The Great Lakes Entomologist

Volume 50
Numbers 1 & 2 -- Spring/Summer 2017
Numbers 1 & 2 -- Spring/Summer 2017

Article 4

September 2017

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Cover Page Footnote

My postdoctoral research in Michigan supported by the United States Department of Agriculture-National Institute for Food and Agriculture Specialty Crop Research Initiative; project 2012-01534: Developing Sustainable Pollination Strategies for U.S. Specialty Crops during this research. I also appreciate the willingness of Fenner Nature Center staff to allow research to be conducted on the Center's grounds.

Notes on the Nests of *Augochloropsis metallica fulgida* and *Megachile mucida* in Central Michigan (Hymenoptera: Halictidae, Megachilidae)

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Abstract

Notes on the nesting biology of two ground-nesting bee species are provided from Central Michigan. A single nest of *Augochloropsis metallica* (Fabricius) *fulgida* (Smith) was excavated on 12 July 2014 in Shiawassee County. There were two female nest inhabitants. Examination of mandibular wear, wing wear and ovarial development suggests one female was acting as a worker caste. Also, a nesting aggregation of *Megachile mucida* Cresson was observed in Ingham County. Information on nest architecture and cell construction is based on excavations of several nests during 7–15 June 2014. *Megachile mucida* is recorded as a new host species for the cleptoparasite *Coelioxys sodalis* Cresson. This is the first record of *M. mucida* in Michigan, additional collection records of this species in Michigan are also reported.

Introduction

The bee families Halictidae and Megachilidae are remarkable for their varied nesting habits (Medler and Lussenhop 1968; Michener 1974, 2007; Yanega 1997; Litman et al. 2011; Gibbs et al. 2012), however basic natural history remains limited for many species. This is problematic for taxa where social behavior or nesting biology varies within a genus, which is commonplace among halictid and megachilid bees. Since there is a lack of published information on many bee species, even brief notes can be informative.

The New World tribe Augochlorini (Hymenoptera: Halictidae) is most diverse in the Neotropical region (Michener 2007), but four species in three genera are known to occur in Michigan: *Augochlora pura* (Say), *Augochlorella aurata* (Smith), *Augochlorella persimilis* (Viereck), and *Augochloropsis metallica* (Fabricius) *fulgida* (Smith). The nests of *A. pura* and both *Augochlorella* species have been studied in detail (Ordway 1966, Stockhammer 1966, Packer et al. 1989, Mueller 1996). *Augochlora pura* is a solitary, wood-nester (Stockhammer 1966) commonly found in rotting logs in the eastern United States, including southern Michigan. *Augochlorella aurata* and *A. persimilis* form eusocial, occasionally semisocial or solitary, underground-nests (Ordway 1966, Packer et al. 1989, Packer 1990, Mueller 1996). There are no published studies of the nests of *A. metallica*. Some data on laboratory colonies are mentioned by Eickwort and Sakagami (1979) in reference to the subgenus *A.* (*Paraugochloropsis*), but specific details for *A. metallica* are not provided. Five species of Neotropical *Augochloropsis* from Brazil and Costa Rica have been studied in detail (Michener and Lange 1959, Michener and Seabra 1959, Gimenes et al. 1991, Coelho 2002) and a broad spectrum of social behaviors were documented, including solitary, communal, semisocial, and eusocial nesting. The Nearctic species *A. sumptuosa* (Smith) was studied in both New Jersey (Smith 1901) and Kansas (Michener and Lange 1959), using the specific epithet *humeralis* (Patton), and found to be communal or semisocial.

Bees in the genus *Megachile* (Megachilidae: Megachilini) are commonly referred to as leaf-cutter bees for their use of masticated or cut leaves in cell construction (Medler and Lussenhop 1968, Litman et al. 2011), but other materials may also be used instead, including plant resins (Krombein 1967, Medler and Lussenhop 1968, Litman et al. 2011, O'Neill and O'Neill 2016). Leaf-cutter bees nest in both pre-existing cavities (Fye 1965, Krombein 1967) and underground burrows (Krombein 1953, Eickwort et al. 1981, Sheffield et al. 2011). Members of the subgenus *M.* (*Xanthosarus*), which includes *Megachile mucida* Cresson, nest in both underground burrows (Graenicher 1905, Sladen 1918, Hobbs and Lilly 1954, Cane et al. 1996) and

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logs or stems (Stephen 1956, Medler and Lussenhop 1968). Two Michigan species, *M. gemula* Cresson and *M. melanophaea* Smith, are strikingly similar morphologically to *M. mucida*, but differ in their nesting biology (Graenicher 1905, Fye 1965, Medler and Lussenhop 1968). *Megachile gemula* nests in hollow twigs or poplar logs (Fye 1965) and *M. melanophaea* nests in the ground (Graenicher 1905). Given the differences between close relatives, it is worth documenting the nesting biology of *M. mucida*.

