

Nest architecture and pollen hosts of the borealpine osmiine bee species *Hoplitis (Alcidamea) tuberculata* (Hymenoptera, Megachilidae)

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Abstract

Although *Hoplitis tuberculata* is a rather common bee species in the upper montane and subalpine zone of the Alps, its biology is only fragmentarily known. In the present publication, both nest architecture and pollen host spectrum are described. *H. tuberculata* nests in insect borings in dead wood, where one to several brood cells are built in a linear series. Examination of four nests obtained from trap nests revealed three peculiar characteristics of its nest architecture: i) the 0.3–0.5 cm thick partitions between the brood cells are three-layered consisting of two walls built from masticated leaves which enclose an interlayer that is densely packed with pebbles, earth crumbs and other small particles; ii) in the majority of the nests, a vestibule varying in length from 2.2–8.9 cm and loosely filled with small particles is present between the outermost cell partition and the nest plug; iii) the nest is sealed by a 1.2–1.9 cm long plug consisting of two walls of masticated leaves which enclose a space that is densely packed with small particles and divided up by one to three additional walls. The nest architecture of *H. tuberculata* is unique among Palaearctic osmiine bees; however, it corresponds to that of three North American species closely related to *H. tuberculata*. Microscopical analysis of female pollen loads and brood cell provisions revealed that *H. tuberculata* is polylectic with a strong preference for Fabaceae. Among the Fabaceae, *Lotus* and *Hippocrepis* were by far the most important pollen hosts. Non-Fabaceae taxa represented by substantial proportions in pollen loads or cell provisions were *Helianthemum* (Cistaceae), *Vaccinium* (Ericaceae) and *Rubus* (Rosaceae).

Keywords

Apiformes, *Hoplitis tuberculata* species group, *Monumetha*

Introduction

Osmiine bees are famous for their very diverse and often spectacular nest building behaviours as well as for their high proportion of species that exhibit narrow host plant specializations (Friese 1923, Malyshev 1937, Westrich 1989, O'Toole and Raw 1991, Müller et al. 1997, Cane et al. 2007, Sedivy et al. 2008, 2013a,b,c, Gotlieb et al. 2014, Haider et al. 2014, Müller 2015). While the biology of most Central European osmiine bee species is well known, gaps of knowledge exist for several species mainly occurring in the Alps.

Hoplitis (Alcidamea) tuberculata is a boreoalpine species, which has a disjunct distribution area encompassing the Alpine arc from France to Austria and some neighbouring mountains such as Jura and Schwarzwald on the one hand and the boreal zone from Scandinavia and northeastern Europe to easternmost Asia on the other hand (Tkalců 1977, Müller 2015). It belongs to a clade of six species, which were formerly treated as members of the subgenus *Monumetha* (Michener 2007, Ungricht et al. 2008), but recently merged as *Hoplitis tuberculata* species group into the large subgenus *Alcidamea* (Sedivy et al. 2013c, Müller 2015). While *H. tuberculata* is restricted to the Palearctic region, all the other species occur in North America with some species reaching as far north as arctic Alaska (Michener 1947, 2007, Hurd and Michener 1955, Ascher and Pickering 2015), clearly suggesting a nearctic origin of the *Hoplitis tuberculata* species group (Sedivy et al. 2013c).

Hoplitis tuberculata is rather common in the upper montane and subalpine zone of the Alps, where it inhabits open forests, forest edges or windfalls between 900m a.s.l. and the timberline (Amiet et al. 2004). Its nesting biology is only fragmentarily known. While the species has repeatedly been observed to nest in insect burrows in dead wood (Giraud 1861, Frey-Gessner 1880, Friese 1923, Stoeckhert 1933, Grünwaldt 1939, Käpylä 1978, Westrich 1989, Amiet et al. 2004; Fig. 1), its nest architecture is unknown and available information on the material used to build cell partitions and nest plug is contradictory. According to Käpylä (1978), a combination of small stones, masticated leaves and pieces of rotten wood is used to seal the nest. In contrast, Westrich (1989) considered mud to be the exclusive nest building material, which - according to Amiet et al. (2004) - is sometimes combined with masticated leaves. Although current knowledge suggests that *H. tuberculata* is a pollen generalist collecting pollen from the flowers of at least seven plant families (Käpylä 1978, Westrich 1989), its host plant preferences in Central Europe have never been analyzed in detail.

