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Colleen D. Satyshur
Department of Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle, Saint Paul, MN 55108, USA, csatyshu@umn.edu

Thea A. Evans
Department of Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle, Saint Paul, MN 55108, USA, evans676@umn.edu

Britt M. Forsberg
versity of Minnesota Extension, University of Minnesota, 135 Skok Hall, 2003 Upper Buford Circle, St. Paul, MN 55108, USA, forsb118@umn.edu

Robert B. Blair
Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, 135 Skok Hall, 2003 Upper Buford Circle, St. Paul, MN 55108, USA, blairrb@umn.edu

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Minnesota State Records for *Osmia georgica, Megachile inimica,* and *Megachile frugalis* (Hymenoptera, Megachilidae), Including a New Nest Description for *Megachile frugalis* Compared with Other Species in the Subgenus *Sayapis*

Colleen D. Satyshur[1,*], Thea A. Evans[1], Britt M. Forsberg[2] and Robert B. Blair[3]

[1] Department of Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle, Saint Paul, MN 55108, USA

[2] University of Minnesota Extension, University of Minnesota, 135 Skok Hall, 2003 Upper Buford Circle, St. Paul, MN 55108, USA

[3] Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, 135 Skok Hall, 2003 Upper Buford Circle, St. Paul, MN 55108, USA

* Corresponding author: (e-mail: csatyshu@umn.edu)

Abstract

In this article, we report the first Minnesota state records of *Osmia (Helicosmia) georgica* Cresson 1878, *Megachile (Sayapis) inimica* Cresson 1872, and *Megachile (Sayapis) frugalis* Cresson 1872, which were collected in 2018. We also provide the first description of the nest structure of *M. frugalis*. All three species typically have more southern distributions. The nest of *M. frugalis* shows similar structure to other species in the subgenus *Sayapis* Titus, such as *M. inimica* and *M. pugnata* Say, particularly in that the longitudinal nest cell walls lack a lining of leaf pieces, and the cell partitions are made from a layer of leaf pieces followed by a layer of masticated vegetation and soil particles.

Keywords: *Megachile inimica*, *Megachile frugalis*, *Sayapis*, *Osmia georgica*, natural history, cavity-nesting, trap nest, solitary bees, nest architecture

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In this paper, we report the first records of *Osmia georgica* Cresson, *Megachile inimica* Cresson, and *Megachile frugalis* Cresson in the state of Minnesota. Prior to this, *O. georgica* has shown a predominantly southeastern distribution in the United States of America, with digitized records showing it present along the entire eastern coast and west through Michigan, Nebraska and Texas. Both *Megachile* Latreille species have been recorded across the southern USA, extending northwards into southern Wisconsin, Michigan, New England and south into Mexico and central America (Medler and Lussenhop 1968, Gibbs et al. 2017, GBIF.org 2020). These new records for Minnesota add to the 18 species of *Osmia* Panzer and 22 species of *Megachile* currently known from the state (MNDNR 2019). In the United States as a whole there are 140 species of *Osmia* and 138 species of Megachile (Ascher and Pickering 2020). Bees in the genera *Osmia* and *Megachile* are solitary-nesting bees that typically use vegetative matter or mud to construct nest cells, although some species do use resin (Cane et al. 2007, Michener 2007, Sheffield et al. 2011).

The two new Megachile species reported here both belong to the subgenus *Sayapis* Titus. Prior to this, Minnesota has had only a single representative of the subgenus: *Megachile pugnata* Say. Species in the subgenus *Sayapis* have unusual nest structure compared with other congeners. Among the (*Sayapis*) species found in the United States, nests have been described for *M. pugnata*, *M. inimica*, *Megachile policaris* Say, and *Megachile zaptlana* Cresson (Table 1; Mitchel 1937, Medler 1964, Krombein 1967, Medler and Lussenhop 1968, Frohlich and Parker 1983, Raw 1984, MacIvor 2016, dos Santos et al. 2020). Two others, *Megachile fidelis* Cresson and *Megachile newberryae* Cockerell, have been recorded nesting in stems or wood, but their nest structure information is lacking (Mitchell 1937, Butler 1965, Barthell et al. 1998, Frankie et al. 1998). We know of no references of nests of *Megachile mellitarsis* Cresson or *M. frugalis*.

