JHR 96: 641–656 (2023)
doi: 10.3897/jhr.96.109255
https://jhr.pensoft.net

RESEARCH ARTICLE

JOURNAL OF Hymenoptera RESEARCH
A peer-reviewed open-access journal
The International Society of Hymenopterists

Two new *Hoplitis* species of the subgenus *Hoplitis* Klug, 1807 (Hymenoptera, Megachilidae) and the nesting biology of *H. astragali* sp. nov. in Dagestan

Alexander V. Fateryga[1], Andreas Müller[2,3], Maxim Yu. Proshchalykin[4]

1 *T.I. Vyazemsky Karadag Scientific Station, Nature Reserve of RAS, Branch of A.O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Nauki Str. 24, Kurortnoye, 298188 Feodosiya, Russia* **2** *ETH Zurich, Institute of Agricultural Sciences, Biocommunication and Entomology, Schmelzbergstrasse 9/LFO, 8092 Zurich, Switzerland* **3** *Natural History Museum Bern, Department of Invertebrates, Bernastrasse 15, 3005 Bern, Switzerland* **4** *Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences, 100-let Vladivostoku Ave. 159, 690022 Vladivostok, Russia*

Corresponding author: Alexander V. Fateryga (fater_84@list.ru)

Academic editor: Jack Neff | Received 9 July 2023 | Accepted 8 August 2023 | Published 15 August 2023

https://zoobank.org/FB63186E-9043-4571-A1FE-EE27E3FA9D1D

Citation: Fateryga AV, Müller A, Proshchalykin MYu (2023) Two new *Hoplitis* species of the subgenus *Hoplitis* Klug, 1807 (Hymenoptera, Megachilidae) and the nesting biology of *H. astragali* sp. nov. in Dagestan. Journal of Hymenoptera Research 96: 641–656. https://doi.org/10.3897/jhr.96.109255

Abstract

Hoplitis astragali **sp. nov.**, a member of the *H. monstrabilis* species group, and *H. dagestanica* **sp. nov.**, a member of the *H. adunca* species group, are described. The former species is known from Dagestan in Russia, Azerbaijan, and Turkmenistan, the latter only from Dagestan. Nests of *H. astragali* are described. Females of this species excavated burrows in a vertical clay cliff, but sometimes chose a horizontal surface for nest excavation, particularly at the entrance of old burrows of *Xylocopa olivieri* (Apidae). The nest burrows of *H. astragali* were either sub-vertical or sub-horizontal. The nests were composed of one to three brood cells, an empty vestibule in front of the outermost cell, and a closing plug at the nest entrance made of moistened mud. The inner surface of the cells was covered with a thin wall composed of compact soil, most probably built by the female bee after cell excavation. The pollen loaf was very liquid and had a spherical shape. The egg was deposited on its top. The cocoon consisted of a single thin layer, which uniformly covered the whole inner surface of the cell. There was one generation per year. The prepupae hibernated. *Sapyga caucasica* (Sapygidae) was recorded in the nests as a kleptoparasite. Both females and males of *H. astragali* exclusively visited flowers of two species of the genus *Astragalus* (Fabaceae).

Keywords

Bionomics, Caucasus, megachilid bees, osmiine bees, Palaearctic region, taxonomy

Introduction

Hoplitis Klug, 1807 is the largest genus of the osmiine bees (Hymenoptera, Megachilidae, Osmiini) with 387 species described so far (Müller 2023). It is distributed in the Palaearctic, the Nearctic, and the Afrotropical region; a few species also occur in the Oriental region (Michener 2007). The genus *Hoplitis* is especially diverse in the Palaearctic region, where 14 subgenera and 311 species occur (Praz et al. 2008; Ungricht et al. 2008; Sedivy et al. 2012a; Müller 2023). The largest subgenus of the genus *Hoplitis* is *Hoplitis* s. str., which is confined to the Palaearctic region. It contains 91 species described so far and a large number of still undescribed species amounting to more than 50. The subgenus comprises several species groups. Among them, the *Hoplitis adunca* species group is the largest and one of the taxonomically most challenging osmiine bee taxa due to the high morphological uniformity among its species, especially in the female sex (Müller 2016, 2023). Members of this species group nest either in various pre-existing cavities (such as rock and stone crevices, hollow stems, abandoned nests of other bees and wasps, insect burrows in wood, rarely empty snail shells) or construct cells freely on the surface of rocks or stones, usually in depressions (Sedivy et al. 2013). The building material used for nest construction is always mud, often combined with small pebbles or gravel. Members of the *Hoplitis annulata* and the *H. monstrabilis* species groups nest in self-excavated burrows in the ground and the *H. erythrogastra* species group contains kleptoparasites, which develop in nests of members of the *H. annulata* species group (Michener 2007; Sedivy et al. 2013; Müller 2023).

The megachilid bee fauna of the Republic of Dagestan (Russia) is very poorly known. A list of just 30 species, including one species later synonymized, was published 150 years ago (Morawitz 1873); six of them were described as new, of which four are currently recognized as valid species. Some recently published papers (Fateryga 2017; Fateryga et al. 2019; Fateryga and Proshchalykin 2020; Litman et al. 2021) added 46 species increasing the total species number to 75, which is expected to be still very far from the true number of megachilid bee species occurring in Dagestan. The present contribution is a part of the currently ongoing study of the megachilid bees of Dagestan. Several field expeditions were made to various districts of this republic in 2015–2022, which resulted in about 2000 newly collected specimens of Megachilidae. The complete list of species will be published in a separate paper, while the purpose of the present contribution is to describe two new *Hoplitis* species of the subgenus *Hoplitis*. Since nests of one of these species were discovered, its bionomics is briefly described in the present paper.

Material and method

The material for the present study was collected in Dagestan in 2018–2022 and deposited in the collections of the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia [**ZISP**], the Federal Scientific Center of the East

Asia Terrestrial Biodiversity of the Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, Russia [**FSCV**], the Entomological Collection of ETH Zurich, Switzerland [**ETHZ**], and the research collection of A.V. Fateryga, Feodosiya, Russia [**CAFK**].