Based on the investigation of four nests recently discovered in the Swiss Alps and the microscopical analysis of 87 pollen loads of females collected across the Alpine arc, the present publication aims to fill the knowledge gaps still existing on both the nesting biology and the flower preferences of *Hoplitis tuberculata*.

Material and methods

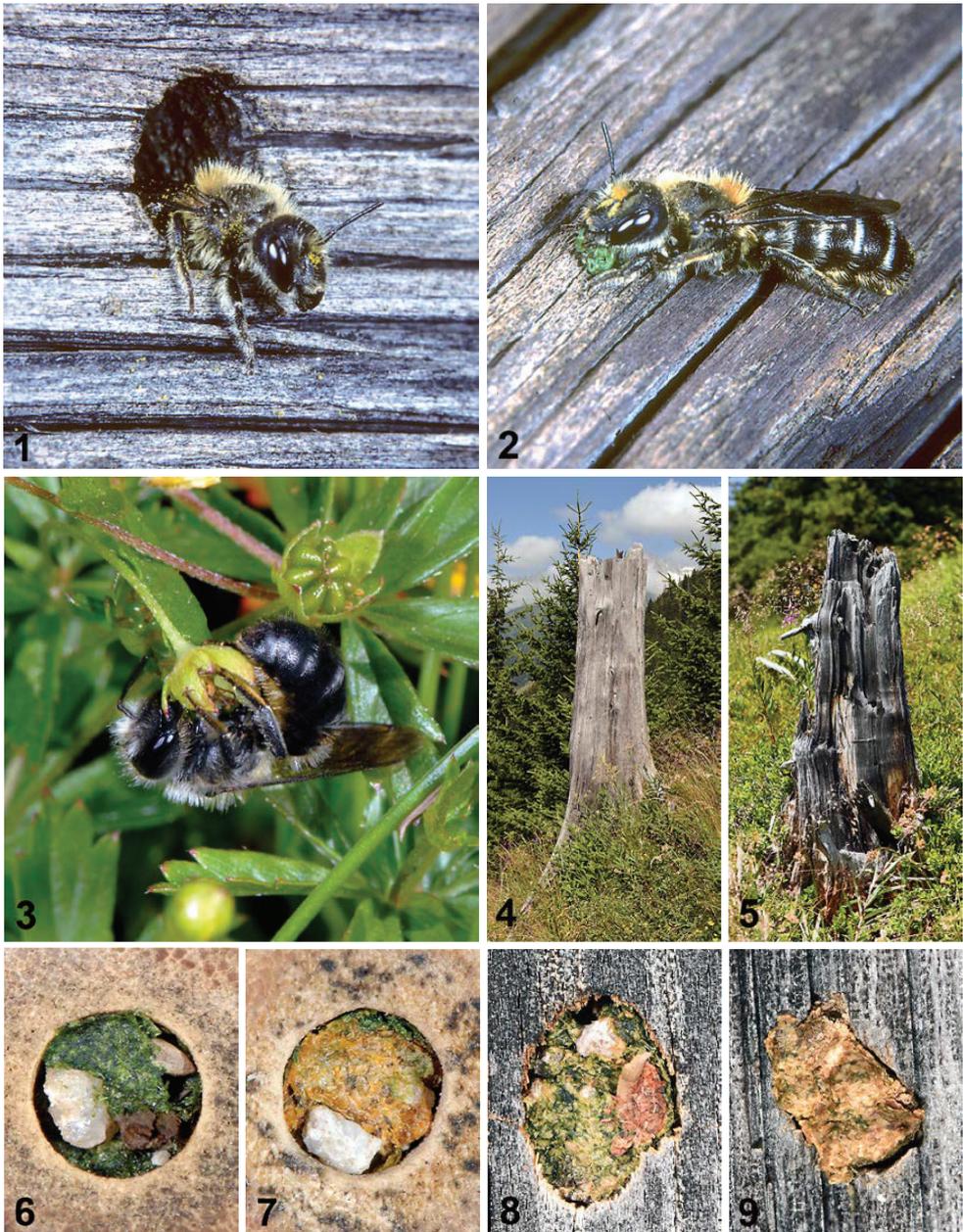
In spring 2014 and 2015, a total of 20 trap nests were fixed at a height of 0.2–1.5 m to sun exposed dead wood in an open subalpine forest above Sedrun (Grisons, Switzerland) between 1650 m and 1800 m a.s.l., where *Hoplitis tuberculata* had been found to be common. Each trap nest consisted of a bundle of about 30 hollow bamboo sticks. The diameter of the burrows in the bamboo sticks varied between 3 mm and 8 mm. During the flight period of *H. tuberculata*, which lasted from the beginning of June to the end of July, the trap nests were checked twice for sealed nests or for nests still being provisioned. Sealed nests were opened in the laboratory by splitting them longitudinally with a knife, before nest architecture and nest building material were analyzed. To get additional information on the material used to construct nest plugs, trunks and stumps of dead trees in the vicinity of the trap nests were searched for sealed nests of *H. tuberculata*.

