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Biology of the Bee *Hoplitis (Hoplitis) monstrabilis* Tkalçú and Descriptions of Its Egg and Larva (Megachilidae: Megachilinae: Osmiini)

JEROME G. ROZEN, JR.,¹ HIKMET ÖZBEK,² JOHN S. ASCHER,³ AND
MOLLY G. RIGHTMYER⁴

ABSTRACT

Herein we describe the nesting biology of the solitary ground-nesting bee *Hoplitis (Hoplitis) monstrabilis* Tkalçú from eastern Turkey. Its shallow nests in the ground differ from the known nests of members of subgenus *Hoplitis*, most of which make mortar and pebble nests either on the exposed surfaces of rocks or within stems or other cavities. Cells are not lined with flower petals or other vegetative tissue, as expected for subgenus *Hoplitis*, but unlike other ground-nesting species of *Hoplitis* belonging to other subgenera such as *Anthocopa*. The egg of this bee is also described and illustrated, as is the fifth (last) larval instar.

ABSTRAKT

Bu çalışmada bireysel yaşama sahip, toprakta yuva yapan *Hoplitis (Hoplitis) monstrabilis* Tkalçú'nun yuva yapma biyolojisi Doğu Anadolu (Türkiye)'de çalışılmıştır. Yuva, toprakta yüzeysel bir şekilde yer almaktadır. Aynı alt cinsde ait yuvaları bilinen türlerin yuvalarından az farklılık göstermekte, istisna olarak bu alt türde hücrelerin iç cidarları çiçeklerin taç yaprakları veya diğer bitkisel dokularla astarlanmamış durumdadır. *Hoplitis (Hoplitis) monstrabilis*'in yumurta ve beşinci (son) larva dönemi tanımlanmış ve çizimleri yapılmıştır.

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INTRODUCTION

This paper reports on the nesting biology and describes the mature larva of *Hoplitis* (*Hoplitis*) *monstrabilis* Tkalčú resulting from the excavation of two nests found on the campus of Atatürk University in Erzurum, Turkey. Andreas Müller identified the two female voucher specimens, each taken from a nest, and additional females and one male collected nearby. This recently described species belongs to a small species group diagnosed by Tkalčú (2000), also including the sympatric *H. erzurumensis* Tkalčú and *H. lapidaria* (Morawitz). Males of this groups, referred to here as the *lapidaria* species group, have highly modified male hind legs (illustrated by Tkalčú, 2000), with greatly expanded hind tibiae and inner tibial spurs. Females appear similar to those of subgenus *Annosmia*, and Warncke (1991) therefore placed *H. lapidaria*, known only from the female, in that subgenus.

We present information on *H. monstrabilis* to expand knowledge of ground-nesting behavior in genus *Hoplitis* and to provide evidence pertinent to the phylogenetic placement of the *lapidaria* species group. More generally, we hope to augment our limited understanding of the biology of the Osmiini and of the range of larval variation within Megachilidae.