In addition to details of these new state records, we also provide the first description of the nest structure of *M. frugalis* in comparison with *M. inimica* and published nest descriptions of other species within the

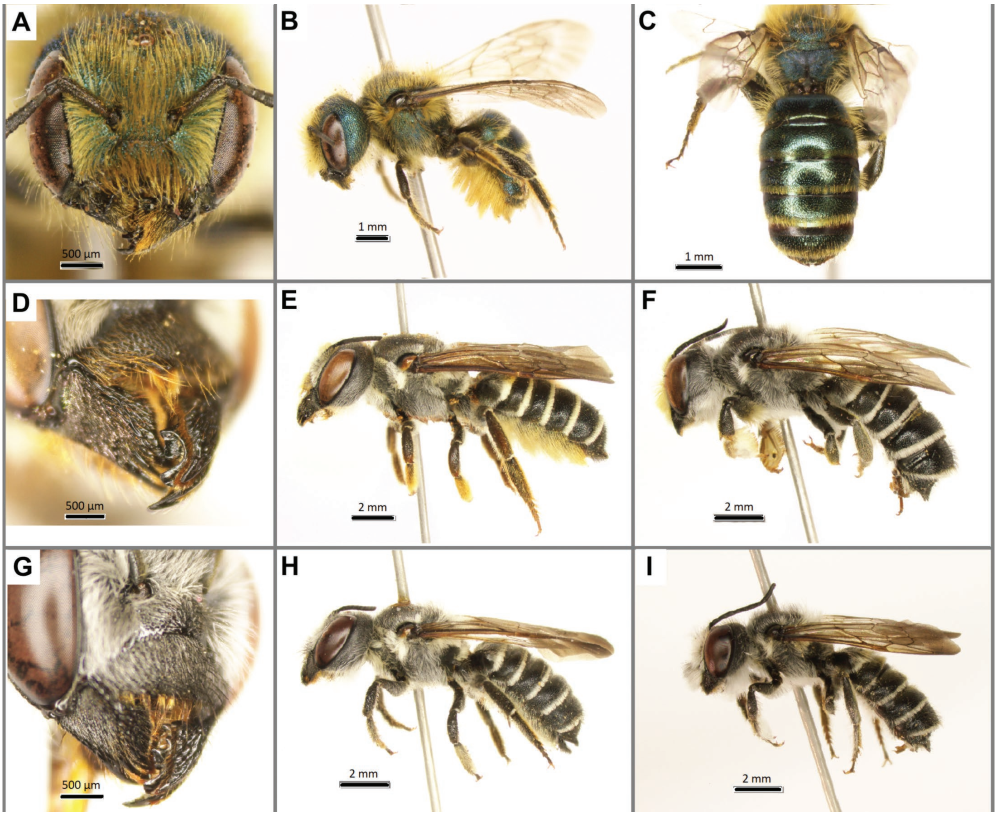

Figure 1: A) Female *O. georgica* mandible. B) *O. georgica* female side, note projection on mandible and yellow scopa. C) *O. georgica* male abdomen, note propodeal slit and T6 notch. D) *M. inimica* female mandible, note central point on clypeus. E) *M. inimica* female side. F) *M. inimica* male side, note lack of black brush on expanded forebasitarsis. G) *M. frugalis* female mandible, note black hair on clypeus. H) *M. frugalis* female side I) *M. frugalis* male side. (Photos courtesy of Thea Evans).

subgenus *Sayapis* which inhabit the United States.

Methods and Materials

Bees were collected with nest blocks as part of the citizen science project "Minnesota Bee Atlas" (https://z.umn.edu/beeatlas). Blocks were made from untreated pine or Douglas fir, with a roof of cedar shingling. Each block measured approximately 8.9 × 14 × 27.9 cm (3.5 × 5.5 × 11 in.) and contained five tunnels each of six different diameters: 3.18 mm, 4.76 mm, 6.35 mm, 7.94 mm, 9.53 mm, and 11.11 mm. Tunnels were approximately 11.43 cm (4.5 in.) deep and spaced 2.54 cm (1 in.) away from other tunnels or the block edge. Each block was identified by a unique number, and tunnels within blocks by unique letter-number combinations.

Volunteers across the state of Minnesota were selected to hang and monitor a nest block in a semi-natural habitat. In March 2018, a total of 140 nest blocks were sent out. Recommended block placement was 0.9–1.5 meters high facing south or east in a semi-sunny location. Volunteers were asked to record specific mounting conditions of their block and report every 2–3 weeks on evidence of nesting. All records discussed in this paper come from southern Minnesota. The nest block that yielded *O. georgica*, number 502, was placed in Winona County, Minnesota, southeast of the town of Lewiston (43.94986°N, –91.82164°W). According to volunteer observation, it was mounted next to several acres of Conservation Reserve Program (CRP) land containing trees, grasses, and native wildflowers, at a height of 1.22 m, facing southeast. The five *M. inimica* nests were distributed between two blocks. One block, number 453, was located near Revere in Cottonwood County (44.13895°N, –95.3601°W), and hung 1.2–1.4 m high,

