage (1971; and later Michener [1981]) placed them in the family

¹ University of Mons, Laboratory of Zoology, place du parc 20, 7000 Mons, Belgium, e-mail: denis.michez@umons.ac.be

² Agricultural Research Council, Private Bag X134, 0121 Queenswood, Pretoria, South Africa. School of Biological and Conservation Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville, Pietermaritzburg, 3209, South Africa, e-mail: eardleyc@arc.agric.za

³ Institute of Landscape Ecology, University of Münster, Robert-Koch-Str. 26, D-48149 Münster, Germany, e-mail: kimtimmermann@gmx.de

⁴ Department of Entomology, Comstock Hall, Cornell University, Ithaca, NY 14853-0901, e-mail: bnd1@cornell.edu

* Corresponding author.

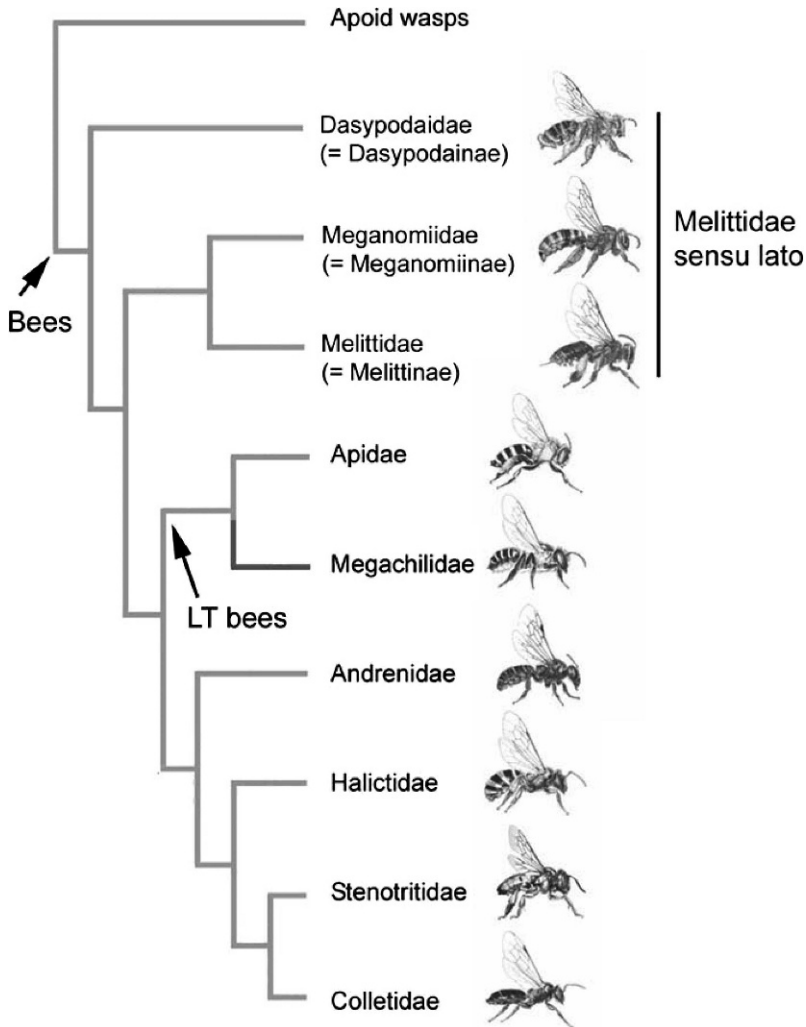


Fig. 1. Phylogeny of bees according to Danforth *et al.* (2006). Danforth *et al.* (2006) consider subfamilies of Melittidae as family level. LT = Long tongued bees.

Melittidae. Recent molecular analyses have placed Meganomiinae as sister to Melittinae (Fig. 1) (Danforth *et al.*, 2006).

Meganomiine species are robust bees with three sub-marginal cells, extensive yellow markings on the whole body and many unique modifications of the legs and hidden sterna of the male (Michener, 1981). They are restricted to Sub-Saharan Africa except for one undescribed *Meganomia* species recorded from Yemen. Michener (1981), Michener and Brooks (1987) and Michener *et al.* (1990) reviewed the four included genera and the 12 species: *Ceratonomia* Michener 1981 (one described species), *Meganomia* Cockerell 1931 (four described species and one undescribed species), *Pseudophilanthus* Alfken 1939 (four described species) and *Uromonia* Michener 1981 (two described species).