The objective of this paper is to provide brief notes on the nests of *Augochloropsis* (*Paraugochloropsis*) *metallica fulgida* and *Megachile* (*Xanthosarus*) *mucida*, since published information on these species is otherwise lacking. The descriptions below are intended to fill gaps in knowledge of bee natural history and to demonstrate the potential value of such observations even when not conducted as part of a detailed scientific study.

Methods

A single nest of *A. m. fulgida* was discovered on 12 July 2014 while collecting bees in a small clearing at Rose Lake Wildlife Area, Shiawassee County (N42.8075, W84.363). The nest entrance was completely obscured from above by a leaf (Figs. 1A, 1B), and the nest was only recognized by seeing a returning female. Flowers at the site included *Monarda fistulosa* L. and *Asclepias tuberosa* L. No other *Augochloropsis* nests were found in the vicinity, although *M. texana* Cresson was seen nesting in the same clearing. The nest was excavated by spraying dry plaster of plaster down the entrance. A grass stem was also carefully slid down into the burrow to help track the path of the nest. A hole approximately 20 cm deep was dug to one side of the entrance. The soil was carefully scraped away from the side until the burrow and cell cluster were found. Two or three cells were opened immediately to appease my curiosity or the immatures were damaged during removal of the cells. The remainder of the cells were returned to the lab and individuals reared to adulthood. Dissections of the metasomata were made from adult females active in the nest and two lab reared females. The metasomata from pinned specimens were rehydrated in water overnight before dissection. Mandibles and wings were assessed for wear using the newly emerged females as a standard for comparison.

Records of *M. mucida* for Michigan were based on my own collections, deposited at the J. B. Wallis / R. E. Roughley Museum of Entomology (JBWM), and re-examination of material in the A.J. Cook Arthropod Research Collection (MSUC). Since *M. mucida* had never before been recorded in Michigan and because it could be easily mistaken for either *M. gemula* or *M. melanophaea*, historical collections of these two latter species were re-examined to verify their determinations. Identifications of *M. mucida* and *Coelioxys sodalis* Cresson were based on information from published keys (Mitchell 1935, 1962; Baker 1975) and comparison to identified material in the MSUC.

A nesting aggregation was discovered on a former farm lane currently used as a walking path at Fenner Nature Center, Ingham County (N42.7089, W84.5226). The site was on a slight south-facing slope, with sandy soil and sparse weedy vegetation (e.g., Brassicaceae and Oxalidaceae). Observations and nest excavations were made haphazardly over the course of four weeks at the Fenner Nature Center. Eight nests were excavated using methods similar to those above. Nests were selected based on female activity allowing association of the bee to the nest contents. Completed cells were returned to the lab to be reared. Cells were stored in an unheated building during the winter before being brought back to the lab in spring and kept at room temperature.

Results

Augochloropsis (*Paraugochloropsis*) *metallica fulgida*

A nest of *A. m. fulgida* was discovered and excavated on 12 July 2014. The burrow extended nearly straight down from the horizontal surface for approximately 15 cm before taking a 90 degree turn towards the adjacent cluster of vertical cells (Figs. 1C, 1D). The nest architecture fits the category IbLV (Sakagami and Michener 1962, Eickwort and Sakagami 1979). The cluster of approximately 15 cells was damaged slightly during the excavation, and was removed leaving a small fist-sized space in the soil (Fig. 1D). Two adult females were found inside the nest. These were captured for later dissection. Emergences began on the 17th of July and continued every 1–2 days and was over by mid-August. In total, 9 males and 4 females were reared from the nest in the following order: 1 ♂ (17 Jul.), 1 ♂ (19 Jul.), 1 ♂ (21 Jul.), 1 ♂ (24 Jul.), 1 ♂ (25 Jul.), 1 ♂and 1 ♀ (26–27 Jul.), 1 ♂ (28 Jul.), 1 ♀ (29 Jul.), 1 ♀ (31 Jul.), and 2 ♂♂ and 1 ♀ (2–12 Aug.). The last three individuals, two males and one female, emerged between the 2–12 August, when I was absent from the lab. Based on the regular emergence of the other individuals these three likely emerged in sequence by no later than the 6th of August.