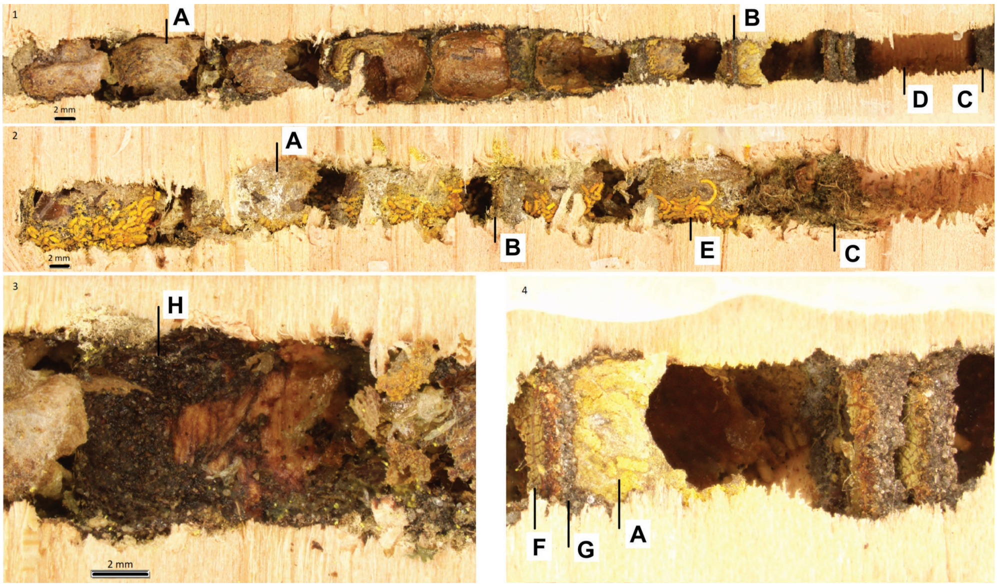

Figure 2. Nests of *M. frugalis* (top) and *M. inimica* (middle), with entrances to right, A=cocoon, B=cell partition, C=final nest plug, D=vestibule, E=frass. Bottom left: close up of 2nd cell of *M. frugalis* nest with cocoon removed - note partial lining of cell walls (H) with chewed vegetation. Bottom right: Close up of 8th cell of *M. frugalis* nest showing partition construction in more detail, F=leaf piece, G=chewed vegetation and soil particles. (Photos courtesy of Thea Evans).

facing southeast. The other block, 467, was located on the edge of Dover in Olmstead County (43.96863°N, –92.1343°W), and hung four feet high, facing south. The block was situated in a lawn with hostas, a highbush cranberry and arborvitae, very close to farmland and grassland. The block containing the *M. frugalis* nest, number 472, was located near Bingham Lake in Cottonwood County, (43.92406°N, –95.0407°W), and hung 1.37 m high, facing south. The volunteer described the location as bordering Conservation Reserve Program land with abundant flowers and near a lake.

In the late fall, blocks were returned to the University of Minnesota where they were surveyed by otoscope, overwintered and reared to emergence in a growth chamber the following year. Warming for emergence was conducted with constant temperature steps, rather than by tracking local daily fluctuations, therefore bee emergence dates suggest relative seasonality rather than actual emergence in field conditions. To capture emerging bees, a hollowed-out plastic test-tube cap was glued over each tunnel entrance and a replaceable test tube was inserted in the cap. Emerged bees in test tubes were removed daily and new tubes placed on tunnels. Bee identification was done by C. D. Satyshur using Mitchell (1962), Sandhouse (1939), and Discover Life keys (Andrus et al. 2020, Griswold et al. 2020, Nelson and Droege 2020a,b). Specimens were compared to materials in the University of Minnesota Insect Collection, which were available for all but *M. frugalis* females, and specimen photographs were reviewed by Jason Gibbs. Bees are deposited in the University of Minnesota Insect Collection; photographs are included in Fig. 1 and within the Minnesota Bee Atlas Species Guide (University of Minnesota Extension 2020).

After the emergence season, the *M. frugalis* and *M. inimica* nest tunnels were split open. Nests were photographed and measured using digital calipers and the Olympus cellSense Standard program. Composite photographs of the nests were created using the Olympus cellSense Standard, CombineZP, and Paint programs. A voucher nest for each species is housed in University of Minnesota insect collection. The *O. georgica* nest tunnel was not opened, because these bees were not identified until after block disposal. Nest descriptions for *O. georgica* can be found in the literature (*e.g.* Hartman et al. 1944, Krombein 1967, Hawkins 1975).

Table 1: Summaries of nesting records of Megachile (Sayapis) which inhabit the United States, encompassing the varying levels of information available.