To uncover the pollen host preferences of *Hoplitis tuberculata*, the scopal pollen contents of 87 female specimens collected at 87 different localities in Switzerland (n=67), Austria (n=11), Liechtenstein (n=3), Germany (n=3) and Italy (n=3) from 1905 to 2015 were microscopically analyzed using the method outlined by Westrich and Schmidt (1986). Before removing pollen from the metasomal scopae, the degree to which they were filled was estimated. The amount of pollen in the scopae was assigned to five classes, ranging from 5/5 (full load) to 1/5 (filled to one-fifth). The pollen grains were stripped off the scopae with a fine needle and embedded in glycerol gelatin on a slide. When a pollen load was composed of different pollen types, their percentages were estimated by counting the grains along two transects chosen randomly across the cover slip at a magnification of 400x. Pollen types represented by less than 5% of the counted grains were excluded to prevent a potential bias caused by contamination. For pollen loads consisting of two or more different pollen types, the percentages of the number of pollen grains were corrected by their volume. After assigning different weights to scopae according to their degree of filling (full loads were weighted five times more strongly than scopae filled to only one-fifth), the estimated percentages were summed up over all pollen samples. The pollen grains were identified at a magnification of 400x with the aid of the literature cited in Westrich and Schmidt (1986), Beug (2004) and an extensive reference collection. In addition, the pollen provisions in six brood cells of two nests detected at the study site were analysed. To estimate the proportion of the different pollen types in the provisions, the amount of each pollen type was assigned to one of five quantity classes.

Results

Nest architecture

Four nests of *Hoplitis tuberculata* in three different trap nests were found. Five further nests were found in tree trunks and stumps in the vicinity of the trap nests (Figs 4, 5).



Figures 1–9. Nesting biology of *Hoplitis tuberculata*: **1** Female leaving her nest in a preexisting burrow in dead wood **2** Female transporting leaf pulp in her mandibles **3** Female collecting leaf pulp from the sepals of *Potentilla erecta* **4–5** Dead tree stumps with beetle burrows used as nesting sites (Sedrun, Grisons, Switzerland) **6–8** Sealed nests with outermost wall of nest plug with pebbles and earth crumbs embedded in the leaf pulp matrix **9** Sealed nest with outermost wall of nest plug consisting of leaf pulp only.

The maximal diameter of the nine burrows selected by the bees as nesting sites was 4 mm (n=1), 4.5 mm (n=6), 5 mm (n=1) and 6 mm (n=1).