Only one of the adult females found in the nest had evidence of ovarial development including a well-developed ovariole. The

Figure 1. A-D Nesting site of *Augochloropsis metallica fulgida*. A. Nest entrance of *A. m. fulgida* obscured by leaves. B. Nest entrance of *A. m. fulgida* with leaves removed. White powder surrounding entrance from plaster of Paris sprayed in nest. C. Cell cluster at base of entrance tunnel (marked with white plaster of Paris). Arrow points to vertical cell with pollen at bottom. D. Entire nest with vertical tunnel from surface (marked with white plaster of Paris) and space with cell cluster removed. E-H. Nesting aggregation of *Megachile mucida*. E. Trail at Fenner Nature Center with *M. mucida* nests. F. Female *M. mucida* entering nest with cut leaf held with mandibles. G. Curved trail of soil material removed during nest excavation (black arrows). H. Excavated nest of *M. mucida* showing depth from surface and partially exposed cells.

other had slender ovaries, but these were still more developed than newly emerged females. Both adults in the nest had evidence of wear, but there was substantially more wear to both the mandibles and wings of the female with undeveloped ovaries.

Megachile (Xanthosarus) mucida

Megachile mucida has been taken from the following locations in Michigan: ***Berrien Co.:*** 5 km E of Paw Paw Lake, 29 Jul. 2011 (1 ♀ MSUC); ***Clinton Co.:*** Sleepy Hollow State Park, 15 Jun. 2014 (1 ♂ JBWM); ***Ingham Co.:*** MSU Beal Botanical Garden, 8 Jun. 2014 (1 ♀ JBWM); MSU Horticultural Demonstration Garden, 9 Jun. 2013 (3♀ 1 ♂ JBWM), 31 May 2014 (1 ♂ JBWM), 1 Jun. 2014 (1 ♂ JBWM); MSU Radiology garden, 15 Jun. 2014 (1 ♀ JBWM), 21 Jun. 2014 (2 ♀ JBWM); Fenner Nature Center, 31 May 2014 (2 ♀ JBWM), 7 Jun. 2014 (2 ♀ JBWM), 14 Jun. 2014 (2 ♂ JBWM); ***Ionia Co.:*** Clarksville Research Center, 42.8708 -85.2544, 22 Jun. 2016, *Penstemon digitalis* (2 ♀ MSUC); ***Van Buren Co.:*** 25 May 2005 (2♂ MSUC); South Haven, 3 mi. S,. 12 Jun. 2006 (2 ♂ MSUC). Historical specimens identified as *M. gemula* and *M. melanophaea* in the MSUC were not found to include misidentified *M. mucida*.

On 31 May 2014, no nesting activity was observed at the site (Fig. 1E), but two female *M. mucida* were collected. When the site was revisited on 7 June 2014, the nesting aggregation was at peak activity and bees could be observed entering and exiting nests at a high frequency (Fig. 1F). The aggregation was recognizable from a distance of several meters due to the many females engaged in nest construction and cell provisioning. The nesting aggregation was approximately 7.5 m by 5 m in size and nests were commonly separated by 20–25 cm. In one case, a female *M. mucida* was observed repeatedly attempting to enter a nest occupied by another *Megachile*. The female was repelled each time by the occupant. By 14 June 2014, activity had reduced dramatically. The nesting aggregation was still recognizable by the nest entrances, but active females were no longer visible from a distance. Bees were observed leaving and returning to nests at regular intervals, but typically only 1 or 2 females were visible at one time. In the fourth week, the aggregation was almost completely unrecognizable. Nest entrances were closed and no foraging females were observed.

On 7 June 2014, females were observed dragging dirt from the nest entrance for 15–20 cm making a visible trail which typically curved perpendicular to the direction of the nest entrance in a J-shape (Fig. 1G). Females would then either quickly walk or make a short flight back to the nest entrance and repeat the excavation behavior multiple times. Nests were built at an oblique angle into sandy soil. Nest depth was typically much less than 10 cm, often only 3–4 cm below the surface (Fig. 1H). Nest entrances were approximately 8 mm in diameter. Cells were composed of a simple tunnel extending approximately 10 to 15 cm with cells built in series at the terminus (Fig. 2A) or occasionally side-by-side. Some nests had a single cell others had 3 cells in series. One excavated nest appeared to have separate groups of cells in series, but it was unclear if these represented a single nest or multiple nests built one on top of the other.