Species	Location	Substrate	Materials and construction	Reference
M. fidelis	Sequoia Natl. Park, CA, USA	"small log"	1 nest.	Mitchell 1937
M. fidelis	Central Valley, CA, USA	pine trap nests	25 nests, 6.5–8.0 mm diameter.	Barthell et al. 1998
M. fidelis	San Joaquin Valley, CA, USA	Wooden trap nests	NA	Frankie et al. 1998
M. frugalis	Near Bingham Lake, MN, USA	pine/ Douglas fir wooden nesting block	1 nest, 7.94 mm diameter. Eight cells av. 10.1 mm long. Partitions made from leaf circles covered with masticated vegetation, which was also plastered on lower walls. Plug single layer of soil particles and masticated vegetation. Vestibule present.	This work
M. inimica inimica	San Antonio, TX, USA	"worm holes in mesquite trees or fenceposts."	Unknown number of nests. "Lined with circles cut from leaves of *Monisia pallida* Planch." (Probably *Celits pallida* Planch).	Mitchell 1937, H.B. Parks pers com.
M. inimica sayi	Sioux City, IA, USA	"mine in apple wood"	NA	Mitchell 1937, p 193
M. inimica inimica	Sand scrub in Florida, USA	Traps made from borings into wood	1 nest, 6.4 mm diameter. Cells 22–31 mm long. Partition before cells, cells unlined by leaf pieces, partitions "consisting of 1 or 2 circular leaf cuttings on the inner surface and 3-4 mm of agglutinated sand which also formed the base of the next cell." Vestibule 8 mm long, plug "17 mm thick of loosely arranged, more or less circular leaf cuttings."	Krombein 1967
M. inimica sayi	Desert floor, Arizona, USA	Traps made from borings into wood	2 nests, 6.4 mm diameter. Cells 17–25 mm long. Partition before cells. Partitions 1.5 or 2-3 mm thick, "had several leaf cuttings at the inner end then a layer of fine pebbles and leaf pulp". Vestibule 17 mm long. Plug 5 mm thick with leaf cuttings, pebbles and leaf pulp "which hardened into a firm plug."	Krombein 1967
M. inimica sayi	Ipswich, southern Wisconsin, USA	Sumac stem Traps	2 nests. Built against pith at tunnel bottom. "Not enclosed in pieces of leaf…but consisted only of the partitions formed of chewed leaf material."	Medler and Lussenhop 1968
M. inimica	Near Revere and Dover, MN, USA	pine/ Douglas fir wooden nesting block	5 nests, 6.35-9.53 mm diameter. Cells av. 12.8 mm long. Partitions made from one cut leaf piece, followed by a thin layer of soil particles, sometimes covered with chewed vegetation. Sometimes vegetation plastered on lower cell walls. Plug made of two layers of partitions with grass or wood pressed into it. No vestibule.	This work
M. newberryae	Arizona, USA	holes in *Prosopis*	Cutting leaves of *Celits.*	Butler 1965

Species	Location	Substrate	Materials and construction	Reference
M. pugnata	Wisconsin, USA	sumac stick trap-nests	20 nests, 6.25, 7.8 mm diameter, cells av. 15.27 mm long. "Cells were made with basal and apical partitions consisting of leaf discs, chewed leaf materials and soil." Vestibule present. Plug of layered partitions.	Medler 1964
M. pugnata	Captive rearing, Utah, USA	tunnels in elderberry, or glass tubes	Many nests. 8–9 mm diameter, some excavation. *Oenothera hookeri* for building material. Partitions made by masticating vegetation and smearing it on back and sides to make a rim. Leaf pieces attached to the rim, filling tunnel diameter. Another layer of masticated vegetation placed in a rim, smeared to the middle, and with soil particles pressed into it. Then "female laid on her back and groomed the posterior portion of the abdomen and again passed a droplet of liquid to the middle and fore-legs. This time the secretion was placed between the mandibles and chewed vigorously. The female then chewed and licked the outer surface of the partition." Almost all had vestibules.	Frohlich and Parker 1983
M. pugnata	Toronto, ON, Canada	Cardboard tube traps in PVC housing	45 nests. "Mud and chewed leaves to line its brood cells, and makes partitions between adjacent cells using circular pieces of leaves laid one over the other."	MacIvor 2016
M. policaris	Arizona and Florida, USA	Traps made from borings into wood	8 nests, 6.4 or 12.7 mm diameter. Single-larvae cells:13-30 mm long, communal brood cells: 17–78 mm long. "gummy leaf pulp" before cells, cells unlined by leaf material. Many large communal brood cells with multiple pollen balls or a long pollen ball. Partitions "2 layers of small compressed leaflets 2–9 mm long separated by thin septa of hardened, gummy leaf pulp. Occasionally several alternating layers . . . Closing plugs . . . were constructed of the same material in alternating layers." Vestibular cell frequently lacking. Leaf pieces from "*Prosopis* (mesquite), *Mimosa biuncifera* (cat claw acacia), *Eysenhardtia polystachya* (kidneywood)" and an unidentified shrub. Arizona bees used small whole leaflets vs circles.	Krombein 1967, W. Niles
M. zaptlana	Southern and coastal plains, Jamaica	"old beetle burrows in fence posts"	129 nests, cells av. 9.8 mm diameter. Cells av. 19.9 mm long. Base of the first cell lined with pieces of leaves and intercellular partitions constructed but longitudinal walls of cells unlined.	Raw 1984
M. zaptlana	Iguarassu, Pombos, PE, Brazil	Cardboard tubes in wooden traps, and wooden and clear plastic traps	157 nests, 6 mm diameter. Cells av. 6–9.3 mm long. Cells unlined by leaf pieces. Partitions between cells made of a rim of chewed leaves, followed by larger leaf pieces which were covered with chewed vegetation and sand. Most nests had 1 vestibule, some had up to 4. The final plug consisted of 2–5 juxtaposed partitions.	dos Santos et al. 2020

Table 2: Nests of new species records for Minnesota from 2018 season, with emergence dates of males (m) and females (f) listed in the timeline column.