Morphological terminology and definitions for body measurements follow Michener (2007) with the following specifications: i) the distance between lateral ocellus and preoccipital margin was measured in top view rather than in lateral view; ii) the diameter of an ocellus includes the ocellar border, which is often of the same colour as the surrounding cuticle thereby differing from the usually light colour of the central part of the ocellus; iii) the length of a segment of the labial palpus was measured from its sclerotized base to the sclerotized base of the subsequent segment; iv) the length of an antennal article was measured along its lower margin, while its width corresponds to the maximal width of the article; v) numbering of antennal articles starts from the scapus, which is antennal article 1, and ends with the last flagellomere, which is antennal article 12 (females) or 13 (males); vi) the number of a segment belonging to a segmented body part is put into parentheses if a character of that segment is not developed in all individuals; thus, "terga (2)3–6 strongly shagreened" means that tergum 2 is strongly shagreened as terga 3–6 in some but not all specimens. Measurements to the nearest 0.1 mm or 0.5 mm (for body length) were taken using an ocular micrometer on an Olympus VNT stereomicroscope. Photomicrographs were taken with a Keyence VHX-2000 digital microscope.

The nesting biology of *Hoplitis astragali* sp. nov. was investigated 6 km northwest of Chirkey in the Buynaksky district (43°00'10"N, 46°53'51"E) in 2022. Six nesting females were recorded on 27 May at a clay cliff. One of them was sealing her nest with soil; this nest was dissected immediately after the female had finished the closing plug. The other five nests were marked with two triangular pieces of red plastic each; the markers were inserted in an equal distance of about 10 cm from the nest entrance, so that the latter lay in the middle between them. The second visit to this place on 31 May revealed that four of the five nests still open on 27 May were sealed with soil plugs and that an additional nest was built and sealed near one of them. All five sealed nests were extracted from the cliff together with the surrounding earth excavated with the help of a shovel. The earth lumps were transferred to the laboratory and the nests were dissected in October 2022 by removing the surrounding earth layer by layer with a knife. In total, six nests were studied, including the freshly sealed one. Plans of the nest structure were drawn on paper and the direction of the nesting burrows and brood cells determined with a compass. Contents of nest cells from the dissected nests were placed into glass tubes sealed with cotton plugs and then kept under outdoor conditions. Photographs of the nests were taken with a Canon EOS RP digital camera, a Sigma AF 105 mm f/2.8 and a Canon RF 35 mm f/1.8 macro lens, and a Yongnuo YN-14EX macro flash. Additional observations on flower visits by both new species of *Hoplitis* were made in Tsudakhar in the Levashi district (42°19'40"N, 47°09'48"E) in 2018–2022.

Taxonomy

***Hoplitis* (*Hoplitis*) *astragali* Fateryga, Müller & Proshchalykin, sp. nov.**
https://zoobank.org/69FC78C0-D4DA-473E-9538-FFCF4E52C810
Fig. 1A–H

Type material. *Holotype*. Russia. Dagestan, Levashi district: Tsudakhar, 42°19'40"N, 47°09'48"E, 10.6.2019, ♂ (leg. A. Fateryga). Deposited in ZISP.

***Paratypes*. Russia. Dagestan, Buynaksky district:** 6 km NW Chirkey, 43°00'10"N, 46°53'51"E, 26–27.5.2022, 1 ♀, 7 ♂ (leg. A. Fateryga), 7 ♀, 2 ♂ (leg. M. Proshchalykin); **Dagestan, Kumtorkalinsky district:** Sarykum sand dune, 43°00'08"N, 47°14'15"E, 28–29.5.2019, 8 ♀, 1 ♂ (leg. M. Proshchalykin, V. Loktionov); ibid., 30.5.2019, 2 ♀ (leg. M. Mokrousov); **Dagestan, Levashi district:** Tsudakhar, 42°19'40"N, 47°09'48"E, 23.6.2018, 1 ♂ (leg. A. Fateryga); ibid., 1.6.2019, 2 ♀ (leg. M. Proshchalykin, V. Loktionov), 5 ♂ (leg. A. Fateryga); ibid., 10–11.6.2019, 12 ♀, 4 ♂ (leg. A. Fateryga); ibid., 16.6.2021, 1 ♂ (leg. A. Fateryga); ibid., 28–29.5.2022, 1 ♀, 2 ♂ (leg. A. Fateryga), 5 ♀, 15 ♂ (leg. M. Proshchalykin); **Dagestan, Laksky district:** vicinity of Turtsi, 42°11'34"N, 47°09'33"E, 22.5.2021, 4 ♀ (leg. A. Fateryga). **Azerbaijan. Nakhchivan Autonomous Republic:** Babek, Sirab, 1.6.2020, 1 ♀ (leg. M. Maharramov). **Turkmenistan:** Ashgabat environs, 15.5.1993, 3 ♀, 1 ♂ (leg. M. Halada). Deposited in ZISP, FSCV, ETHZ, and CAFK.

Diagnosis. Among the western Palaearctic *Hoplitis* species of the subgenus *Hoplitis* s. str., the female of *H. astragali* (Fig. 1A) is unequivocally characterised by the following combination of characters: i) apical margin of sternum 6 without submarginal carina; ii) tibial spurs of hind leg apically blunt with very short tip oriented at right angles to the longitudinal axis of the spur (Fig. 1G); iii) clypeus medially with impunctate longitudinal zone, which is usually continuous, well delimited, about 2–5× as wide as diameter of adjacent punctures and roughly parallel-sided (Fig. 1C); iv) declivous lateral side of apical part of labrum about as high as length of last antennal article (Fig. 1E); v) marginal zones of terga 1–5 with long, dense and uninterrupted band of cream-coloured hairs, which turn to white in worn specimens. The male of *H. astragali* (Fig. 1B) is easily diagnosed by the following combination of characters: i) apical margin of tergum 7 medially truncate to slightly rounded (Fig. 1H); ii) gonoforceps apically with finger-like projection directed inwards at right angles to its longitudinal axis (Fig. 1H); iii) sterna (2)3–4 medially with inconspicuous, very narrow and little raised longitudinal keel; iv) antennal articles 4–13 longer than wide and ventrally weakly keeled (Fig. 1D); v) marginal zone of sterna 2–4 with rather dense white hair band (Fig. 1F); vi) lobes of bilobed membranous appendage at apical margin of sternum 6 roughly quadrangular in shape and separated from each other by narrow longitudinal zone beset with reddish-brown spines (Fig. 1F).