Females were observed returning to nests with leaf pieces of various sizes. Leaves were either an oval leaf as long as or longer than the female herself (Fig. 1F) or a roughly circular leaf disc. Females would spend between 1 and 2 minutes inside the nest before leaving for another leaf piece. Females were observed flying north of the aggregation on these flights towards a wooded area. Some damaged cottonwood leaves were observed north of the aggregation (Fig. 2B), but no females were ever observed cutting leaf pieces. A typical trip for a leaf piece lasted approximately 2 minutes. Each cell was a cylinder composed of overlapping oblong leaf pieces. Three pieces were required to complete the full circumference of the cell. Several overlapping layers of leaves were used, resulting in 20–30 leaf pieces. Circular leaf pieces were placed at both ends of the cell (Fig. 2C). Several layers of circular leaf discs were used to cap the cell. Prior to cell capping, the nest was provisioned with pollen and nectar. In early stages of cell provisioning, pollen appeared to be dry. In capped cells, pollen was a solid mass (Fig. 2D) presumably held together by nectar and any glandular fluids the female might secrete.

Females of the cleptoparasitic bee *Coelioxys sodalis* (Fig. 2E) were observed flying over the aggregation during the second and third weeks. On 14 June 2014, a *C. sodalis* female was observed entering a *M. mucida* nest. After approximately 1 min., the cleptoparasite emerged and was captured. The nest was then excavated and the cells retained. Attempts were made to rear the specimens in the lab allowing them to first overwinter in an unheated building, but adults never emerged. Cells were opened and mature larva were alive inside but after a year following their overwintering period, they never completed development. A bombyliid fly, identified as *Hemipenthes sinuosa* (Wiedemann), was commonly seen at the nesting aggregation (Fig. 2F), but was never directly associated with *Megachile* nests.