The ecology and floral choices of Meganomiinae are poorly known. *Meganomia gigas* Michener 1981 is the only species whose nesting behaviour has been described (Rozen, 1977). *M. gigas* presents a nesting behaviour which can be regarded as functionally intermediate between that of Dasypodainae and Melittinae. Females are gregarious and dig a deep nest (120 cm) in sandy soil, as in Dasypodainae, but they apply a waterproof lining to the cell walls, as in Melittinae. Moreover, the females of *M. gigas* moisten the pollen with nectar during their foraging trips and their larvae spin cocoons, as in Melittinae. Provisioning behaviour has been described for *M. gigas* and *Ceratonomia rozenorum* Michener 1981 (Rozen, 1977). Both species appear to be oligolectic on Fabaceae (on *Crotalaria podocarpa* and *Indigofera* sp., respectively). Lastly Gess and Gess (2004, 2006) and Eardley and Urban (2010) listed floral records for both previous species and for *M. binghami*. *M. gigas* was recorded on *Crotalaria* and *C. rozenorum* on *Indigofera*, confirming earlier observations by Rozen. Field records of *M. binghami* indicate various host-plants suggesting polylectic behaviour or possibly the existence of multiple cryptic, oligolectic species. But these field records do not distinguish pollen and nectar collection and palynological analyses are necessary to confirm pollen preferences (e.g., Westrich and Schmidt, 1986; Westrich, 1990; Müller, 1996; Sipes and Tepedino, 2005).

Hereafter we present a review and new data on one species, *M. binghami*. We reviewed material from collections (309 specimens) allowing us to diagnose accurately the species and describe its distribution. Lastly, we performed palynological analyses of the pollen from female scopae. We compare pollen loads of *M. binghami* with available pollen loads of *M. gigas* and *M. andersoni*. We discuss the results of these palynological analyses in relation to the evolution of host-plant specialization in the Melittidae.

Material and Methods

One of us (DM) studied the type material of *M. binghami* in the collections of the Natural History Museum (NHM, London, UK). Additional specimens belonging to the Kansas University collection (KU, USA), American Museum of Natural History (AMNH, USA), Oberösterreichisches Landesmuseum Linz (OOLL, Austria), Cornell University Insect Collection (CUIC, USA), University of Liège Gembloux agro-Bio Tech (FSAGX, Belgium), Musée royal d'Afrique central de Tervuren (MRACT, Belgium), Plant Protection Research Institute Pretoria (NCSA, South Africa), Zoological Institute of Saint Petersburg (ZIS, Russia) and the University of Mons (UMons, Belgium) were also examined. Review of this material allowed us to evaluate the extent of morphological variation in the species.

We used the glossary of Michener (2007) for the description of the morphology. The cuticular ultrastructures were studied using SEM (JEOL JSM-6100) linked to the software package "Semafore" (JEOL, Sollentuna, Sweden).

The map (Fig. 3) is based on 309 specimens. Biogeographical data have been included in the *Banque de Données Fauniques Gembloux-Mons* (BDFGM). They were managed using Data Fauna Flora 2.0 (Barbier *et al.*, 2000). Conventional geographic coordinates of the records have been searched in the numeric gazetteer included in the software (CFFGazet). Data were mapped using Carto Fauna Flora 2.0 (Barbier and Rasmont, 2000). A Gall geographical projection was used for mapping the data.

The label data provided information on the floral visits of 116 specimens of *Meganomia binghami* (92 females and 24 males). We identified the pollen from the scopae of 23 *M. binghami* females from three different localities. Moreover, we analysed the pollen from 3 females of *M. gigas* and 4 females of *M. andersoni*.

The pollen was gently removed with a pin and embedded in glycerol gelatine on microscope slides. Pollen samples were identified by light microscopy at a magnification of 400 \times . Pollen composition was investigated by identification of 400 pollen grains randomly chosen from each sample (Table 1). Pollen grains representing less than 5% of each load were assumed to be contamination and were ignored (Westrich and Schmidt, 1986). According to the definitions of Müller and Kuhlmann (2008), we designated a species as oligolectic if more than 95% of the total pollen originated from one host-plant family. If not, we considered the species to be mesolectic or polylectic depending on the diversity of the alternative host-plants.

Pollen samples were determined by K. Timmerman. Pollen determination is not easy in Africa due to the high diversity of plants and the poor knowledge on the pollen morphology. However, a likely determination is possible and identification of “morphopollen” is possible.

Results

Meganomia binghami (Cockerell 1909)

Nomia (*Meganomia*) *binghami* Cockerell 1909: 402–403. Original designation of the locus typicus: “*Damara Land*”. Holotype ♀, two paratypes ♂.