Assignment to species group. The *Hoplitis monstrabilis* species group of *Hoplitis* (*Hoplitis*) includes several species that are morphologically and biologically intermediate between the members of the *H. adunca* species group and the *H. annulata* species

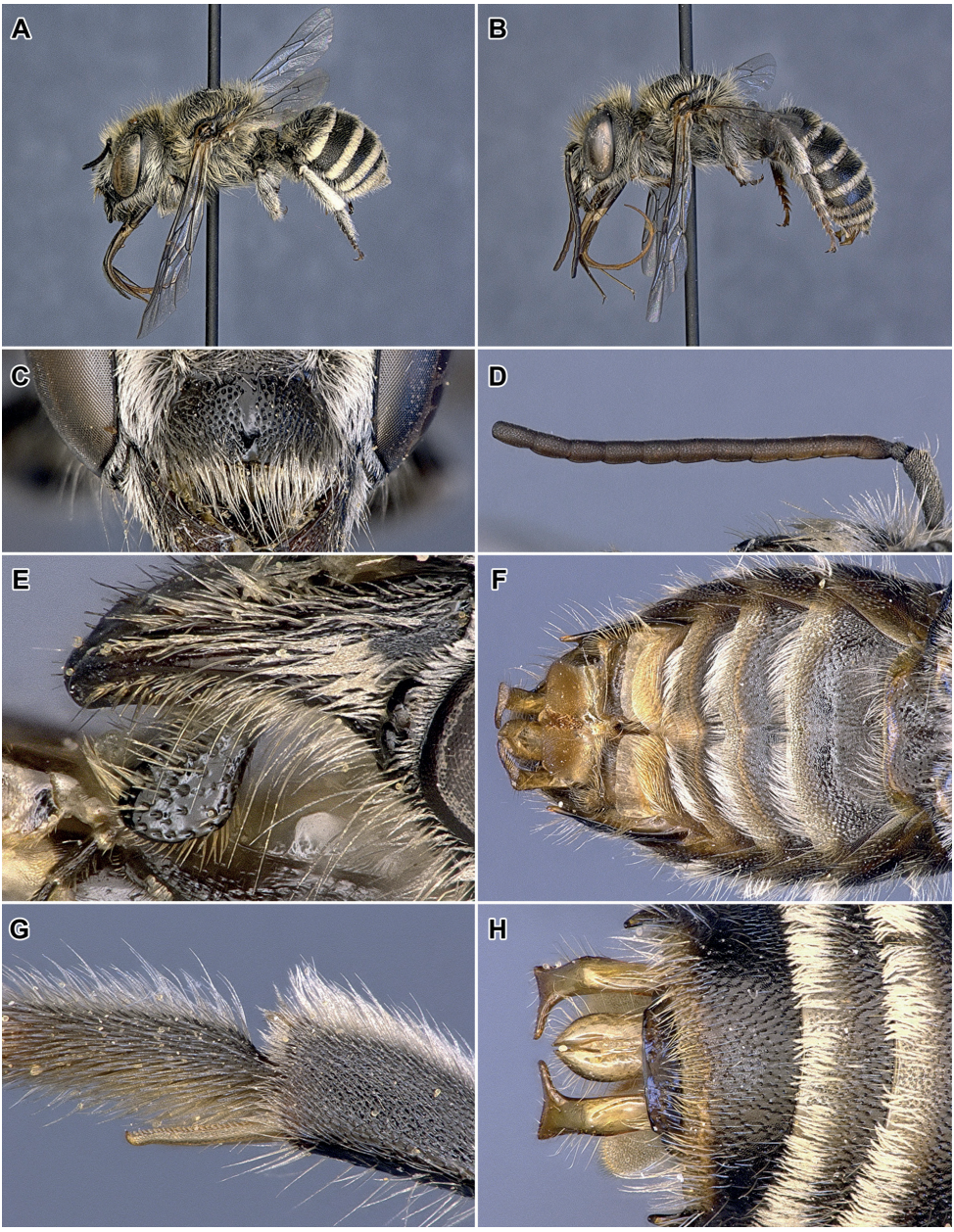

Figure 1. *Hoplitis astragali* sp. nov. **A, C, E, G** female **B, D, F, H** male **A, B** habitus in lateral view **C** clypeus in front view **D** antenna in front view **E** mandible and labrum in lateral view **F** sterna 1–6 in ventral view **G** part of hind leg with inner tibial spur **H** terga 4–7 and genitalia in dorsal view.

group (Sedivy et al. 2012b, 2013; Müller 2023). The representatives of the *H. monstrabilis* species group differ from those of the *H. adunca* species group by the absence of a submarginal carina on female sternum 6 and their habit of nesting in self-excavated

burrows in the ground rather than in pre-existing cavities or stone irregularities above ground. They differ from the *H. annulata* species group by the shape of male tergum 7, which is apically truncate to rounded rather than bidentate. In accordance with these differences, *H. astragali* is assigned here to the *H. monstrabilis* species group.

Description. Due to the uniform morphology of the numerous species of *Hoplitis* (*Hoplitis*), the following description is restricted to characters, which are relevant for the recognition of the new species.

Female. Body length 7–9 mm. ***Head*****:** Head 0.85–0.9× as long as wide. Distance between lateral ocellus and preoccipital margin 2.3–2.4× as long as ocellar diameter. Second segment of labial palpus 1.6–1.7× as long as first segment and 0.8–0.9× as long as compound eye. Proboscis reaching coxa of fore leg when folded. Mandible three-toothed, its preapical zone reddish. Clypeus densely punctate except for median impunctate longitudinal zone, which is usually continuous, well delimited, maximally 4–5× as wide as diameter of adjacent punctures and roughly parallel-sided (Fig. 1C). Apical margin of clypeus medially straight to very shallowly emarginate and weakly crenulate. Yellowish-white pilosity at apical margin of clypeus long, its longest hairs almost as long as maximal length of clypeus (Fig. 1C). Punctation of supraclypeal area and frons very dense and finer than that of clypeus. Labrum basally impunctate, its lateral sides apically strongly declivous (Fig. 1E) and about as high as length of last antennal article. Antennal article 3 about 1.5× as long as apically wide and 1.4–1.6× as long as article 4. Anterior side of antennal articles (4)5–10(11) partly reddish-brown. ***Mesosoma*****:** Tegula predominantly yellowish-red. Scutum and scutellum densely punctured with interspaces not reaching the diameter of one puncture except medially and laterally, where interspaces may exceed the diameter of one puncture. Basal area of propodeum shagreened except for more or less extended polished zone along lower lateral borders. Posterior surface of propodeum polished with scattered punctures. Propodeal pit polished. Tibial spur of fore leg elongated into tip, which is slightly longer than basally wide and connected to more basal part of spur by straight to weakly concave margin. Tibial spurs of hind leg yellowish, almost parallel-sided and apically blunt with very short tip oriented at right angles to longitudinal axis of spur; inner spur slightly longer than outer spur and roughly 10× as long as maximally wide (Fig. 1G). ***Metasoma*****:** Punctation of tergal discs dense with interspaces reaching the diameter of one to two punctures. Marginal zone of terga 1–5 reddish to yellowish and covered with long, dense and uninterrupted band of cream-coloured hairs (Fig. 1A), which are medially slightly longer than last antennal article. When seen from behind, longest erect hairs on median half of tergum 1 more than half to almost as long as maximal length of lateral hair tuft. Declivous lateral part of tergum 1 and marginal zone of sterna 2–5 yellowish. Apical margin of sternum 6 without submarginal carina. Scopa white.