BIOLOGY OF HOPLITIS (*HOPLITIS*) *MONSTRABILIS*

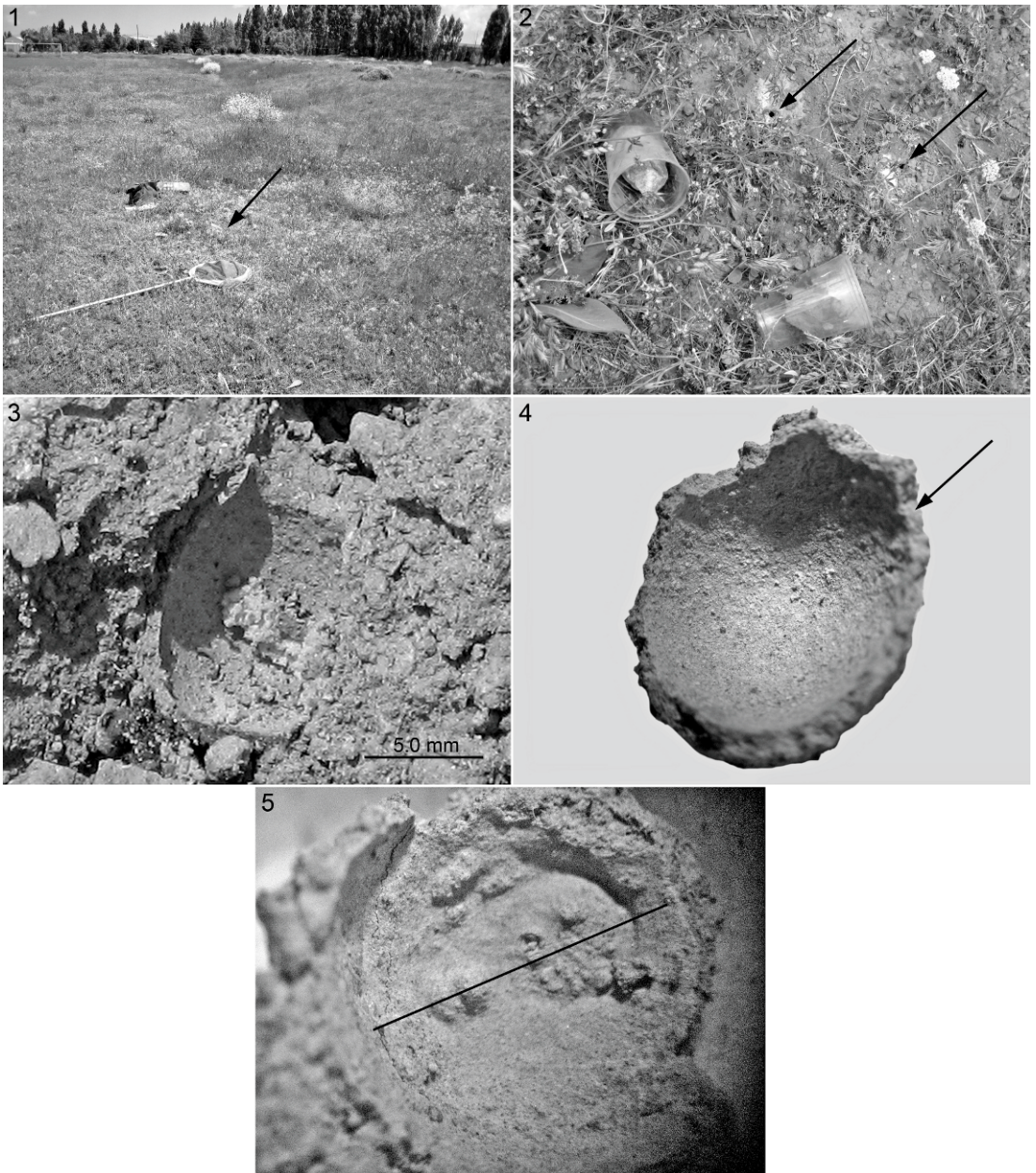
DESCRIPTION OF NESTING SITE: On July 6, 2007, M.G.R. discovered the two nest entrances of this species, about 15 cm apart, as both females repeatedly entered and left their respective nests for short periods ranging from 30 sec. to about 2 minutes apart. This activity suggested that they were removing soil and dropping it a short distance away, thus accounting for the lack of tumuli around the open entrances. The ground surface was horizontal with sparse, low herbaceous vegetation between which the surface was barren (fig. 2). The site was within 1 m of a dense but low patch of vegetation that had grown over the excavated nesting site of *Rophites* (*Rophitoides*) *canus* Eversmann that had been studied in 2005 (Rozen and Özbek, 2008) at the edge of a seldom-used soccer field

on the campus (fig. 1). We excavated the two *Hoplitis* nests on July 11, 2007. The soil was consolidated and compact without visible moisture in the vicinity of the cells, although we found darker, moister soil starting at a depth of about 5 cm.

J.S.A. located another *Hoplitis* nest, possibly of this species, on a bare (devoid of vegetation) horizontal surface at 22 km southwest of Oltu, Erzurum, on July 7, 2007, but this nest was not studied. A photo of the female at the nest entrance is available at http://www.discoverlife.org/mp/20p?see=L_JSA484.