Bee species	Minnesota County	Nest ID and tunnel diameter	Offspring	Emergence timeline
O. georgica	Winona Co.	502(F3) 4.76 mm (3/16 in.)	7	10-Mar-19: 2m 11-Mar-19: 4m 13-Mar-19: 1f
M. inimica	Cottonwood Co.	453(G2) 7.94 mm (5/16 in.)	4	1-May-19: 1m 7-May-19: 3f 9-May-19: 1f
M. inimica	Cottonwood Co.	453(H2) 7.94 mm (5/16 in.)	5	4-May-19: 2m 7-May-19: 3f
M. inimica	Olmstead Co.	467(D1) 9.53 mm (3/8 in.)	6	4-May-19: 6f
M. inimica	Olmstead Co.	467(E1) 9.53 mm (3/8 in.)	3	6-May-19: 2f 7-May-19: 1f
M. inimica	Olmstead Co.	467(E2) 6.35 mm (1/4 in.)	4	28-Apr-19: 1m 4-May-19: 1f Upon opening: 2f dead
M. frugalis	Cottonwood Co.	472(F2) 7.94 mm (5/16 in.)	8	15-Apr-19: 3m,1f 16-Apr-19: 4f

Results

Warming for emergence began on 4 March 2019 (Table 2). Six males and one female *O. georgica* emerged from a single nest between 10–13 March (Fig. 1). Three males and five female *M. frugalis* emerged from a single nest between 15–16 April 2019. Bees emerged from the five *M. inimica* nests between 28 April–7 May 2019. A total of *22 M. inimica* were collected, four males and 18 females, with an average of 4.4 bees/nest. In all cases above, males emerged before females within nests and there were no other organisms that emerged from these tunnels.

The *O. georgica* nest was in the 4.76 mm diameter tunnel F3 in block 502. The volunteer reported partial plugs of "mud/sand" on 2 June and 24 June 2018, and a full plug of the same material on 25 July 2018. Upon return to the University of Minnesota, we used the otoscope to record a complete outer nest plug of masticated vegetation, rather than mud/sand, which was a common misinterpretation among reporters. Despite frequent volunteer reports and helpful pictures of the five *M. inimica* nest blocks, nesting phenology information is sparse, possibly because these nests were plugged well inside tunnel entrances, making them difficult to see. Volunteer reports include grass material in 467(E1) on 7 July 2018, and a full plug of unknown material in 467(E2) on 28 September 2018. Upon return to the University of Minnesota, we recorded the following plug materials in the five tunnels that later produced *M. inimica:* three complete grass plugs, one complete plug of leaf/petal pieces, and one complete mud/sand plug. Variation in otoscope-recorded plug materials within a species can indicate incomplete nests, or that a species adds extra material to the final plug, or that another species has built a second nest in the tunnel, closer to the opening. Evidence from opening nest tunnels suggests the first two situations are likely for these nests as no evidence of other species' nests were seen. The *M. frugalis* nest was made in block 472(F2). The volunteer submitted six observations, with no activity in this tunnel. However, volunteer photographs show a full plug on 10 August 2018, which was absent on 22 July 2018, indicating the nest was completed between those dates. Upon return to University of Minnesota, we observed a full plug of masticated vegetation in the tunnel.

All five *M. inimica* nests were opened and a composite photograph of nest 453(H2) was created (Fig. 2). Four of the five nests were complete and measured on average 81.8 mm long, with final plugs recessed on average 26.2 mm from the tunnel entrance.

Three complete nests had five cells, one had six, and the incomplete nest had four cells. The average cell length was 12.8 mm (range: 8.3–17.6 mm). However, the cell lengths were longer in narrower diameter tunnels and shorter in wider diameter tunnels. The average cell length was 10.1 mm in the two 9.53 mm diameter tunnels, 14.0 mm long in the two 7.94 mm diameter tunnels and 15.7 mm long in the 6.35 mm diameter tunnel. In one nest, the innermost cell failed early, leaving a mass of pollen stores. In two other nests, there was a cell that did not produce an emerging adult, but these must have failed after cocoons were spun, as all cells contained evidence of cocoons. There was no evidence that the nests were parasitized, and no dead pupae or adults were found. Emerging bees can chew through dead offspring or adults, sometimes pushing debris out of the tunnel as they go and leaving little evidence behind. The average thickness of partitions between cells across all nests was 1.9 mm. The partitions were made from one whole leaf piece, followed by a thin layer of soil particles, in some cases with chewed vegetation on top. Cell walls were generally unlined by any leaf or soil material, although sometimes mud or masticated vegetation was spread part way up the sides of cells from the lower partition. The bees' cocoons were clearly evident, made of parchment-like material with yellowish orange frass distributed over the outside. No complete nest contained a vestibule. Despite the otoscope records of grass nest plugs, all final plugs consisted primarily of two consecutive partitions, of similar construction to cell partitions, with grass or wood fibers only pressed into the outermost surface of some. Plugs averaged 7.4 mm thick (range 6.6–8.3 mm).