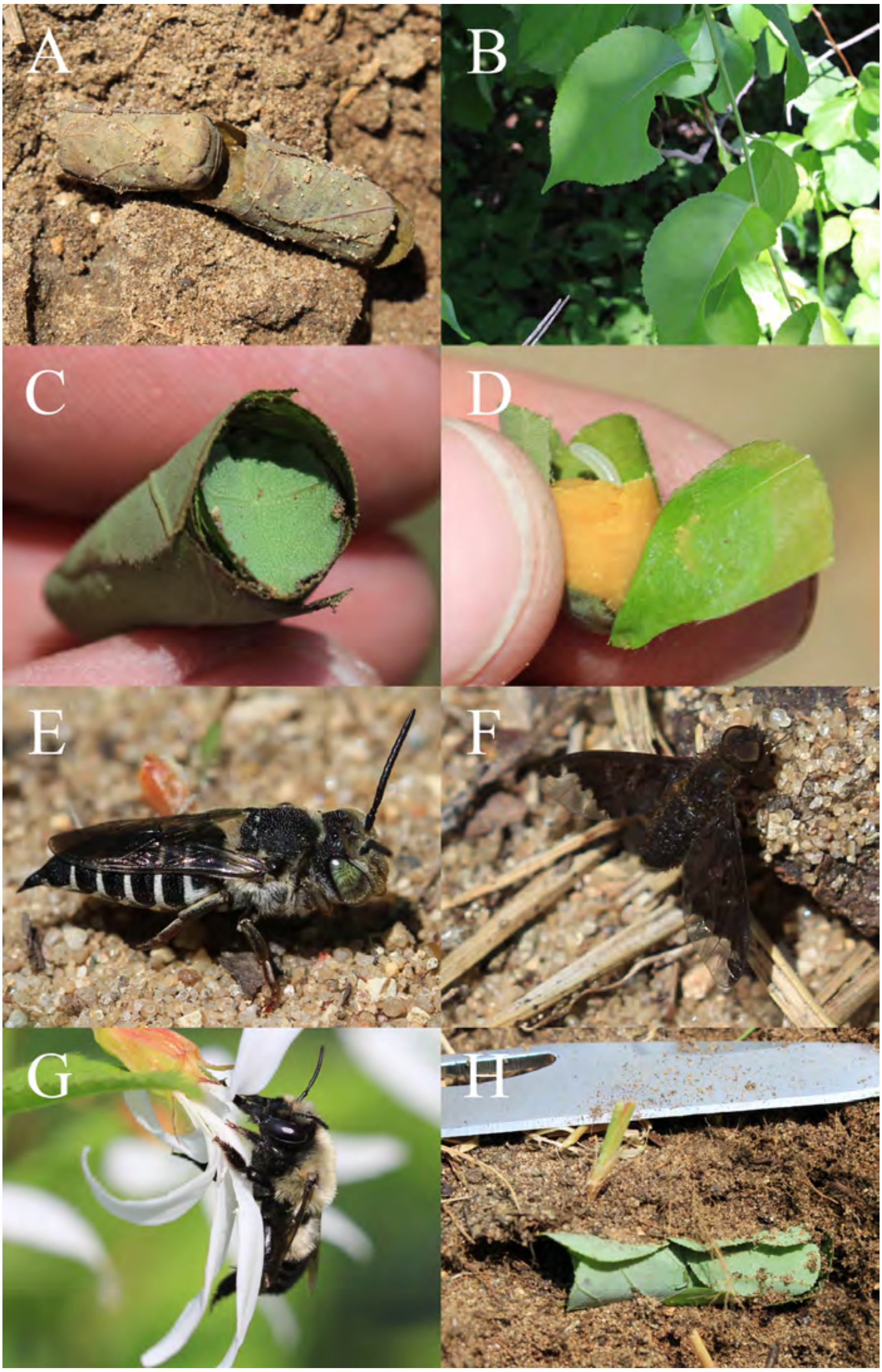

Figure 2. A-D Nesting aggregation of *Megachile mucida*. A. Two cells of *M. mucida* in series. B. Cottonwood leaves at north end of aggregation showing possible signs of *Megachile* damage. C. Complete cell of *M. mucida* showing circular leaf pieces used to close the cell. D. Opened cell of *M. mucida* showing pollen mass with attached egg. E-F. Insects associated with nesting aggregation. E. *Coelioxys sodalis* female. F. *Hemipenthes sinuosa*. G. *Megachile mucida* visiting *Gillenia trifoliata* at the Beal Botanical Garden. H. Excavated nest of *M. texana*.

In one instance, a female was observed closing a nest. She was seen pulling soil down around the nest entrance. She then flew away for approximately 1 min. before returning to continue closing the nest entrance for 30 sec. This pattern was repeated 5 times. It is unclear if these flights were normal behavior or if they were made in response to the close observation of her activity.

Males were never observed at the nesting aggregation. Males were collected patrolling at a patch of *Rubus* approximately 120 m to the south of the aggregation. No mating was observed and females were never observed on flowers near the aggregation. Males were also observed patrolling flowers on MSU campus at both the Beal Botanical Garden and Horticulture Demonstration Gardens. *Baptisia* spp. and *Gillenia trifoliata* (L.) Moench (Fig. 2G) seemed to be the preferred plant of females in the gardens.

Discussion

In *Augochloropsis m. fulgida*, the nest architecture closely matches the that of *A. (P.) iris* (Schrottky) (Michener and Lange 1959, Coelho 2002), a putatively eusocial species. The regular sequence of offspring emergence suggests that approximately one cell is provisioned every 1 or 2 days. The sex ratio of the lab-reared individuals was biased towards males, which might suggest that the excavation interrupted the construction of female cells. Only two adults were found in the nest, but the excavation occurred at approximately 2 pm, so it is possible that other foraging occupants were missed. The different levels of ovarial development observed between nest-mates of *A. m. fulgida* is strongly suggestive of division of labor. The extensive wing and mandibular wear suggest the undeveloped ovaries were not a consequence of being newly emerged. In fact, it suggests that a greater amount of nest cell construction and foraging was performed by this female (Michener et al. 1955, Ordway 1965, Packer and Knerer 1986, Mueller and Wolf-Mueller 1993). Semi-sociality, division of labor between sisters, is more commonly reported in the Augochlorini than division of labor between generations, *i.e.* eusociality (Danforth and Eickwort 1997). *Augochloropsis metallica* has been recorded as solitary or communal in some faunal studies (Wolf and Ascher 2009, Goldstein and Ascher 2016), but this may not be the case. Given the small size of the colony and the behavioral variability observed in other augochlorine species (Michener and Lange 1959, Packer 1990), it is possible that this species displays polyethism.