Male. Body length 7.5–10 mm. ***Head*****:** Head 0.84–0.87× as long as wide. Distance between lateral ocellus and preoccipital margin 1.7–2× as long as ocellar diameter. Second segment of labial palpus 1.6–1.7× as long as first segment and 0.8–0.9× as long as compound eye. Proboscis reaching coxa of fore leg when folded. Mandible two-toothed, its preapical zone black to more or less reddish. Clypeus rather strongly

convex in profile, its punctation dense except sometimes for its median part, where interspaces between punctures may be larger forming a small polished area or a non-continuous midline. Apical margin of clypeus medially straight to very shallowly emarginate and weakly crenulate. Antennal article 3 about 1.3× as long as apically wide and articles 4–13 1.5–2× as long as wide. Ventral side of antennal articles 4–13 with weakly delimited and rounded longitudinal keel. Ventral and anterior side of antennal articles 3–13 more or less light brown to yellowish-brown (Fig. 1D). ***Mesosoma*:** Tegula predominantly yellowish-red. Scutum and scutellum densely punctured with interspaces hardly reaching the diameter of one puncture except medially and laterally, where interspaces may exceed the diameter of one puncture. Basal area of propodeum shagreened except for more or less extended polished zone along lower lateral borders. Posterior surface of propodeum polished with scattered punctures. Propodeal pit polished. Tibial spur of fore leg elongated into tip, which is about as long as basally wide and connected to more basal part of spur by straight to weakly concave margin. Tibial spurs of hind leg yellowish and almost parallel-sided except for apex, which is slightly curved. ***Metasoma*:** Punctation of tergal discs rather dense with interspaces reaching the diameter of two to three, rarely more punctures. Marginal zone of terga 1–5 reddish to yellowish and covered with long, dense and usually uninterrupted whitish hair band (Fig. 1B). Tergum 6 laterally toothed, its marginal zone yellowish and ciliated with yellowish hairs. Apical margin of tergum 7 medially truncate to slightly rounded (Fig. 1H). Declivous lateral part of tergum 1 and marginal zone of sterna (1)2–5 yellowish. Apical margin of sternum 1 straight, of 2–4 medially shallowly emarginate and of 5 distinctly emarginate (Fig. 1F). Marginal zone of sterna 2–4 with rather dense white hair band (Fig. 1F). Sterna (2)3–4 medially with inconspicuous, very narrow and little raised longitudinal keel. Sternum 5 medially with very narrow longitudinal row of yellowish hairs directed backwards. Sternum 6 basally with pair of membranous flaps. Lobes of bilobed membranous appendage at apical margin of sternum 6 roughly quadrangular in shape (Fig. 1F) and separated from each other by narrow longitudinal zone beset with reddish-brown spines. Gonoforceps slightly wider than penis valve and apically with finger-like projection, which is directed inwards at right angles to its longitudinal axis and about 3× as long as maximally wide (Fig. 1H).

Distribution. Mountainous Dagestan in Russia (from 75 to 1350 m a.s.l.), Nakhchivan Autonomous Republic of Azerbaijan, and southernmost Turkmenistan.

Etymology. The species epithet refers to the flowers of *Astragalus* L. (Fabaceae) exploited by the species for pollen and nectar (see below).

Hoplitis (*Hoplitis*) *dagestanica* Fateryga, Müller & Proshchalykin, sp. nov.

https://zoobank.org/33893507-BAC4-4602-9B50-EFB4869722AF

Fig. 2A–H

Type material. *Holotype*. Russia. Dagestan, Levashi district: Tsudakhar, 42°19'40"N, 47°09'48"E, 11.6.2019, ♂ (leg. A. Fateryga). Deposited in ZISP.

***Paratypes*. Russia. Dagestan, Levashi district:** Tsudakhar, 42°19'40"N, 47°09'48"E, 1.6.2019, 2 ♂ (leg. A. Fateryga), 3 ♂ (leg. M. Proshchalykin, V. Loktionov); ibid., 10.6.2019, 2 ♂ (leg. A. Fateryga); ibid., 28–29.5.2022, 1 ♀, 1 ♂ (leg. A. Fateryga), 2 ♀, 13 ♂ (leg. M. Proshchalykin); **Dagestan, Rutul district:** near Kufa village, 6 km NW Rutul, 41.565178°N, 47.362029°E, 1500 m, 1.7.2018, 1 ♂ (leg. M. Proshchalykin, V. Loktionov, M. Mokrousov). Deposited in ZISP, FSCV, ETHZ, and CAFK.

Diagnosis. Among the western Palaearctic *Hoplitis* species of the subgenus *Hoplitis* s. str., the female of *H. dagestanica* (Fig. 2A) is unequivocally characterised by the following combination of characters: i) sternum 6 lateroapically with distinct submarginal carina and medioapically not elongated into distinct and well delimited tooth of narrowly triangular to linear shape; ii) proboscis not reaching till trochanter of hind leg in repose and second segment of labial palpus distinctly shorter than maximal length of mesosoma measured in lateral view (Fig. 2A); iii) clypeus and galea of proboscis normally haired, without apically curved or wavy pollen-collecting bristles; iv) lateral lobes of pronotum not inflated; v) apex of inner tibial spur of hind leg strongly curved at an angle of 60 to 80 degrees (Fig. 2G); vi) clypeus medially without uninterrupted sharp and narrow longitudinal carina; vii) disc of tergum 5 covered with rather dense and appressed cream-coloured to yellowish-white pilosity (Fig. 2C); viii) when seen from behind, longest erect hairs on median half of tergum 1 only about 1/7 to 1/8 as long as maximal length of lateral hair tuft (Fig. 2E); ix) punctation of lateroapical part of scutum with interspaces reaching the diameter of one puncture; x) metasomal scopa yellowish (Fig. 2A); xi) anterior side of antennal articles (5)6–11 partly dark reddish-brown. The male of *H. dagestanica* (Fig. 2B) is easily diagnosed by the following combination of characters: i) apical margin of tergum 7 medially rounded (Fig. 2H); ii) second segment of labial palpus shorter than compound eye (Fig. 2B); iii) last article of antenna almost twice as long as basally wide and tapering towards apex with ventral margin slightly concave (Fig. 2D, F); iv) posterior side of antenna with roundish bump near distal end of articles (4)5–6 and small pointed tubercle near distal end of articles 7–11(12) (Fig. 2F); iv) ventral margin of antennal articles (4)5–10(11) distally slightly widened (Fig. 2D); v) antennal article 3 1.4–1.5× as long as apically wide and longer than article 4 (Fig. 2D); vi) lateral lobes of bilobed membranous appendage at apical margin of sternum 6 densely haired, distinctly wider than long, laterally elongated into a distinct and more or less acute tip and separated from each other by only a rather shallow median emargination (Fig. 2H); vii) marginal zone of sterna 4–5 reddish and very densely punctured with interspaces much narrower than the diameter of one puncture (Fig. 2H).