The *M. frugalis* tunnel 472(F2) was opened and a composite photograph of the nest was created (Fig. 2). The nest had eight cells, corresponding to eight emerged adults. The nest occupied the full length of the 106.7 mm tunnel. Mud and possibly masticated vegetation were plastered on the innermost end of the nest, measuring 2.4 mm thick. The average nest cell length was 10.1 mm (range 9.6–10.7 mm) and partition thickness was 0.8 mm (range 0.3–1.1 mm). Each cell had a thin layer of masticated vegetation plastered on the inner 1/3–1/2 of the wall length, while the remaining wall area was covered with a shiny material over the bare wooden tunnel wall (Fig. 2). The bees' cocoons were clearly evident, made of parchment-like material with a small amount of brown frass, primarily on the outer ends. The upper partition of the last cell was made of two layers instead of one and measured 3.2 mm. All partitions were made of a single layer of leaf pieces, followed by a thin layer of masticated vegetation and sand. The nest contained a 13.1 mm long vestibule between the last cell and the final plug. The final plug was located at the tunnel entrance and composed of a single layer of soil particles mixed with masticated vegetation that was 2.3 mm thick.

Discussion

Our understanding of all three species' distributions is expanded somewhat northward by these new records for Minnesota. Among digitized bee records, the closest prior records for *O. georgica* are found in northern Indiana, Illinois, Kansas, and Missouri (GBIF.org 2020). It's also reported from nine counties in the Lower Peninsula of Michigan (Gibbs et al. 2017). *Megachile inimica* has been recorded in southern Wisconsin (Medler and Lussenhop 1968) and in Kalamazoo county in the Lower Peninsula of Michigan (Gibbs et al. 2017). The nearest digitized records are in Nebraska and Illinois (GBIF.org 2020). *Megachile frugalis* has also been recorded from eight counties in southern Michigan (Gibbs et al 2017) and there are also digitized records from Missouri and Kansas (GBIF.org 2020). Whether the northern records reported here are due to a change in the species' ranges or increased sampling effort is difficult to say from these data.

Our available nesting and emergence phenology point to mid or late summer nesting by *M. inimica* and *M. frugalis*. *Megachile frugalis* had clear nest plug data for late July to early August. The sparse nesting information for *M. inimica* nests came in July and September, somewhat corresponding to the flight period reported for southern Wisconsin of 4 July to 2 September (Medler and Lussenhop 1968). *Megachile inimica* also emerged at the very end of rearing, later than the rest of the bees. As we rear at fixed temperatures, and bee and wasp species emerge in a predictable order each year, the greater degree-days before emergence of *M. inimica* could point to a possible mechanism for the species primarily being found in areas with longer growing seasons. It also could point to a mechanism for a possible northward expansion of the species' distribution, as the freeze-free season in southern Minnesota has lengthened by 16 days from 1951–2012 (GLISA 2020).

Similarly, the full plug date for *O. georgica* reported by the volunteer (between 24 June and 25 July) would be late compared to other *Osmia* species seen in this project, which often complete nest building by early to mid-June. However, the partial plug noted by the volunteer in early June may actually represent the nest completion date, and the offspring emerged in the growth chamber in the same timeframe as other small *Osmia*. Hawkins (1975) reports *O. georgica* completed nests between the end of May and the end of June in Tennessee.

With the addition of the *M. frugalis* nest in this work, seven of the eight (*Sayapis*) species in the US now have at least one record of a nesting substrate, or the material in which a nest is made (Table 1). Natural nests have been documented in wood substrates for *M. fidelis, M. inimica inimica* Cresson, *M. inimica sayi* Cresson, *M. newberryae* and *M. zaptlana* (Mitchell 1937, Butler 1965, Raw 1984). Others are only known from trap nests, which, while suggestive and in some cases well documented, does not necessarily fully encompass their nesting biology. For example, one predominantly ground nesting bee species, *Megachile wheeleri* Mitchell, has been caught in trap nests (Gordon 2000). O*smia lignaria* Say, which is managed using trap nests, can also nest in the ground (Rau 1937, Linsley and MacSwain 1941, Levin 1966). Other species may show flexibility in the use of nest substrate, such as *Megachile brevis* Say. This bee species can be found in trap nests, but also has been found in standing dead stems, in a termite hole in a garage door, among leaves — both alive and dead, in prostrate corn stalks, under cow chips and mats of prairie grass, among small rocks on the ground, and in holes actually in the ground (Michener 1953).