DIAGNOSIS: The morphology of male and female of *M. binghami* is very constant. Shapes, cuticular structure, yellow maculations and pilosity are unchanging among populations. Females can be distinguished from other *Meganomia* by their yellow clypeus from side to side with a pair of basomedian black areas extending across more than the middle of the clypeus, the scutum is black with a narrow yellow band on the anterior margin; the metanotum is fully yellow and the yellow band across the first tergum is interrupted medially. Males can be separated by the fifth sternum having two apical combs (Fig. 2C) and the shapes of hidden sterna 6–8 and genitalia (Fig. 2D–H).

EXAMINED MATERIAL: **ANGOLA**. 1♀, road Espinheira to Namibe, 15°18'36"S 12°09'56"E, 23.I.2009, leg. C. Eardley, on *Crotalaria* sp., NCSA. **BOTSWANA**. 1♂, Palapye [22.55°S 27.13°E], FSAGX; 1♀, Ghanzi [21.57°S 21.78°E], 26.I.1994, leg. Konaka, NCSA. **SOUTH AFRICA**. 1♀, Langjan Nature Reserve [22.85°S 29.21°E], 24.I.1982, leg. Eardley, NHM; 1♂, Noeniepoort [29.23°S 18.78°E], 13.II.1984, leg. Whitehead, NHM; 1♀, Pomfret [25.82°S 23.53°E], 26.II.1980, leg. Whitehead, NHM; 1♀/5♂, Hotazel [27.23°S 22.97°E], 15.I.2004, on *Tribulus* sp., leg. Danforth, CUIC; 15♀/1♂, idem, 14.I.2004; 15♀/1♂, Van Zylsrus [26.98°S 22.07°E], 16.I.2004, on *Tribulus* sp., leg. Danforth, CUIC; 37♀/7♂, Vivo [23.05°S 29.28°E], 07.I.2004, on *Cleome* sp., leg. Danforth, CUIC; 1♀, Kalahari Gemsbok National Park [25.68°S 20.33°E], 28.III.1990, leg. Schwarz, FSAGX; 1♂, Olifantshoek [27.93°S 22.73°E], 25.III.1990, leg. Schwarz, FSAGX; 11♂, Beit Bridge [22.21°S 29.98°E], 09.III.1990, leg. Eardley, NCSA; 4♀/3♂, Hotazel [27.23°S 22.97°E], 17.I.2004, leg. Eardley, NCSA; 1♀, Kruger National Park [22.26°S 31.12°E], 20–24.I.1985, leg. Eardley, NCSA; 25♀/18♂, Langjan Nature Reserve [22.83°S 29.23°E], 10.III.1990, leg.

Table 1. Palynological analyses of pollen from female scopae. SA = South Africa. Fil. = Degree of filling; 5 = 100% filled. Pollens A–D seem different from the likely pollen of Aizoaceae, *Cleome* (Cleomaceae), Geraniaceae and *Tribulus* (Zygophyllaceae).