Assignment to species group. Due to the presence of a submarginal carina on female sternum 6 and the apically rounded male tergum 7, *H. dagestanica* is clearly a member of the *H. adunca* species group.

Description. Due to the uniform morphology of the numerous species of *Hoplitis* (*Hoplitis*), the following description is restricted to characters, which are relevant for the recognition of the new species.

Figure 2. *Hoplitis dagestanica* sp. nov. **A, C, E, G** female **B, D, F, H** male **A, B** habitus in lateral view **C** terga 4–6 in dorsal view **D** antenna in front view **E** terga 1–2 from behind **F** antenna in top view **G** part of hind leg with inner tibial spur **H** sterna 5–6 and tergum 7 in ventral view.

Female. Body length 7–8 mm. ***Head*:** Head about 0.95× as long as wide. Distance between lateral ocellus and preoccipital margin about 1.75× as long as ocellar diameter. Second segment of labial palpus about 1.35× as long as first segment and about 0.75× as long as compound eye. Proboscis reaching coxa of fore leg when folded. Mandible three-toothed, its preapical zone weakly reddish. Clypeus densely punctured with interspaces rarely surpassing the diameter of half a puncture and without distinct polished midline. Antennal article 3 almost 2× as long as apically wide and about 2× as

long as article 4. Anterior side of antennal articles (5)6–11 partly dark reddish-brown. ***Mesosoma*:** Tegula yellowish-brown except for black anterior third and black inner margin. Scutum and scutellum densely punctured with interspaces rarely surpassing the diameter of one and a half punctures except lateroapically on scutum and medially on scutum and scutellum, where interspaces may reach the diameter of one puncture. Basal area of propodeum shagreened throughout. Posterior surface of propodeum shagreened with scattered punctures. Propodeal pit polished. Tibial spur of fore leg elongated into tip, which is slightly longer than basally wide and angularly stepped from more basal part of spur. Tibial spurs of hind leg yellowish; inner spur slightly tapering towards apex, which is strongly curved at an angle of 60 to 80 degrees (Fig. 2G); outer spur slightly shorter than inner spur, its apex curved at an angle of about 45 degrees. ***Metasoma*:** Punctation of tergal discs moderately dense with interspaces reaching the diameter of two to three punctures on discs 1–3 (Fig. 2E). Marginal zone of terga 1–5 covered with uninterrupted band of cream-coloured to yellowish-white hairs (Fig. 2A), which may be interrupted on tergum 1 in worn specimens (Fig. 2E). Tergal discs 1–4 with short erect pilosity of yellowish hairs, which are shorter than antennal article 2. When seen from behind, longest erect hairs on median half of tergum 1 only about 1/7 to 1/8 as long as maximal length of lateral hair tuft (Fig. 2E). Disc of terga 5–6 covered with rather dense and appressed cream-coloured to yellowish-white pilosity. Sternum 6 lateroapically with distinct submarginal carina and medioapically without well delimited tooth (Fig. 2C). Scopa yellowish.

Male. Body length 7.5–9.5 mm. ***Head*:** Head about 0.85× as long as wide. Distance between lateral ocellus and preoccipital margin about 1.75× as long as ocellar diameter. Second segment of labial palpus about 1.35× as long as first segment and 0.75× as long as compound eye. Proboscis reaching coxa of fore leg when folded. Mandible two-toothed and predominantly black, sometimes with dark reddish-brown preapical zone. Clypeus rather strongly convex in profile, its punctation very fine and dense without polished interspaces. Apical margin of clypeus medially straight and crenulate. Antennal article 1 about 2× as long as maximally wide (Fig. 2D). Antennal article 3 1.4–1.5× as long as apically wide and almost 1.5× as long as article 4 (Fig. 2D). Posterior side of antenna with roundish bump near distal end of articles (4)5–6 and small pointed tubercle near distal end of articles 7–11(12) (Fig. 2F). Ventral margin of antennal articles (4)5–10(11) distally slightly widened (Fig. 2D). Last article of antenna almost twice as long as basally wide and tapering towards apex with ventral margin slightly concave (Fig. 2D). Antenna predominantly yellowish-red; black to dark brown are articles 1, 2, base of 3, apex of 13, and sometimes dorsal side of articles 3–7 (Fig. 2F). ***Mesosoma*:** Tegula predominantly yellowish-red. Scutum and scutellum densely punctured with interspaces hardly surpassing the diameter of one puncture. Basal area of propodeum shagreened throughout. Posterior surface of propodeum shagreened with scattered punctures. Propodeal pit polished. Tibial spur of fore leg elongated into tip, which is slightly longer than basally wide and angularly stepped from more basal part of spur. Tibial spur of hind legs yellowish, tapering towards apex and apically curved. ***Metasoma*:** Punctation of tergal discs moderately dense with interspaces reaching the

diameter of three to four punctures on discs 1–4. Marginal zone of terga 1–5 covered with uninterrupted band of yellowish-white hairs (Fig. 2B). Tergum 6 laterally toothed, its marginal zone reddish, ciliated with yellowish hairs, apically crenulate and medially usually slightly emarginate. Apical margin of tergum 7 medially rounded (Fig. 2H). Marginal zone of sterna 2–5 reddish and very densely punctured with interspaces much narrower than the diameter of one puncture. Apical margin of sterna 1–4 almost straight and of 5 weakly rounded and medially shallowly emarginate. Marginal zone of sterna 2–4 with loose whitish hair band. Sterna 2–5 with preapical transverse swelling, which is sparsely punctured and medioapically emarginate on sterna 3–5. Sternum 6 basally with pair of membranous flaps (Fig. 2H). Lobes of bilobed membranous appendage at apical margin of sternum 6 densely haired, distinctly wider than long, laterally elongated into a distinct and more or less acute tip and separated from each other by only a rather shallow median emargination (Fig. 2H). Gonoforceps very narrow, slightly bent inwards and downwards in its apical third and apically with dense and short tuft of white hairs. Outer margin of penis valve ciliated with white bristles, of which the longest are slightly longer than the maximal valve width.