To date, internal nest architecture appears to be fairly conserved within the subgenus *Sayapis* in the United States. There is now information of varying detail for five of the eight species (Table 1). All available information indicates they construct nest cells that are unlined by leaf pieces, in contrast with most other *Megachile* which fully line the longitudinal walls of their nest cells with cut leaf pieces. Partitions between cells are also similar for these five (*Sayapis*) species, consisting of a layer of leaf pieces on the inner side covered with a mix of soil particles and masticated vegetation.

There are some differences between species. All United States (*Sayapis),* in contrast with many other *Megachile,* make use of soil particles in nest building to some degree. However, nest accounts indicate that the ratio of soil to masticated vegetation may differ between species in the subgenus. For example, we recorded final nest plugs of *M. inimica* covered with soil particles with grass or wood pressed into it, while the *M. frugalis* plug was primarily masticated vegetation. The *M. frugalis* nest also had masticated vegetation plastered on the lower walls of cells (Fig. 2), which is more wall lining than reported for *M. inimica* or *M. pugnata.* The *M. frugalis* nest contained a vestibule, similar to reports for *M. pugnata* and *M. inimica* (Medler 1964, Krombein 1967). In contrast, we did not see vestibules in our *M. inimica* nests. The most unusual nest structure in United States (*Sayapis*) is reported for *M. policaris.* This species can construct atypically large, multi-offspring cells (Krombein 1967, Michener 2007), unlike the more common single-offspring cells of *M. inimica, M. frugalis, M. pugnata and M. zaptlana (*Table 1; Medler 1964, Krombein 1967, Medler and Lussenhop 1968, Frohlich and Parker 1983, Raw 1984, MacIvor 2016, dos Santos et al. 2020). It is unknown to what degree nest architecture may naturally vary within a species or may differ between nests in trap nests compared to natural substrates.

It would be interesting to see how nest construction of other members of this subgenus compare to the five United States species that have been described. The nests of *M. fidelis* should be attainable from trap nests, and perhaps those of *M. newberryae* also. The final species, *M. mellitarsis*, has two intriguing synonyms (*M. terrestris_homonym* Cockerell 1908a and *M. geophila* Cockerell 1908b), which suggest affiliation for the ground, possibly indicating that it breaks from the other members of the subgenus and nests below-ground. However, Cockerell's (1908a) original description does not mention nesting, simply noting that the bee was flying close to the ground when caught. Future research could focus on nests of *M. mellitarsis,* as well as filling out nest architecture and natural substrate information for the other US (*Sayapis)* species. The results presented in this work add to foundational data on both bee distribution and nesting biology, addressing the lack of nesting information for bee species in the United States (Harmon-Threatt 2020).

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Literature Cited

Andrus, R., S. Droege, and T. Griswold. 2020. Draft guide to the male Osmia of Eastern North America. Available from https://www.discoverlife.org/mp/20q?guide=Osmia_male (accessed December 2019).

Ascher, J.S., and J. Pickering. 2020. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). Available from https://www.discoverlife.org/mp/20q?guide=Apoidea_species (accessed December 2019).

Barthell, J.F., G.W. Frankie, and R.W. Thorp. 1998. Invader effects in a community of cavity nesting Megachilid bees (Hymenoptera: Megachilidae). Environmental Entomology 27(2): 240–247.

Butler, G.D. Jr. 1965. Distribution and host plants of leaf-cutter bees in Arizona. College of Agriculture, University of Arizona Technical Bulletin 167: 19 p.

Cane, J.H., T. Griswold, and F.D. Parker. 2007. Substrates and materials used for nesting by North American Osmia bees (Hymenoptera: Apiformes: Megachilidae). Annals of the Entomological Society of America 100(3): 350–358.

Cockerell, T.D.A. 1908a. Descriptions and records of bees.—XVIII. Annals and Magazine of Natural History 8(i): 259–267.

Cockerell, T.D.A. 1908b. A new name in *Megachile*. The Canadian Entomologist 40:460.

Cresson, E.T. 1872. Hymenoptera Texana. Transactions of the American Entomological Society 4: 153–292.

Cresson, E.T. 1878. Descriptions of new North American Hymenoptera in the collection of the American Entomological Society. Transactions of the American Entomological Society and Proceedings of the Entomological Section of the Academy of Natural Sciences 7: 61–136.

dos Santos, A.A., D. Parizotto, C. Schlindwein, and C.F. Martins. 2020. Nesting biology and flower preferences of *Megachile* (*Sayapis*) *zaptlana*. Journal of Apicultural Research 59(4): 609–625.

Frankie, G.W., R.W. Thorp, L.E. Newstrom-Lloyd, M.A. Rizzardi, J.F. Barthell, T.L. Griswold, J. Kim, and S. Kappagoda. 1998. Monitoring solitary bees in modified wildland habitats: Implications for bee ecology and conservation. Environmental Entomology 27(5): 1137–1148.