All four nests built in the bamboo sticks of the trap nests had a similar structure and consisted of i) a basal wall that sealed the nest against the rear end, ii) a varying number of brood cells each delimited towards the nest entrance by a cell partition, iii) a (facultative) vestibule in front of the last cell and iv) a nest plug that closed the nest at the front end. The distance from the basal wall to the outermost wall of the nest plug was 6.5 cm, 7.6 cm, 8.3 cm and 10.9 cm.

The basal walls consisted of masticated leaves ("leaf pulp") and had a width of about 1 mm. In two nests, a free space between pith and basal wall with a length of 0.4 cm and 3.5 cm, respectively, was present, which was loosely filled with small particles, such as pebbles, wood and leaf fragments, seeds or earth crumbs (Fig. 10). In the other two nests, the basal wall was constructed directly adjacent to the pith that filled the rear of the bamboo sticks (Fig. 14). Some of these particles, which were most probably transported into the nest by the female bees, partly adhered to the inside of the basal wall, suggesting that the females incorporated them into the leaf pulp matrix during the first steps of basal wall construction.

The four nests contained one (n=1), two (n=2) and four (n=1) linearly arranged brood cells, which had a length of 8.5-12.5 mm (Fig. 10, 14). In two nests, which were opened in late fall, the brood cells harboured postdefecating larvae spun in a semi-transparent, brownish-white cocoon, indicating that *Hoplitis tuberculata* overwinters as prepupa. The cell partitions had a width of 3-5 mm and invariably consisted of three layers (Fig. 11): two walls each of 0.5-1 mm width, which had been constructed from leaf pulp, enclosed an interspace of 2-4 mm length, which was densely packed with pebbles, earth crumbs, seeds, wood chips or fragments of leaves and needles. While the outer sides of both walls of the cell partitions were very carefully worked forming a plane surface, the inner sides were more irregular. Some of the particles of the inter-layer were partly incorporated into the leaf pulp matrix of the inside of the outer wall.

Three of the four nests contained a vestibule between the outermost cell partition and the nest plug measuring 2.2 cm, 8.1 cm and 8.9 cm in length (Fig. 10). The vestibule was loosely filled with a small amount of 20 to 30 particles, such as pebbles, earth crumbs, wood chips or fragments of leaves and needles (Fig. 13). In one nest, no vestibule was developed; instead, the outermost cell partition and the nest plug bordered directly at each other (Fig. 12, 14).

The nest plugs measured 1.2 cm, 1.3 cm, 1.4 cm and 1.9 cm in length. They consisted of one wall each at the rear and the front end, which enclosed a space that was divided up by one (n=1) or three (n=3) additional walls (Fig. 10, 12, 14). All interspaces between the walls were usually densely packed with small pebbles, earth crumbs, wood chips or fragments of leaves and needles. The walls of the nest plug had a width of 0.5-1 mm, were built from leaf pulp and partly contained foreign particles on their inside, which had been glued to the leaf pulp matrix during wall construction. In two nests, single pebbles and/or earth crumbs were embedded in the leaf pulp matrix of the outside of the front wall (Fig. 6, 7), whereas in the other two nests the front wall consisted



Figures 10–14. Nest architecture of *Hoplitis tuberculata*: **10** Opened nest in a hollow bamboo stick with – from left to right – i) short space filled with small particles followed by the basal wall, ii) two brood cells, which are delimited towards the nest entrance by a three-layered cell partition, iii) vestibule loosely filled with small particles, iv) nest plug consisting of one wall each at the rear and the front end enclosing a space that is filled with small particles and divided up by three additional walls (the low amount of particles in the space between the third and the fourth wall, the presence of only traces of the fourth and the outermost wall and the lack of particles between the two outermost walls is due to the loss of particles and walls during the splitting of the stick) **11** Three-layered cell partition composed of two walls enclosing an interlayer that is densely filled with particles **12** Three-layered cell partition being flush with the nest plug, which consists of several walls with densely packed small particles in between **13** Vestibule between outermost cell partition and innermost part of the nest plug loosely filled with small particles **14** Opened nest in a hollow bamboo stick with i) basal wall built directly adjacent to the pith in the rear of the stick, ii) four brood cells each delimited by a three-layered cell partition directly followed by iii) the nest plug.

exclusively of leaf pulp. This variability in the presence or absence of small particles incorporated into the front wall was also apparent in the five nests found in the vicinity of the trap nests: the front wall of two nests contained small particles on its outside (Fig. 8), whereas that of the other three nests was built of leaf pulp only (Fig. 9).