It is notable that *M. mucida*, a relatively distinctive species, was not collected in Michigan prior to 2005. There is a substantial bee collection at Michigan State University thanks to collectors such as Roland Fischer (MSU) and Robert Dreisbach (Dow Chemical, Midland), including material examined by a number of bee experts, most notably Theodore Mitchell, who revised the Nearctic *Megachile* (Mitchell 1935) and the bees of the eastern United States (Mitchell 1962). Given that the bee is now relatively common on the MSU campus, it seems unlikely that this species would have been missed by earlier collectors.

Another distinctive species, *Dieunomia heteropoda* (Say), was also recently recorded for the state based on specimens collected since 2003 (Gibbs et al. 2014) as were 'southern' species of *Andrena* (Tuell et al. 2009). These may be simply oversights that have been discovered recently due to increased collection effort, but it could also be that some bees with primarily southern distributions have been moving northward into Michigan in recent years. Such expansions have been speculated for other bee species (Zarrillo et al. 2016). The possibility of climate induced changes in bee distributions, the number of rare and poorly documented species, and the potential pollinator crisis make it increasingly important to document the distribution and natural history of wild bees.

Interestingly, although *M. mucida* is near the northern extreme of its range in central Michigan, its cleptoparasite *C. sodalis* is near the southern boundary of its range in the east (Baker 1975). *Coelioxys sodalis* has been previously recorded invading the nests of *M. melanophaea* (Graenicher 1927, 1935), a close relative of *M. mucida*, and also *M. texana, M. frigida* Smith (Pengelly 1955), and possibly *M. rotundata* (Fabricius) (Hobbs 1968). *Megachile texana* is a similar in size species that also has shallow underground nests (Fig. 2H) (Krombein 1953, 1970). *Megachile rotundata* is a much smaller bee that nests in cavities, but *Coelioxys* size can vary considerably intraspecifically with different host use (Packer et al. 1995). The host breadth of many cleptoparasitic bees remains poorly documented and the hosts of some species remain unknown (Baker 1975). This new association highlights another reason for additional study of bee natural history.

Acknowledgments

My postdoctoral research in Michigan was supported by the National Institute of Food and Agriculture, U.S. Department of Agriculture under award number 2012-51181-20105: Developing Sustainable Pollination Strategies for U.S. Specialty Crops. I also appreciate the willingness of Fenner

Nature Center staff to allow research to be conducted on the Center's grounds. Two anonymous reviewers provided useful comments that improved the final paper.

Literature Cited

Baker, J. R. 1975. Taxonomy of five nearctic subgenera of *Coelioxys* (Hymenoptera: Megachilidae). The University of Kansas Science Bulletin. 50: 49–730.

Cane, J. H., D. Schiffhauer, and L. J. Kervin. **1996**. Pollination, foraging, and nesting ecology of the leaf-cutting bee *Megachile* (*Delomegachile*) *addenda* (Hymenoptera: Megachilidae) on cranberry beds. Annals of the Entomological Society of America. 89: 361–367.

Coelho, B. W. T. 2002. The biology of the primitively eusocial *Augochloropsis iris* (Schrottky, 1902) (Hymenoptera, Halictidae). Insectes Sociaux. 49: 181–190.

Danforth, B. N., and G. C. Eickwort. **1997**. The evolution of social behavior in the augochlorine sweat bees (Hymenoptera: Halictidae) based on a phylogenetic analysis of the genera, pp. 270–292. *In* Choe, J.C., Crespi, B.J. (eds.), The evolution of social behavior in insects and arachnids. Cambridge University Press, New York, New York.

Eickwort, G. C., R. W. Matthews, and J. Carpenter. **1981**. Observations on the nesting behavior of *Megachile rubi* and *M. texana* with a discussion of the significance of soil nesting in the evolution of megachilid bees (Hymenoptera: Megachilidae). Journal of the Kansas Entomological Society. 54: 557–570.

Eickwort, G. C., and S. F. Sakagami. **1979**. A classification of nest architecture of bees in the tribe Augochlorini (Hymenoptera: Halictidae; Halictinae), with description of a Brazilian nest of *Rhinocorynura inflaticeps*. Biotropica. 11: 28–37.