Species	Locality, date, floral record, collector	Fil.	Pollen
<i>M. binghami</i>	SA, Van Zylsrus, 16.I.2004, on <i>Tribulus</i> , B.N. Danforth	2	100% likely <i>Tribulus</i>
<i>M. binghami</i>	SA, Van Zylsrus, 16.I.2004, on <i>Tribulus</i> , B.N. Danforth	3	100% likely <i>Tribulus</i>
<i>M. binghami</i>	SA, Van Zylsrus, 16.I.2004, on <i>Tribulus</i> , B.N. Danforth	3	100% likely <i>Tribulus</i>
<i>M. binghami</i>	SA, Van Zylsrus, 16.I.2004, on <i>Tribulus</i> , B.N. Danforth	2	100% likely <i>Tribulus</i>
<i>M. binghami</i>	SA, Van Zylsrus, 16.I.2004, on <i>Tribulus</i> , B.N. Danforth	2	100% likely <i>Tribulus</i>
<i>M. binghami</i>	SA, Van Zylsrus, 16.I.2004, on <i>Tribulus</i> , B.N. Danforth	2	100% likely <i>Tribulus</i>
<i>M. binghami</i>	SA, Van Zylsrus, 16.I.2004, on <i>Tribulus</i> , E. Almeida	2	100% likely <i>Tribulus</i>
<i>M. binghami</i>	SA, Van Zylsrus, 16.I.2004, on <i>Tribulus</i> , E. Almeida	2	100% likely <i>Tribulus</i>
<i>M. binghami</i>	SA, Vivo, 8.I.2004, on <i>Cleome</i> , E. Almeida	4	55% likely <i>Cleome</i> , 45% pollen A
<i>M. binghami</i>	SA, Vivo, 8.I.2004, on <i>Cleome</i> , E. Almeida	2	100% likely <i>Cleome</i>
<i>M. binghami</i>	SA, Vivo, 8.I.2004, on <i>Cleome</i> , E. Almeida	4	100% pollen A
<i>M. binghami</i>	SA, Vivo, 8.I.2004, on <i>Cleome</i> , E. Almeida	2	100% likely <i>Cleome</i>
<i>M. binghami</i>	SA, Vivo, 8.I.2004, on <i>Cleome</i> , B.N. Danforth	3	100% likely <i>Cleome</i>
<i>M. binghami</i>	SA, Vivo, 7.I.2004, on <i>Cleome</i> , B.N. Danforth	3	100% likely <i>Cleome</i>
<i>M. binghami</i>	SA, Vivo, 8.I.2004, on <i>Cleome</i> , B.N. Danforth	1	100% likely <i>Cleome</i>
<i>M. binghami</i>	SA, Vivo, 8.I.2004, on <i>Cleome</i> , B.N. Danforth	3	70% likely <i>Cleome</i> , 30% likely Geraniaceae
<i>M. binghami</i>	SA, Vivo, 8.I.2004, on <i>Cleome</i> , B.N. Danforth	1	100% likely <i>Cleome</i>
<i>M. binghami</i>	SA, Vivo, 8.I.2004, on <i>Cleome</i> , B.N. Danforth	4	100% likely <i>Cleome</i>
<i>M. binghami</i>	SA, Vivo, 7.I.2004, on <i>Cleome</i> , B.N. Danforth	1	100% likely <i>Cleome</i>
<i>M. binghami</i>	SA, 27 km S Okahandja, 1.III.1977, on <i>Gisekia africana</i> , J. Rozen	5	64% Aizoaceae, 36% likely Geraniaceae
<i>M. binghami</i>	SA, Tshipise, 27.XI.1999, leg. Brzoska	5	100% likely <i>Tribulus</i>
<i>M. binghami</i>	SA, Tshipise, 27.XI.1999, leg. Brzoska	5	100% likely <i>Tribulus</i>
<i>M. andersoni</i>	Tanzania, Mkomazi, 07.I.1995, on <i>Cleome</i> , leg. Stone	4	70% likely <i>Cleome</i> , 30% pollen B
<i>M. andersoni</i>	Tanzania, Mkomazi, 07.I.1995, on <i>Cleome</i> , leg. Stone	2	100% likely <i>Cleome</i>
<i>M. andersoni</i>	Kenya, Magadi, 16.VI.1967, leg. Michener	4	40% pollen C, 60% pollen D
<i>M. andersoni</i>	Kenya, Magadi, 16.VI.1967, leg. Michener	3	30% pollen C, 70% pollen D
<i>M. gigas</i>	Namibia, 8 km N Karabib, 22.III.1976, on <i>Crotalia podocarpa</i> , J. Rozen	5	100% likely Fabaceae
<i>M. gigas</i>	Namibia, 58 km SW Omaruru, 26.III.1976, J. Rozen	4	100% likely Fabaceae
<i>M. gigas</i>	Namibia, 52 km SW Omaruru, 26.III.1976, J. Rozen	4	100% likely Fabaceae

Eardley, NCSA; 1♂, idem, I.1990, leg. Smith, NCSA; 2♀/1♂, idem, leg. Prinsloo, NCSA; 3♀/4♂, idem, leg. Eardley, NCSA; 3♀/5♂, idem, 02.II.1984, on *Justicia flava*, leg. Eardley, NCSA; 1♀, idem, on *Grewia flava* leg. Eardley, NCSA; 2♀/8♂, Messina [22.26°S 29.88°E], 28.I.1993, leg. Uys, NCSA; 9♀, Van Zylsrus [26.58°S 22.04°E],