Frohlich, D.R., and F.D. Parker. 1983. Nest building behavior and development of the sunflower leafcutter bee *Eumegachile* (*Sayapis*) *pugnata* (Say) (Hymenoptera: Megachilidae). Psyche 90(3): 193–209.

GBIF.org (27 May 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.7ys4v9

Gibbs, J., J.S. Ascher, M.G. Rightmyer, and R. Isaacs. 2017. The bees of Michigan (Hymenoptera: Apoidea: Anthophila), with notes on distribution, taxonomy, pollination, and natural history. Zootaxa 4352(1): 1–160.

Gordon, D.M. 2000. Plants as indicators of leafcutter bee (Hymenoptera: Megachilidae) nest habitat in coastal dunes. Pan-Pacific Entomologist. 76(4): 219–233.

Great Lakes Integrated Sciences and Assessments (GLISA). "Historical Climatology: Minneapolis-Saint Paul, Minnesota". Available from http://glisa.umich.edu/media/files/Minn-StPaulMN_Climatology.pdf (accessed January 2020).

Griswold, T., H. Ikerd, S. Droege, J.B. Pascarella, and J. Pickering. 2020. Draft guide to the female Osmia of Eastern North America. Available from https://www.discoverlife.org/mp/20q?guide=Osmia_female (accessed December 2019).

Harmon-Threatt, A. 2020. Influence of nesting characteristics on health of wild bee communities. Annual Review of Entomology 2020 65(1): 39–56.

Hartman, C.G., P. Hartman, P. Hartman, and C. Rettenmeyer. 1944. Notes on the habits of *Osmia georgica* Cresson as ascertained by the glass-tube method. Psyche 51: 162–165.

Hawkins, W.A. 1975. Nesting biology of *Osmia* (*Chalcosmia*) *georgica* (Hymenoptera: Megachilidae). Journal of the Kansas Entomological Society 48(4): 493–499.

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

Levin, M.D. 1966. Biological notes on *Osmia lignaria* and *Osmia californica* (Hymenoptera: Apoidea, Megachilidae). Journal of the Kansas Entomological Society 39: 524–535.

Linsley, E.G. and J. W. MacSwain. 1941. The bionomics of *Ptinus californicus*, a depredator in the nests of bees. Bulletin of the Southern California Academy of Sciences 40: 126–137.

MacIvor, J.S. 2016. DNA barcoding to identify leaf preference of leafcutting bees. Royal Society Open Science 3(3): 1–13. doi: 10.1098/rsos.150623.

Medler, J.T. 1964. A Note on *Megachile* (*Sayapis*) *pugnata pugnata* Say in trap-nests in Wisconsin (Hymenoptera: Megachilidae). The Canadian Entomologist 96(6): 918–921.

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

Michener, C.D. 1953. The Biology of a leafcutter bee (*Megachile brevis*) and its associates. The University of Kansas Science Bulletin 35(3): 1659–1748.

Michener C.D. 2007. The Bees of the World, 2nd ed. Johns Hopkins University Press, Baltimore, MD, USA.

Minnesota Department of Natural Resources (MNDNR). "Minnesota Bees- A preliminary list". Available from https://files.dnr.state.mn.us/eco/mcbs/pollinators/bees_species_list_2019.pdf (Accessed Dec 2019).

Mitchell, T.B. 1937. A revision of the genus *Megachile* in the Nearctic region: Part VII Taxonomy of the subgenus *Sayapis* (Hymenoptera, Megachilidae). Transactions of the American Entomological Society 63(2): 175–206.

Mitchell, T.B. 1962. Bees of the Eastern United States, Vol II. North Carolina Agricultural Experiment Station Technical Bulletin 152: 557 p.

Nelson, R.A. and S. Droege. 2020a. Guide to the female Megachile of Eastern North America. Available from https://www.discoverlife.org/mp/20q?guide=Megachile_female (accessed December 2019).

Nelson, R.A. and S. Droege. 2020b. Guide to the male Megachile of Eastern North America. Available from https://www.discoverlife.org/mp/20q?guide=Megachile_male (accessed December 2019).

Sandhouse, G.A. 1939. North American bees of the genus *Osmia* (Hymenoptera: Apoidea). Memoirs of the Entomological Society of Washington 1: 1–167.

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.

Rau, P. 1937. The Life-history of *Osmia lignaria* and *O. cordata*, with notes on *O. conjuncta*. Annals of the Entomological Society of America 30: 324–343.

Raw, A. 1984. The nesting biology of nine species of Jamaican bees (Hymenoptera). Revista Brasileira De Entomologia 28(4): 497–506.

University of Minnesota Extension. 2020. Minnesota Bee Atlas Species Guide. Available from http://apps.extension.umn.edu/environment/citizen-science/bee-atlas/bee-blocks/SpeciesGuide (accessed August 2020).