In summary, the females used two different materials for nest construction: i) leaf pulp to build all the walls within the nest (Fig. 2) and ii) small particles, which were amassed in interspaces between walls and occasionally also incorporated into the leaf pulp matrix of certain walls. The origin of the leaf pulp is not known in detail; one

female, however, was repeatedly observed to chew sepals of *Potentilla erecta* to collect leaf pulp (Fig. 3). The small particles were most probably all collected from the ground as judged by the observation that several females picked up small pebbles and earth crumbs from a small unpaved path.

Pollen hosts

The microscopical analysis of 87 female pollen loads revealed that *Hoplitis tuberculata* is polylectic harvesting pollen from the flowers of at least eight plant families (Tab. 1). However, pollen of Fabaceae strongly dominated constituting 84.5% of the total pollen grain volume, followed by pollen of Cistaceae represented by 8.9%. Pollen of all other plant families was recorded in small percentages only. The strong preference for Fabaceae pollen is also evident from the finding that all 87 pollen loads contained pollen of this plant family, 54 of which were pure Fabaceae pollen loads. Among the Fabaceae, *Lotus* was by far the most important pollen host (Tab. 1); its pollen represented 63.9% of the total pollen grain volume and was recorded in 84 out of 87 pollen loads, 35 of which were pure *Lotus* pollen loads. The second most important Fabaceae pollen host was *Hippocrepis*; its pollen represented 11.0% of the total pollen grain volume and was recorded in 31 out of 87 loads.

Pollen of *Lotus* was also the most important pollen type recorded in six brood cell provisions of two nests collected at the study site (Tab. 2). All cells contained large to very large amounts of *Lotus* pollen. The provisions of several cells, however, also contained considerable amounts of non-Fabaceae pollen, such as pollen of *Vaccinium* and *Rubus*.

Discussion

Nest architecture

As shown in the present study, *Hoplitis tuberculata* uses leaf pulp to construct the walls of both brood cells and nest plug. The erroneous assumption of mud as being the exclusive or predominant nest building material (Westrich 1989, Amiet et al. 2004) is probably based on the observation of females that collected earth crumbs or pebbles on the ground to amass them later in interspaces within their nests. In fact, among *Hoplitis* species of the large subgenus *Alcidamea* only two species have been recorded so far to use mud for nest construction, i.e. the stem-nesting Nearctic *H. grinnelli*, which constructs its cell partitions with clay while the nest plug consists of alternating layers of clay and pith (Davidson 1896, as *H. producta*), and the Palaearctic *H. fulva*, which seals its nest in preexisting cavities of loess scarps with a plug of mud whereas its brood cells are constructed from leaf pulp alone (Marikovskaya 1968).

Peculiar characteristics of the nest architecture of *Hoplitis tuberculata* include i) the three-layered cell partitions, ii) the presence of a vestibule loosely filled with small

Table 1. Pollen composition of female pollen loads of *Hoplitis tuberculata*. n=87 pollen loads from 87 different localities distributed across the Alps.