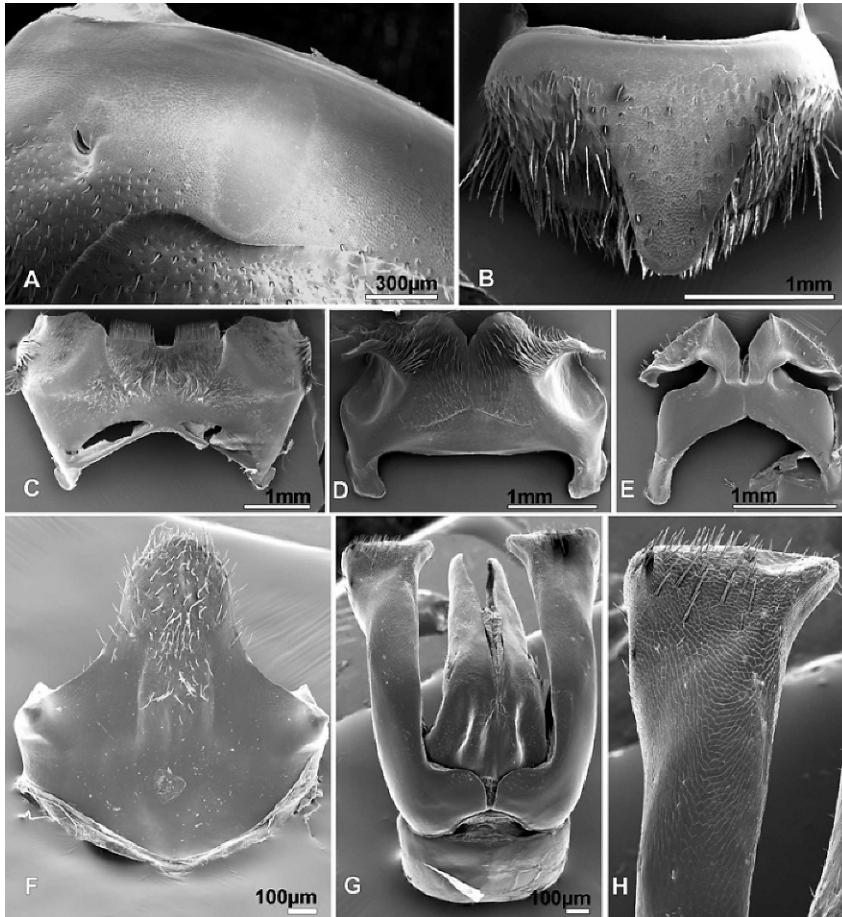


Fig. 2. *Meganomia binghami* male. A, Pregradular stridulatory plate. These structures are present on terga IV–VI in males and terga IV–V in females (Rozen, 1977). The posterior margin of the anterior tergum is scraped across the plate to produce a weak chirping sound during mating (see description in Rozen, 1977). B, pygidial plate. C–F, sterna 5–8. G, genitalia. H, detail of the gonostylus apex.

19.I.1994, leg. Eardley, NCSA; 11♀/4♂, Vivo [23.05°S 29.28°E], 06.I.2004, leg. Eardley, NCSA; 8♀, idem, on *Tribulus* sp., leg. Eardley, NCSA; 6♀/2♂, Vivo [22.56°S 29.33°E], 02.III.1984, on *Cleome diandra*, leg. Mansell, NCSA; 4♀/2♂, idem, on *Cleome diandra*, leg. Eardley, NCSA; 1♀, Kimberley [28.73°S 24.76°E], 22.I.2000, leg. Halada, OOLL; 8♀, Tshipise [22.36°S 30.10°E], 27.XI.1999, leg. Brzoska, KU. **NAMIBIA.** 1♀/1♂, Okahandja [21.98°S 16.92°E], 17.II.1977, on *Gisekia africana*, leg. Rozen, AMNH; 7♀/3♂, Outjo [20.12S 16.15°E], 25.III.1979, leg. Rozen, AMNH; 1♀/1♂, Koës [25.95°S 19.11°E], 09.III.1988, leg. Whitehead, NMH; 4♀, Okahandja [21.98°S 16.92°E], 16.II.1928, leg. Turner, NHM; 1♀, Rundu [17.93°S 19.77°E], 19.I.1993, leg. Schwarz, NHM; 1♀, Okahandja [21.98°S 16.92°E], FSAGX; 1♀/1♂, Rundu [17.93S 19.77E], 23.I.1993, leg. Schwarz, FSAGX; 1♂, Seeheim [26.82°S 17.78°E], 16.II.1934, leg. Ogilviei, FSAGX; 1♂, Kums [28.1S 19.6E], 17.IV.1988, leg. Eardley, NCSA; 6♀/1♂, Rundu [17.93S 19.77E], 19.I.1993, leg. Schwarz, OOLL; 3♀/6♂, idem 23.I.1993, leg. Schwarz, OOLL; 1♂, idem, 19.I.1993, leg. Schwarz, OOLL;

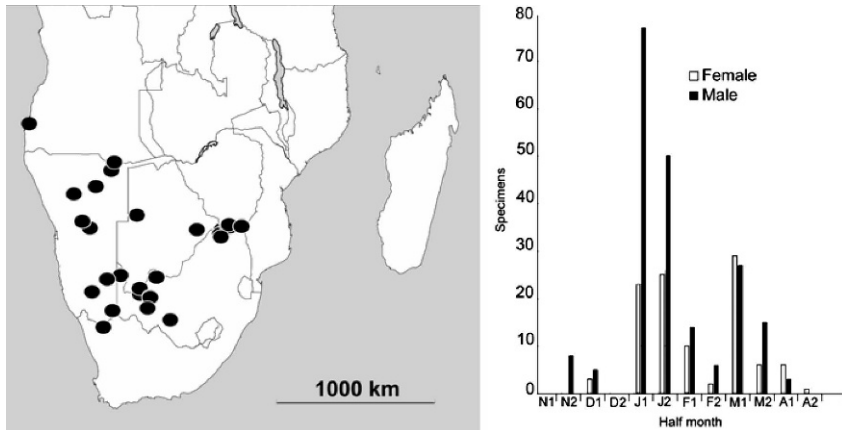


Fig. 3. Collecting localities for *Meganomia binghami* (309 specimens) and phenology of *Meganomia binghami* (N = November, D = December, J = January, F = February, M = March, A = April).