Fye, R. E. 1965. Biology of Apoidea taken in trap nests in northwestern Ontario (Hymenoptera). The Canadian Entomologist. 97: 863–877.

Gibbs, J., S. G. Brady, K. Kanda, and B. N. Danforth. **2012**. Phylogeny of halictine bees supports a shared origin of eusociality for *Halictus* and *Lasioglossum* (Apoidea: Anthophila: Halictidae). Molecular Phylogenetics and Evolution. 65: 926–939.

Gibbs, J., S. Dumesh, and T. L. Griswold. **2014**. Bees of the genera *Dufourea* and *Dieunomia* of Michigan (Hymenoptera: Apoidea: Halictidae), with a key to the *Dufourea* of the eastern United States. Journal of Melittology. 3: 1–15.

Gimenes, M., C. K. Kajiwara, F. A. do Carmo, and L. R. Bego. **1991**. Seasonal cycle and nest architecture of *Augochloropsis notophos* Vachal (Hymenoptera, Halictidae, Halictinae). Revista Brasileira de Entomologia. 35: 767–772.

Goldstein, P. Z., and J. S. Ascher. **2016**. Taxonomic and behavioral composition of an island fauna: A survey of bees (Hymenoptera: Apoidea: Anthophila) on Martha's Vineyard, Massachusetts. Proceedings of the Entomological Society of Washington. 118: 37–92.

Graenicher, S. 1905. Some observations on the life history and habits of parasitic bees. Bulletin of the Wisconsin Natural History Society. 3: 153–167.

Graenicher, S. 1927. On the biology of the parasitic bees of the genus *Coelioxys* (Hymen., Megachilidae). Entomological News. 38: 231–235.

Graenicher, S. 1935. Bee-fauna and vegetation of Wisconsin. Annals of the Entomological Society of America. 28: 285–310.

Hobbs, G. A. 1968. Controlling insect enemies of the alfalfa leaf-cutter bee, *Megachile rotundata*. The Canadian Entomologist. 100: 781–784.

Hobbs, G. A., and C. E. Lilly. **1954**. Ecology of species of *Megachile* Latreille in the mixed prairie region of southern Alberta with special reference to pollination of alfalfa. Ecology. 35: 453–462.

Krombein, K. V. 1953. A note on the nesting habits of *Megachile texana* Cresson (Hymenoptera, Megachilidae). Proceedings of the Entomological Society of Washington. 55: 84–85.

Krombein, K. V. 1967. Trap-nesting wasps and bees: Life histories, nests, and associates. Smithsonian Institution Press, Washington, D.C.

Krombein, K. V. 1970. Another note on the nesting habits of *Megachile texana* Cresson (Hymenoptera: Megachilidae). Proceedings of the Entomological Society of Washington. 72: 415.

Litman, J. R., B. N. Danforth, C. D. Eardley, and C. J. Praz. **2011**. Why do leafcutter bees cut leaves? New insights into the early evolution of bees. Proceedings of the Royal Society, Series B: Biological Sciences. 278: 3593–600.

Medler, J. T., and J. F. Lussenhop. **1968**. Leafcutter bees of Wisconsin. University of Wisconsin Research Bulletin. 274: 1–80.

Michener, C. D. 1974. The social behavior of the bees. Belknap Press, Cambridge, Massachusetts.

Michener, C. D. 2007. The bees of the world, 2nd ed. The Johns Hopkins University Press, Baltimore.

Michener, C. D., E. A. Cross, H. V. Daly, C. W. Rettenmeyer, and A. Wille. **1955**. Additional techniques for studying the behavior of wild bees. Insectes Sociaux. 2: 237–246.

Michener, C. D., and R. B. Lange. **1959**. Observations on the behavior of Brazilian halictid bees (Hymenoptera, Apoidea) IV. *Augochloropsis*, with notes on extralimital forms. American Museum Novitates. 1924: 1–42.

Michener, C. D., and C. A. C. Seabra. **1959**. Observations on the behavior of Brasilian halictid bees, VI, tropical species. Journal of the Kansas Entomological Society. 32: 19–28.

Mitchell, T. B. 1935. A revision of the genus *Megachile* in the Nearctic Region Part III. Taxonomy of the subgenera *Anthemois* and *Delomegachile* (Hymenoptera: Megachilidae). Transactions of the American Entomological Society. 61: 155–205.

Mitchell, T. B. 1962. Bees of the Eastern United States: volume II. N. C. Agricultural Experimental Station Technical Bulletin. 152: 1–557.