Plant family	Plant genus/ subfamily	% pollen grain volume	number (%) of loads with this pollen type	number (%) of pure loads
Fabaceae		84.5	87 (100)	54 (62.1)
Fabaceae	<i>Lotus</i>	63.9	84 (96.6)	35 (40.2)
Fabaceae	<i>Hippocrepis</i>	11.0	31 (35.6)	0 (0)
Fabaceae	<i>Onobrychis</i>	2.9	3 (3.4)	0 (0)
Fabaceae	<i>Trifolium</i>	1.4	2 (2.3)	0 (0)
Fabaceae	unknown	5.2	7 (8.0)	0 (0)
Cistaceae	<i>Helianthemum</i>	8.9	16 (18.4)	0 (0)
Boraginaceae	<i>Echium</i>	1.3	2 (2.3)	0 (0)
Ericaceae	<i>Vaccinium</i>	0.9	2 (2.3)	0 (0)
Rosaceae		1.2	6 (6.9)	0 (0)
Rosaceae	<i>Potentilla</i>	0.7	5 (5.7)	0 (0)
Rosaceae	<i>Rubus</i>	0.5	1 (1.1)	0 (0)
Ranunculaceae	<i>Ranunculus</i>	0.5	2 (2.3)	0 (0)
Asteraceae	Cichorioideae	0.5	3 (3.4)	0 (0)
Lamiaceae		0.4	2 (2.3)	0 (0)
Lamiaceae	Lamioideae	0.4	1 (1.1)	0 (0)
Lamiaceae	Nepetoideae	0.05	1 (1.1)	0 (0)
unknown		1.8	4 (4.6)	0 (0)

Table 2. Pollen composition of brood cells of *Hoplitis tuberculata*. n=6 brood cells from two nests collected near Sedrun (Grisons, Switzerland) on 18.7.2014. The amount of each pollen type was assigned to five quantity classes ranging from +=very small amount to +++++=very large amount.

		Fabaceae: <i>Lotus</i>	Fabaceae: <i>Trifolium</i>	Fabaceae: unknown	Ericaceae: <i>Vaccinium</i>	Rosaceae: <i>Rubus</i>	Asteraceae: Asteroideae
Nest 1	Brood cell 1	++++			++++	++++	
	Brood cell 2	++++			++++	++++	
Nest 2	Brood cell 1	++++		+++	++++	++	
	Brood cell 2	+++++			+++	++	
	Brood cell 3	+++++		++	+	+++	++
	Brood cell 4	+++++	++	+++	+	++	

particles and iii) a nest plug that consists of densely packed layers of small particles sandwiched between at least three walls.

The construction of three-layered cell partitions composed of two walls with an interlayer of densely packed small particles in between seems to be unique among Palearctic osmiine bees, which usually partition linearly arranged brood cells by single walls only (Müller 2015 and references therein). However, such three-layered cell partitions are known from several North American *Hoplitis* species, which are all members of the subgenus *Alcidamea* but differ in their preferred nesting sites. Species, which use preexisting cavities, such as *H. albifrons*, *H. fulgida* and *H. spoliata*, transport small par-

ticles such as pebbles, wood chips, earth crumbs or fragments of conifer needles from outside into their nest to include them into the cell partitions (Fye 1965, Medler 1967, Clement and Rust 1976). Interestingly, these three species are closely related to *H. tuberculata* and also belong to the *Hoplitis tuberculata* species group (see Introduction). Among them, the construction of three-layered cell partitions seems to be the rule in *H. fulgida* and is most common in *H. albifrons*, while *H. spoliata* frequently omits the interlayer resulting in single leaf pulp walls between the brood cells (Fye 1965, Medler 1967, Clement and Rust 1976). In contrast, species, which excavate their own burrows in pithy stems, such as *H. hypocrita*, *H. pilosifrons* or *H. sambuci*, tightly pack particles of pith taken from the burrow walls in between the two leaf pulp layers (Michener 1955, Clement and Rust 1976). Although the latter three species are not members of the *Hoplitis tuberculata* species group, their shared habit of constructing three-layered cell partitions suggests a close relatedness to that group as shown by Sedivy et al. (2013).

The function of the three-layered cell partitions is counterintuitive at first sight as the thick nest plug built by *Hoplitis tuberculata* and its relatives (see below) is expected to already provide enough protection against the intrusion of nest predators. We hypothesize that these strong cell partitions might impede mobile larvae of predators, which already infested a brood cell before the nest was sealed, from invading adjacent cells. In fact, larvae of some *Trichodes* beetle species (Cleridae), which are antagonists of above-ground nesting megachilid bees, attack several brood cells in sequence by breaking through the cell walls (Carré 1980).