5♀/4♂, idem, 30.I.1993, leg. Schwarz, OOLL; 2♀, Outjo [20.12°S 16.15°E], 25.III.1979, leg. Rozen, KU; 1♂, Seeis [22.45°S 17.58°E], 16.III.1976, leg. Rozen, KU; 1♀, Kavango [18.5°S 19.5°E], 10.III.1990, leg. Schwarz, ZIS; 1♂, Rundu [17.93°S 19.77°E], 23.I.1993, leg. Schwarz, ZIS. **ZIMBABWE.** 3♀/3♂, Beitbridge [22.22°S 30.0°E], 12.IV.1932, leg. Ogilviei, NHM; 2♂, idem, leg. Mackie, MRACT; 5♀/3♂, Bubi [22.33°S 31.11°E], 08.XII.1998, leg. Halada, OOLL.

DISTRIBUTION (FIG. 3): The distribution of *Meganomia binghami* corresponds with the Savannah biome in the southern part of Africa.

PHENOLOGY (FIG. 3): The extreme collecting dates are 27th of November and 17th of April. It seems that *Meganomia binghami* is a univoltine summer species. The present data show two peaks of emergence, but this is likely a bias in sampling.

FLORAL VISITS: Labels from pinned specimens provide host-plant records on six different genera and families: *Cleome* (Cleomaceae), *Crotalaria* (Fabaceae), *Gisekia* (Aizoaceae), *Grewia* (Tiliaceae), *Justicia* (Acanthaceae) and *Tribulus* (Zygophyllaceae). The main floral resources are in increasing importance: *Crotalaria* (1 female), *Grewia* (1 female), *Grisekia* (1 female and 1 male), *Justicia* (3 females, 5 males), *Tribulus* (39 females, 7 males) and *Cleome* (47 females, 11 males). Additional records are indicated in the literature (review see Eardley and Urban, 2010): Aizoaceae, *Gisekia africana*; Boraginaceae, *Heliotropium ciliatum*; Cucurbitaceae; Fabaceae, *Crotalaria podocarpa*, *Indigofera* sp., *I. alternans*, *I. charlieriana*, *I. Filipes*, *Lessertia macrostachya*; Moluginaceae, *Limeum arquite-carinatum*, *L. fenestratum*, *L. myosotis*; Neuradaceae, *Neuradopsis austro-africana*; Zygophyllaceae, *Tribulus* sp. As noted before, such visits do not usually distinguish pollen collecting from nectar collecting.

Palynological Analyses

The 23 pollen loads of *Meganomia binghami* show five distinct morphologies from at least four plant families: Aizoaceae, Cleomaceae, Geraniaceae and Zygophyllaceae. Each of these families is in a different angiosperm order: Caryophyllales (Aizoaceae), Brassicales (Cleomaceae), Geraniales (Geraniaceae) and Zygophyllales (Zygophyllaceae) [Stevens (2001 onwards), Angiosperm Phylogeny Website, version

9, June 2008]. We were not able to determine the fifth pollen type (pollen A). 82% of the pollen loads are homogenous containing 100% of the same pollen. Pure pollen loads are from Zygophyllaceae ($n = 9$), Cleomaceae ($n = 8$) and pollen A ($n = 1$). 18% of the pollen loads include two different pollens. The mixed pollen loads are from well-filled scopae and the second pollen is well represented. Therefore the mix does not result from contamination. We can infer that females of *M. binghami* forage on different host plants during the same foraging trip or during distinct foraging trips. According to the definition of Müller and Kuhlmann (2008) we can conclude that *M. binghami* is a polylectic species.

The analysis of the content of the pollen loads in *Meganomia andersoni* (Meade-Waldo, 1916) suggests a polylectic behavior as in *M. binghami*. Three pollen loads are clearly mixed and only one pollen load is homogenous. Determination of pollen is very difficult in flowers from this part of the world (Kenya and Tanzania), but *M. andersoni* probably forage on three different plant families. Additional samples are needed to define a level of host-plant specialization.