Distribution. Mountain Dagestan in Russia (from 1120 to 1450 m a.s.l.).

Etymology. The species epithet refers to the occurrence of the species in Dagestan.

Nesting biology

Six nests of *Hoplitis astragali* were studied 6 km northwest of Chirkey at a clay cliff along a dry riverbed (Fig. 3A). All six nests were burrows in the ground. Two nests were located on strongly inclined surface (Fig. 4A), while four nests were located on almost horizontal surface at the entrance of old burrows of *Xylocopa olivieri* Lepeletier, 1841 (Hymenoptera: Apidae) (Fig. 4B). Thus, the main shaft of the former two nests was sub-horizontal (Fig. 4C), while it was sub-vertical in the latter four nests (Fig. 4E,

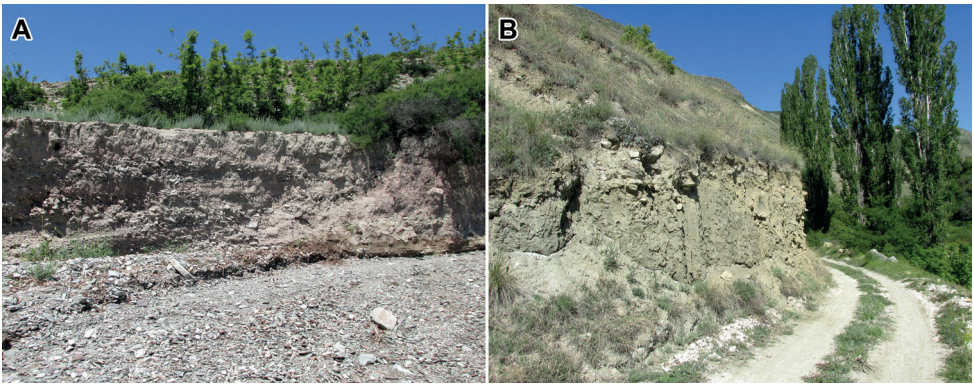

Figure 3. Habitats of the two new species of the genus *Hoplitis* Klug, 1807 in Dagestan **A** clay cliff along dry riverbed 6 km northwest of Chirkey, a nesting site of *H. astragali* sp. nov. **B** clay cliff along unpaved road in Tsudakhar, the type locality of both *H. astragali* and *H. dagestanica* sp. nov.

F). The excavation process was not observed, but it was evident from the following observation that the burrows were self-excavated by the females: two closing plugs were observed on 31 May (Fig. 4D) at the same old *X. olivieri* nest entrance, where there was just one burrow on 27 May (Fig. 4B). Thus, the second burrow was excavated by the female bee, since there was no pre-existing hole available to her. It is noteworthy that the nest entrances were not always circular but sometimes of irregular shape (Fig. 4B).

The nests were composed of one to three brood cells, an empty vestibule, and the closing plug. Of the six nests studied, two had one cell, three were two-celled, and one was three-celled (median two cells per nest). The lengths of the nest burrows were 16–32 mm (median 26 mm). The cells in two- and three-celled nests were linearly arranged in a straight burrow (n = 3, Fig. 4F) or lay in an angled burrow with the longitudinal axis of the brood cells diverging at nearly right angles (n = 1, Fig. 4E). When measured on the inside, the cells were 6.5–9.5 mm long (median 8.0 mm) and maximally 5.5–7 mm wide (median 6.0 mm). The inner surface of the cells was smooth, dull and not covered with any substance other than mud. Although the cell construction process was not observed, the presence of an about 0.4 mm thin and more or less distinct inner cell wall (Fig. 4C, F) suggests that the female covered the inner surface of the cell with an extra layer of mud. As this extra layer was of the same colour as the surrounding substrate, the material for its construction was probably taken from inside the nest. The material used for the construction of the cell plug was apparently also taken from inside the nest as suggested by the irregular shape of the vestibule, indicating that soil material had been harvested from its walls (Fig. 4C, E, F). In contrast, the closing plug was made from soil taken from outside the nest as evidenced by the plug colour, which usually differed from the surrounding substrate (Fig. 4D). One female was observed to harvest dry clay from the cliff surface at a distance of about 0.5 m from the nest, mixed this material with regurgitated liquid, and transported the moistened mud to the nest entrance to build the sealing plug (Fig. A). The space in front of the outermost brood cell was not filled with soil resulting in an empty vestibule of 5–14 mm in length (median 7.0 mm).

The freshly sealed nest contained a single brood cell with an egg and a pollen loaf (Fig. 4C). The pollen loaf was of orange colour and spherical shape, taking about half of the inner volume of the cell. It was very liquid and probably kept its shape due to surface tension and a significant amount of pollen covering it as suggested by the fact that it immediately lost its shape during an attempt to extract it from the cell. The egg was deposited on the top of the pollen loaf and directed with its free end towards the cell plug; its size was about 2.7×0.8 mm. Other cells, dissected in autumn, contained prepupae hibernating in their self-spun cocoons (Fig. 4E, F). The cocoon consisted of a single thin layer; it was whitish and had a slightly shining inner surface. There was no distinct area for air-exchange as known for many other osmiine bees with more complex cocoon structure (Rozen and Praz 2016). Instead, the cocoon of *H. astragali* uniformly covered the whole inner surface of the cell including the inner side of the cell plug. The larval feces were deposited between the cell wall and the cocoon, where they were spread uniformly and sparsely. The prepupae were of deep yellow colour. There