Mueller, U. G. 1996. Life history and social evolution of the primitively eusocial bee *Augochlorella striata* (Hymenoptera: Halictidae). Journal of the Kansas Entomological Society. 69: 116–138.

Mueller, U. G., and B. Wolf-Mueller. **1993**. A method for estimating the age of bees: Age-dependent wing wear and coloration in the wool-carder bee *Anthidium manicatum* (Hymenoptera: Megachilidae). Journal of In\. 6: 529–537.

O'Neill, K. M., and J. F. O'Neill. **2016**. Brood parasitism of the resin bee *Megachile campanulae* (Robertson) by *Coelioxys modesta* Smith (Hymenoptera: Megachilidae). Journal of the Kansas Entomological Society. 89: 117–127.

Ordway, E. 1965. Caste differentiation in *Augochlorella* (Hymenoptera, Halictidæ). Insectes Sociaux. 12: 291–308.

Ordway, E. 1966. The bionomics of *Augochlorella striata* and *A. persimilis* in eastern Kansas. Journal of the Kansas Entomological Society. 39: 270–313.

Packer, L. 1990. Solitary and eusocial nests in a population of *Augochlorella striata* (Provancher) (Hymenoptera; Halictidae) at the northern edge of its range. Behavioral Ecology and Sociobiology. 27: 339–344.

Packer, L., A. Dzinas, K. Strickler, and V. Scott. **1995**. Genetic differentiation between two host "races" and two species of cleptoparasitic bees and between their two hosts. Biochemical Genetics. 33: 97–108.

Packer, L., V. Jessome, C. Lockerbie, and B. Sampson. **1989**. The phenology and social biology of four sweat bees in a marginal environment: Cape Breton Island. Canadian Journal of Zoology. 67: 2871–2877.

Packer, L., and G. Knerer. **1986**. An analysis of variation in the nest architecture of *Halictus ligatus* in Ontario. Insectes Sociaux. 33: 190–205.

Pengelly, D. H. 1955. The biology of bees of the genus *Megachile* with special reference to their importance in alfalfa seed production in southern Ontario. PhD dissertation, Cornell University

Sakagami, S. F., and C. D. Michener. **1962**. The nest architecture of the sweat bees (Halictinae), a comparative study of behavior. The University of Kansas Press, Lawrence, Kansas.

Sheffield, C. S., C. Ratti, L. Packer, and T. Griswold. **2011**. Leafcutter and mason bees of the genus *Megachile* Latreille (Hymenoptera: Megachilidae) in Canada and Alaska. Canadian Journal of Arthropod Identification. 18: 1–107.

Sladen, F. W. L. 1918. Pollination of alfalfa by bees of the genus *Megachile*. Table of Canadian species of the *latimanus* group. The Canadian Entomologist. 50: 301–304.

Smith, J. B. 1901. Notes on some digger bees.—II. Journal of the New York Entomological Society. 9: 52–72.

Stephen, W. P. 1956. Notes on the biologies of *Megachile frigida* Smith and *M. inermis* Provancher (Hymenoptera: Megachilidae). The Pan-Pacific Entomologist. 32: 95–101.

Stockhammer, K. A. 1966. Nesting habits and life cycle of a sweat bee, *Augochlora pura* (Hymenoptera: Halictidae). Journal of the Kansas Entomological Society. 39: 157–192.

Tuell, J. K., J. S. Ascher, and R. Isaacs. **2009**. Wild bees (Hymenoptera: Apoidea: Anthophila) of the Michigan highbush blueberry agroecosystem. Annals of the Entomological Society of America. 102: 275–287.

Wolf, A. T., and J. S. Ascher. **2009**. Bees of Wisconsin (Hymenoptera: Apoidea: Anthophila). The Great Lakes Entomologist. 41: 129–168.

Yanega, D. 1997. Demography and sociality in halictine bees (Hymenoptera: Halictidae), pp. 293–315. *In* Choe, J.C., Crespi, B.J. (eds.), The evolution of social behavior in insects and arachnids.. Cambridge University Press.

Zarrillo, T. A., J. S. Ascher, J. Gibbs, and K. A. Stoner. **2016**. New and noteworthy records of bees (Hymenoptera: Apoidea: Anthophila) for Connecticut. Journal of the Kansas Entomological Society. 89: 138–157.