The pollens collected by females of *M. gigas* are all from Fabaceae, supporting field observations of Rozen (1977) and Gess and Gess (2004). *M. gigas* is therefore very likely oligolectic on this plant family. However, we only sampled three populations localized in the western part of the species distribution. Moreover, these samples originate from specimens collected by Jerry Rozen at the site where he observed the species to exclusively collect pollen on *Crotalaria* (Rozen, 1977). One would need to sample more broadly to confirm that this species is indeed oligolectic.

Discussion

According to the present palynological results and the definition of Müller and Kuhlmann (2008), *M. binghami* is polylectic. But in one population (Van Zylrus), all females foraged on *Tribulus* (Zygophyllaceae). It could mean that some oligolectic “forms” exist in the *M. binghami* species. However, morphology among all populations is very similar. Second, floral fidelity to one host-plant is common in polylectic species (Cane and Sipes, 2006). This so called *floral constancy* is: “a temporary tendency of individual foragers to sequentially visit conspecific flowers” (definition after Cane and Sipes, 2006). The population in Van Zylrus clearly belongs to the same species as the polylectic populations of Vivo and Okahandja, the host plant specialization of the female from the former population is probably local and/or temporal. Polylecty is therefore the most likely behaviour for *M. binghami*.

Alternatively, we could apply the term “eclectic oligolecte” to *M. binghami*. The term was used by Cane and Sipes (2006) to describe bees with a strong preference for a few, very distantly related, host-plants. This could apply to *M. binghami* because our pollen analysis indicates that there is a strong preference for *Tribulus* and *Cleome*. These two genera are in distantly related angiosperm orders (Zygophyllales and Brassicales, respectively). Temporal specialization of the Van Zylrus population could be linked to the presence of only one suitable host plant in bloom at this site. Indeed, we (Danforth and Eardley) did not see *Cleome* at Van Zylrus and *Tribulus* was the only major host plant in bloom at that site.

Recent studies combining bee phylogeny and host-plant records show that closely related species forage mainly on the same host-plants (Müller, 1996; Michez *et al.*, 2004; Sipes and Tepedino, 2005; Michez *et al.*, 2007; Larkin *et al.*, 2008; Müller and

Kuhlmann, 2008; Patiny *et al.*, 2008; Sedivy *et al.*, 2008). Host shifts are rare in bee clades. Polylecty of *M. binghami* is therefore unexpected because most melittid bees (>90%) are oligolectic (Michez *et al.*, 2008). Extrapolation of polylectic behaviour of *M. binghami* to other Meganomiinae is premature. *M. andersoni* could be polylectic as indicated by our results but *C. rozenorum* and *M. gigas* are very likely oligolectic. We do not have any record of floral choices for the eight other meganomiine species.

Oligolectic behaviour appears to be a plesiomorphic feature in most bee groups (Danforth *et al.*, 2006; Patiny *et al.*, 2008; Sedivy *et al.*, 2008). Oligolectic behaviour seems the most likely behaviour for Melittinae and Dasypodainae. A few derived species have been described as polylectic in the genera *Dasygaster*, *Hesperapis* and *Melitta* (Michez *et al.*, 2004, 2008). However, as there is no hypothesis on the phylogenetic relationships among *Meganomia* species, it is impossible to define if the polylectic behaviour of *M. binghami* is ancestral or derived in the genus *Meganomia*.

Acknowledgement

Thanks to the curators of the bee collections: the late Y. Pesenko (ZIS), F. Gusenleitner (OOLL), J Rozen (AMNH) and J. Ascher (AMNH). Thank you to M. Vanderplanck (UMons) for her kind proofreading.