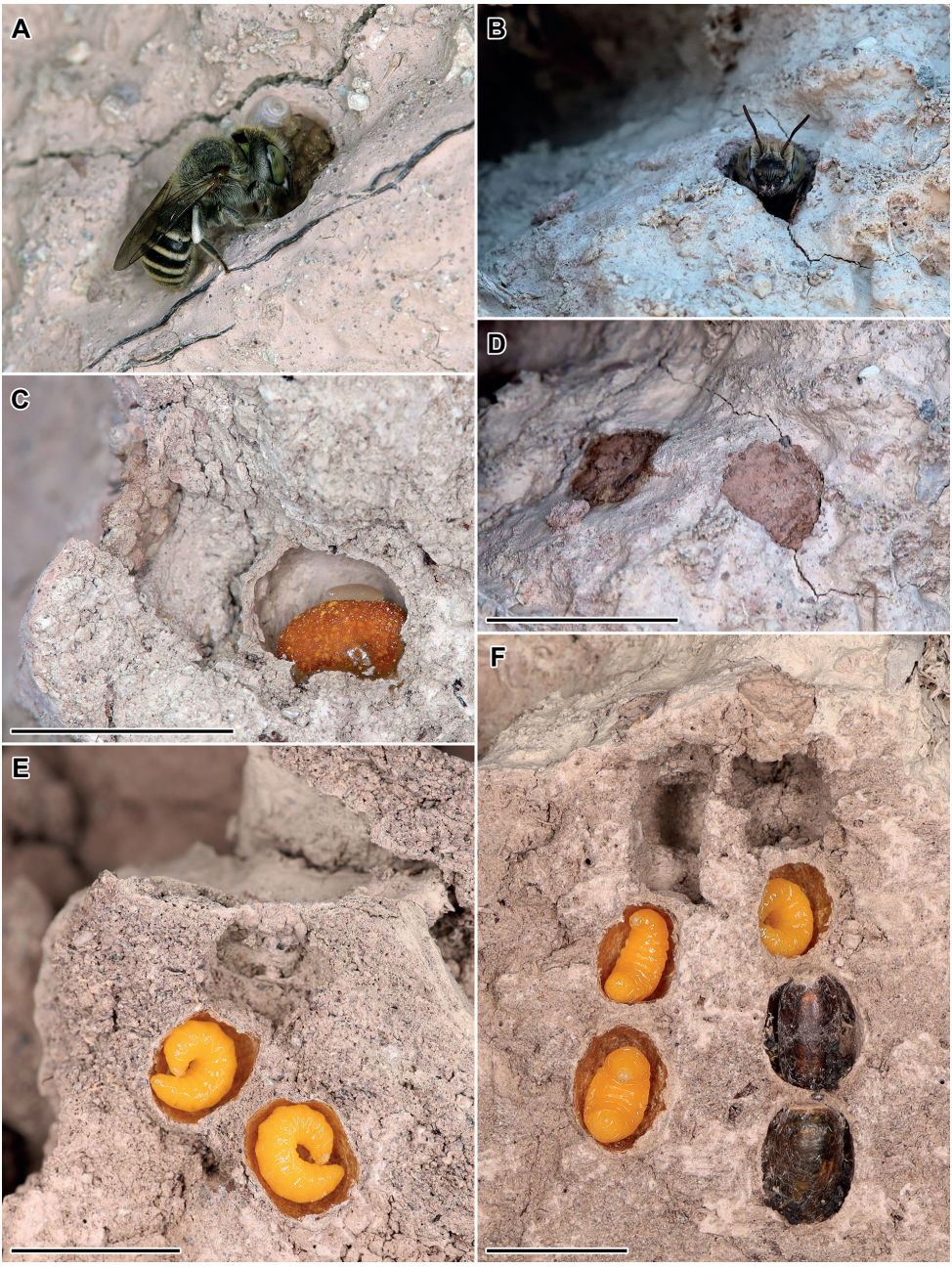

Figure 4. Nesting biology of *Hoplitis astragali* sp. nov. **A** female closing her nest with a plug of mud **B** female inside her nest burrow **C** freshly sealed one-celled nest in lateral view showing a cell with pollen loaf and egg **D** closing plugs of two nests (the right one the same as shown in **B**) **E** two-celled nest in lateral view with hibernating prepupae **F** two nests (the same as in **D**) in lateral view with hibernating prepupae and cocoons of *Sapyga caucasica* Radoszkowski, 1880. Scale bars: 1 cm.

was a single generation, i.e., the progeny of the females nesting in May hibernated. Six prepupae were obtained in 2022 and observed. Two females and two males emerged in 2023, while two prepupae remained alive but did not pupate; they obviously continued hibernation for a second winter.

Cocoons of the kleptoparasitic wasp *Sapyga caucasica* Radoszkowski, 1880 (Hymenoptera: Sapygidae) (Fig. 4F) were found in three of the 11 cells (27%). This wasp hibernates as an imago allowing for its immediate identification to the species level. Several individuals of *S. caucasica* were also observed in May inspecting the surface of the clay cliff where *H. astragali* was nesting.

Flower associations

In Tsudakhar, both new species were observed in the vicinity of a clay cliff along an unpaved road (Fig. 3B). Here, flower-visiting imagines were exclusively recorded on flowers of *Astragalus* (Fabaceae). Two species of this genus were abundant and in flower during the observation period: *Astragalus haesitabundus* Lipsky and *A. onobrychioides* M. Bieb. Females and males of *Hoplitis astragali* as well as a single male of *H. dagestanica* were observed only on the flowers of the former species, whereas no visits to the flowers of the latter species were recorded. In the vicinity of Chirkey *A. haesitabundus* was also abundant and in flower, but here most females and males of *H. astragali* visited the flowers of another *Astragalus* species, *A. bungeanus* Boiss.

Discussion

Hoplitis astragali is the sixth described species of the *H. monstrabilis* species group, while *H. dagestanica* is the 51st described species of the *H. adunca* species group (Müller 2023). Among the members of the *H. monstrabilis* species group, nests were already known for *H. monstrabilis* Tkalců, 2000 and *H. tenuiserrata* (Benoist, 1950) (Rozen et al. 2009; Sedivy et al. 2013; Le Goff 2017). The present contribution supplements those data with the information on the nests of *H. astragali*. All three species excavate their nests in the ground. The nests of *H. monstrabilis* and *H. tenuiserrata*, however, were recorded in horizontal ground and their burrows were sub-vertical. *Hoplitis astragali* nested in vertical cliffs but most of its nests had sub-vertical burrows due to their location at the entrance of horizontal old burrows of *Xylocopa olivieri*. The nests of *H. astragali* have a vestibule, i.e., the burrow between the last brood cell and the sealing plug is not filled with soil. Whether such an empty vestibule is also present in the nests of other members of the *H. monstrabilis* species group is unknown, since all discovered nests of *H. monstrabilis* (n = 2) and *H. tenuiserrata* (n = 1) were incomplete (Rozen et al. 2009; Le Goff 2017). As in *H. astragali*, the cells of *H. monstrabilis* and *H. tenuiserrata* were also found to have a thin wall of compact soil covering the inner cell surface. In the latter two species, it was not clear whether this wall was applied by the female or whether it merely resulted from the smoothing of the inner surface of the

newly excavated cell (Rozen et al. 2009; Le Goff in Müller 2023). Our observations on *H. astragali* suggest that *H. monstrabilis* and *H. tenuiserrata* also cover the inner surface of the cell with an extra layer of mud. Lining the brood cells with an extra layer of mud is also known from members of the *Hoplitis adunca* species group, such as *H. adunca* (Panzer, 1798) and *H. manicata* (Morice, 1901) (Müller 2023 and references therein).