The presence of a vestibule filled with small particles seems to be another typical trait common to the members of the *Hoplitis tuberculata* species group except for *H. spoliata*, where the vestibule is empty (Fye 1965, Medler 1967, Clement and Rust 1976). As in *H. tuberculata*, vestibules may occasionally be absent in nests of *H. albifrons* and *H. fulgida* with the last provisioned cell being flush with the nest plug (Fye 1965, Clement and Rust 1976). In contrast to the three-layered cell partitions, which seem to be a unique character of only a few species of the subgenus *Alcidamea*, vestibules with amassed small particles are rather widespread among osmiine bees. They are known from some *Hoplitis* species of the subgenera *Anthocopa* and *Alcidamea* other than the *Hoplitis tuberculata* species group, from several *Osmia* species of the subgenera *Erythrosmia*, *Neosmia* and *Pyrosmia* as well as from *Wainia elizabethae* (Gess and Gess 1988, Müller 2015 and references therein).

The architecture of the nest plug varies both within and among the North American members of the *Hoplitis tuberculata* species group. The nest plug of *H. spoliata* usually consists of a single layer of leaf pulp, rarely of three or four layers with short empty spaces in between (Medler 1967). In contrast, the nest plug of *H. albifrons* and *H. fulgida* is usually three-layered with two walls enclosing an interspace tightly packed with small particles (Fye 1965, Clement and Rust 1976). In the latter species, one or two additional walls are occasionally present in the particle-filled space between the rear and the front wall of the nest plug, mirroring the situation found for *H. tuberculata* in the present study. As in *H. tuberculata*, small pebbles are often but not always cemented into the leaf pulp matrix of the front wall in *H. fulgida* and *H. spoliata* (Hicks 1926, Fye 1965, Medler 1967).

In summary, although the nest architecture of *Hoplitis tuberculata* is unique among Palearctic osmiine bees, it corresponds to that of its closest North American relatives, indicating that nesting site, nest building material and nest structure are conserved traits within the *Hoplitis tuberculata* species group.

Pollen hosts

The present study shows that *Hoplitis tuberculata* is polylectic and collects pollen from the flowers of at least eight different plant families, among which Fabaceae clearly dominate. Fabaceae pollen was recorded in each pollen load and constituted almost 85% of the total pollen grain volume. In contrast, several brood cell provisions contained considerable amounts of non-Fabaceae pollen suggesting that pollen hosts other than Fabaceae may locally also play an important role for larval nourishment. Indeed, the significance of Fabaceae pollen as deduced from the analysis of pollen loads of females, which most probably all had been collected during flower visits, might have been overestimated. The probability that specimens of *H. tuberculata* are collected at flowers of *Lotus* or *Hippocrepis* rather than at flowers of e.g. *Vaccinium* or *Rubus* is likely higher because the conspicuously yellow Fabaceae flowers act as true magnet for each bee researcher due to the fact that they attract a multitude of different bee species. Considering this possible bias, the host plant spectrum of *H. tuberculata* recorded in the present study is similar to that found in Finland (Käpylä 1978). Here, pollen of seven different plant families represented by at least 3% per load was recorded in 16 pollen loads of females collected both at flowers and nesting sites. As in the present study, Fabaceae (*Caragana*, *Lathyrus*, *Lotus*), Ericaceae (*Vaccinium*), Rosaceae (*Geum*, *Potentilla*, *Rubus*), Ranunculaceae (*Anemone*, *Ranunculus*) and Asteraceae (*Leontodon*) were among the plant families exploited for pollen. In addition, flowers of Asparagaceae (*Convallaria*, *Polygonatum*) and Violaceae (*Viola*) also served as pollen hosts, the former being the most important pollen sources followed by flowers of the Fabaceae.

In summary, the pollen hosts of *Hoplitis tuberculata* known so far belong to ten different plant families, among which Fabaceae predominate but probably not to that large degree as might be expected from the analysis of the female pollen loads from the Alps alone.

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