Literature Cited

- Alexander, B. A., and C. D. Michener. 1995. Phylogenetic studies of the families of short-tongued bees (Hymenoptera: Apoidea). The University of Kansas Science Bulletin 55:377–424.
- Barbier, Y., and P. Rasmont. 2000. Carto Fauna-Flora 2.0. Guide d'utilisation, Mons. 59 pp.
- Barbier, Y., P. Rasmont, M. Dufrière, and J. M. Sibert. 2000. Data Fauna-Flora. Guide d'utilisation, Mons. 107 pp.
- Cane, J. H., and S. D. Sipes. 2006. Characterizing floral specialization by bees: analytical methods and a revised lexicon for oligolecty. In N. M. Waser and J. Ollerton (eds.). Specialization and Generalization in Plant-Pollinator Interactions, pp. 99–122. University of Chicago Press, Chicago.
- Danforth, B. N., S. D. Sipes, J. Fang, and S. G. Brady. 2006. The history of early bee diversification based on five genes plus morphology. Proceedings of the National Academy of Sciences of the United States of America 103:15118–15123.
- Eardley, C. D., and D. Urban. 2010. Catalogue of afrotropical bees (Hymenoptera: Apoidea: Apiformes). Zootaxa 2455:1–548.
- Gess, S. K., and F. W. Gess. 2004. A comparative overview of flower visiting by non-*Apis* bees in the semi-arid to arid areas of Southern Africa. Journal of the Kansas Entomological Society 77:602–618.
- Gess, S. K., and F. W. Gess. 2006. Survey of flower visiting by aculeata wasps and bees in the semi-arid to arid areas of Southern Africa. Annals of the Eastern Cape Museums 5:1–51.
- Larkin, L. L., J. L. Neff, and B. B. Simpson. 2008. The evolution of a pollen diet: host choice and diet breadth of *Andrena* bees (Hymenoptera: Andrenidae). Apidologie 39:133–145.
- Michener, C. D. 1979. Biogeography of the bees. Annals of the Missouri Botanical Garden 66:277–342.
- Michener, C. D. 1981. Classification of the bee family Melittidae with a review of species of Meganomiinae. Contribution of the American Entomological Institute 18:1–135.
- Michener, C. D. 2007. The bees of the world, second edition. The Johns Hopkins University Press, Baltimore. 913 pp.
- Michener, C. D., and R. W. Brooks. 1987. The family Melittidae in Madagascar. Annales de la Société entomologique de France (n.s.) 23:99–103.
- Michener, C. D., R. W. Brooks, and A. Pauly. 1990. Little-known meganomiine bees with a key to the genera (Hymenoptera: Melittidae). Journal of African Zoology 104:135–140.
- Michez, D., M. Terzo, and P. Rasmont. 2004. Phylogénie, biogéographie et choix floraux des abeilles oligolectiques du genre *Dasygaster* Latreille 1802 (Hymenoptera, Apoidea, Melittidae). Annales de la Société entomologique de France (n. s.) 40:421–435.

- Michez, D., C. D. Eardley, M. Kuhlmann, and S. Patiny. 2007. Revision of the bee genus *Capicola* (Hymenoptera: Apoidea: Melittidae) distributed in the Southwest of Africa. *European Journal of Entomology* 104:311–340.
- Michez, D., S. Patiny, P. Rasmont, K. Timmermann, and N. J. Vereecken. 2008. Phylogeny and host-plant evolution in Melittidae *s.l.* (Hymenoptera: Apoidea). *Apidologie* 39:146–162.
- Michez, D., S. Patiny, and B. N. Danforth. 2009. Phylogeny of the bee family Melittidae (Hymenoptera: Anthophila) based on combined molecular and morphological data. *Systematic Entomology* 34:574–597.
- Müller, A. 1996. Host-plant specialization in Western Palearctic anthidiine bees (Hymenoptera: Apoidea: Megachilidae). *Ecological Monographs* 66:235–257.
- Müller, A., and M. Kuhlmann. 2008. Pollen hosts of western palaeartic bees of the genus *Colletes* (Hymenoptera: Colletidae): the Asteraceae paradox. *Biological Journal of the Linnean Society* 95:719–733.
- Patiny, S., D. Michez, and B. N. Danforth. 2008. Phylogenetic relationships and host-plant evolution within the basal clade of Halictidae (Hymenoptera, Apoidea). *Cladistics* 24:255–269.
- Rozen, J. G. 1977. Biology and immature stages of the bee genus *Meganomia* (Hymenoptera, Melittidae). *American Museum Novitates* 2630:1–27.
- Sedivy, C., C. J. Praz, A. Müller, A. Widmer, and S. Dorn. 2008. Patterns of host-plant choice in bees of the genus *Chelostoma*: The constraint hypothesis of host-range evolution in bees. *Evolution* 62:2487–2507.
- Sipes, S. D., and V. Tepedino. 2005. Pollen-host specificity and evolutionary patterns of host switching in a clade of specialist bees (Apoidea: *Diadasia*). *Biological Journal of the Linnean Society* 86:487–505.
- Stage, G. I. 1971. Family placement of the African genus *meganomia* cockerell with a review of the included species (Hymenoptera: Apoidea). *Proceeding Entomological Society Washington* 73:306–313.
- Stevens, P. F. 2001 onwards. Angiosperm Phylogeny Website. Version 9, June 2008 [<http://www.mobot.org/mobot/research/apweb/welcome.html>]
- Westrich, P., and K. Schmidt. 1986. Methoden und Anwendungsgebiete der Pollenanalyse bei Wildbienen (Hymenoptera, Apoidea). *Linzer biologische Beiträge* 18:341–360.
- Westrich, P. 1990. *Die Wildbienen Baden-Württembergs*. Ulmer Verlag, Stuttgart. 972 pp.