Trophic relationships of *H. astragali* appear to be typical of the *H. monstrabilis* species group. Both *H. monstrabilis* and *H. tenuiserrata* are oligolectic on Fabaceae (Rozen et al. 2009; Sedivy et al. 2012b; Müller 2023). We observed *H. astragali* exclusively visiting flowers of two species of *Astragalus* (Fabaceae), which might indicate narrow oligolecty on a single plant genus (Müller and Kuhlmann 2008). However, more flower visiting data including microscopical analysis of pollen contained in the female scopae are needed to clarify the species' degree of host plant specialization. One male of *H. dagestanica* was also observed on flowers of *Astragalus*. However, as this was the only flower visiting record for this species, any assumption on its pollen host preference is premature, although many members of the *H. adunca* species group exclusively or predominantly exploit Fabaceae for pollen (Müller 2016, 2023; Sedivy et al. 2012b).

Acknowledgements

Mikhail Mokrousov (Nizhny Novgorod, Russia) kindly identified the species of *Sapyga* from the nests of *Hoplitis astragali*. Max Kasparek (Heidelberg, Germany) and one anonymous reviewer carefully reviewed the manuscript and provided helpful suggestions to improve it. John Neff kindly improved our English.

The research was carried out within the state assignments of the Ministry of Science and Higher Education of the Russian Federation, No. 121032300023-7 (for A.F.) and No. 121031000151-3 (for M.P.).

References

Fateryga AV (2017) New data on megachilid bees (Hymenoptera: Megachilidae) of the European part of Russia. Proceedings of the Russian Entomological Society 88(2): 86–90. https://doi.org/10.47640/1605-7678_2017_88_2_86

Fateryga AV, Proshchalykin MYu (2020) New records of megachilid bees (Hymenoptera: Megachilidae) from the North Caucasus and the South of European Russia. Caucasian Entomological Bulletin 16(2): 225–231. https://doi.org/10.23885/181433262020162-225331

Fateryga AV, Proshchalykin MYu, Astafurova YuV, Popov IB (2019 ["2018"]) New records of megachilid bees (Hymenoptera, Megachilidae) from the North Caucasus and neighboring regions of Russia. Entomological Review 98(9): 1165–1174. https://doi.org/10.1134/S0013873818090026

Le Goff G (2017 ["2016"]) Note sur la nidification dans le sol de deux *Hoplitis* du Maroc: *Hoplitis* (*Anthocopa*) *zaianorum* Benoist 1927 et *Hoplitis* (*Hoplitis*) *tenuiserrata* Benoist

1950 (Apoidea – Megachilidae – Osmiini). Osmia 6: 9–11. https://doi.org/10.47446/OSMIA6.3

Litman JR, Fateryga AV, Griswold TL, Aubert M, Proshchalykin MYu, Le Divelec R, Burrows S, Praz CJ (2021) Paraphyly and low levels of genetic divergence in morphologically distinct taxa: revision of the *Pseudoanthidium scapulare* (Latreille, 1809) complex of carder bees (Apoidea, Megachilidae, Anthidiini). Zoological Journal of the Linnean Society 195(4): 1287–1337. https://doi.org/10.1093/zoolinnean/zlab062

Michener CD (2007) The Bees of the World (2nd edn.). Johns Hopkins University Press, Baltimore, [xvi +] 953 pp. [+ 20 pls]

Morawitz F (1873 ["1874"]) Die Bienen Daghestans. Horae Societatis Entomologicae Rossicae 10(2–4): 129–189.

Müller A (2016) *Hoplitis* (*Hoplitis*) *galichicae* spec. nov., a new osmiine bee species from Macedonia with key to the European representatives of the *Hoplitis adunca* species group (Megachilidae, Osmiini). Zootaxa 4111(2): 167–176. https://doi.org/10.11646/zootaxa.4111.2.5

Müller A (2023) Palaearctic Osmiine Bees, ETH Zürich. http://blogs.ethz.ch/osmiini [Accessed 12 July 2023]

Müller A, Kuhlmann M (2008) Pollen hosts of western palaearctic bees of the genus *Colletes* (Hymenoptera: Colletidae): the Asteraceae paradox. Biological Journal of the Linnean Society 95(4): 719–733. https://doi.org/10.1111/j.1095-8312.2008.01113.x

Praz CJ, Müller A, Danforth BN, Griswold TL, Widmer A, Dorn S (2008) Phylogeny and biogeography of bees of the tribe Osmiini (Hymenoptera: Megachilidae). Molecular Phylogenetics and Evolution 49(1): 185–197. https://doi.org/10.1016/j.ympev.2008.07.005

Rozen Jr JG, Özbek H, Ascher JS, Rightmyer MG (2009) Biology of the bee *Hoplitis* (*Hoplitis*) *monstrabilis* Tkalců and descriptions of its egg and larva (Megachilidae: Megachilinae: Osmiini). American Museum Novitates 3645: 1–12. https://doi.org/10.1206/646.1

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

Sedivy C, Dorn S, Müller A (2012a) Molecular phylogeny of the bee genus *Hoplitis* (Megachilidae: Osmiini) – how does nesting biology affect biogeography? Zoological Journal of the Linnean Society 167(1): 28–42. https://doi.org/10.1111/j.1096-3642.2012.00876.x

Sedivy C, Dorn S, Müller A (2013) Evolution of nesting behaviour and kleptoparasitism in a selected group of osmiine bees (Hymenoptera: Megachilidae). Biological Journal of the Linnean Society 108(2): 349–360. https://doi.org/10.1111/j.1095-8312.2012.02024.x

Sedivy C, Dorn S, Widmer A, Müller A (2012b) Host range evolution in a selected group of osmiine bees (Hymenoptera: Megachilidae): the Boraginaceae-Fabaceae paradox. Biological Journal of the Linnean Society 108(1): 35–54. https://doi.org/10.1111/j.1095-8312.2012.02013.x

Ungricht S, Müller A, Dorn S (2008) A taxonomic catalogue of the Palaearctic bees of the tribe Osmiini (Hymenoptera: Apoidea: Megachilidae). Zootaxa 1865: 1–253. https://doi.org/10.11646/zootaxa.1865.1.1