NEST DESCRIPTION: Both nests on the campus of Atatürk University agreed in lacking tumuli around open entrances and in being extremely shallow. Some cells were only 2–2.5 cm below the ground surface. The main tunnels, open their entire lengths, descended more or less diagonally with considerable twisting and turning. There were no laterals (i.e., side branches) leading to cells; cells were attached directly to the main tunnels or to one another. One nest contained five cells arranged in two sets of two cells in a linear series and a single open cell incompletely provisioned. The second nest contained a total of eight cells; the three closest to the ground surface were singletons, while the remaining five cells were grouped as a descending series, one connected to the other, none separated by intercalary cells or short tunnel lengths (probably arranged like those pictured by Westrich, 1989: 196, for *Hoplitis mocsaryi* (Friese) [cited as *Osmia mocsaryi*], though without petal linings).

Cells (fig. 3) were oriented with their long axis approximately horizontal, and all were identical in being very broad for their length; one measured 7.0 mm in maximum diameter and 11 mm long. Cells seemed symmetrical around their long axes, and their front and rear ends were equally rounded. Each exhibited a uniformly thin (ca 1–2 mm thick) cell wall (fig. 4) composed of compact soil that tended to separate here and there from the substrate during our excavation. The inner wall surface was smooth and matt (fig. 4), entirely lacking a visible reflective lining as found in many bee cells. However, it was waterproof; during testing, a droplet of water remained beaded on the surface for more than 2 min. None of the



Figs. 1–5. Photographs of nesting site and nest components of *Hoplitis monstrabilis*. **1, 2.** Nesting site (arrow) of *Hoplitis monstrabilis* on campus of Atatürk University, Erzurum, Turkey, and close-up of nest entrances (marked by dry plaster of Paris) identified by arrows, respectively. **3.** Cell showing shape, lateral view from above. **4.** Close-up of cell wall showing matt texture; note cell wall composed of compact soil (arrow). **5.** Cell closure, inner view.

cells was lined with petals or other vegetative material as has been reported for other ground-nesting species of genus *Hoplitis* species (see below). Five cell closures each measured

approximately 5.0 mm in diameter, had a thickness about equal to that of the cell wall, and were slightly concave on the inside, conforming to the general curvature of the

front end of the cell. When observed with a stereomicroscope, the inner surface of the closure lacked a distinct spiral pattern; it was smooth with some irregularities as if formed from very moist soil that soon dried after deposition (fig. 5). When tested with a droplet of water, the inner surface seemed water retardant though perhaps not as strongly so as the cell wall.

PROVISIONS: We collected no adults on flowers, but the single type of pollen in the provisions was almost certainly that of *Onobrychis* (Fabaceae) because of its barrel-like shape. This plant grew abundantly nearby. Of the well known European species of *Hoplitis* (*Hoplitis*), *H. loti* (Morawitz) and *H. ravouxi* (Pérez) are oligolectic on Fabaceae, whereas *H. adunca*, *H. anthocopoides*, and *H. lepeletieri* are narrowly oligolectic on *Echium* (Boraginaceae) (Westrich, 1989). Completed provisions were an ovoid, homogeneous mass of orange pollen and nectar on the floor of the cell. Although appearing solid, the mass was so fluid that it deformed with the airflow from the aspirator used to blow away loose soil during our excavations. When the airflow stopped, it reformed as an oblong ovoid, thus suggesting the shape was dictated by the viscous nature of the mixture in combination with the shape of the lower part of the cell. Interestingly, provisions placed in Kahle's solution with eggs or young larvae tended not to disassemble as one might expect due to their semiliquid condition. Freshly deposited provisions in the single cell still open consisted of mostly dry pollen, on top of which had been deposited a large amount of partly clear nectar. Presumably, after bringing in the final provision load, the foraging female mixes and shapes the mass into its ovoid form.

EGG DESCRIPTION AND DEPOSITION: Freshly deposited eggs are white, i.e., the color of the yolk as seen through their transparent chorions. Their shape (fig. 6) is elongate, gently curved, parallel sided, and approximately equally rounded at both ends. One measured 3.05 mm long and 0.875 mm in maximum diameter at approximate midlength. This species egg index is 77, as calculated by dividing the egg length by the average intertegular distance of 3.95 mm of the two adults collected (Iwata and Sakagami, 1966; Rozen, 2003). This index falls into the

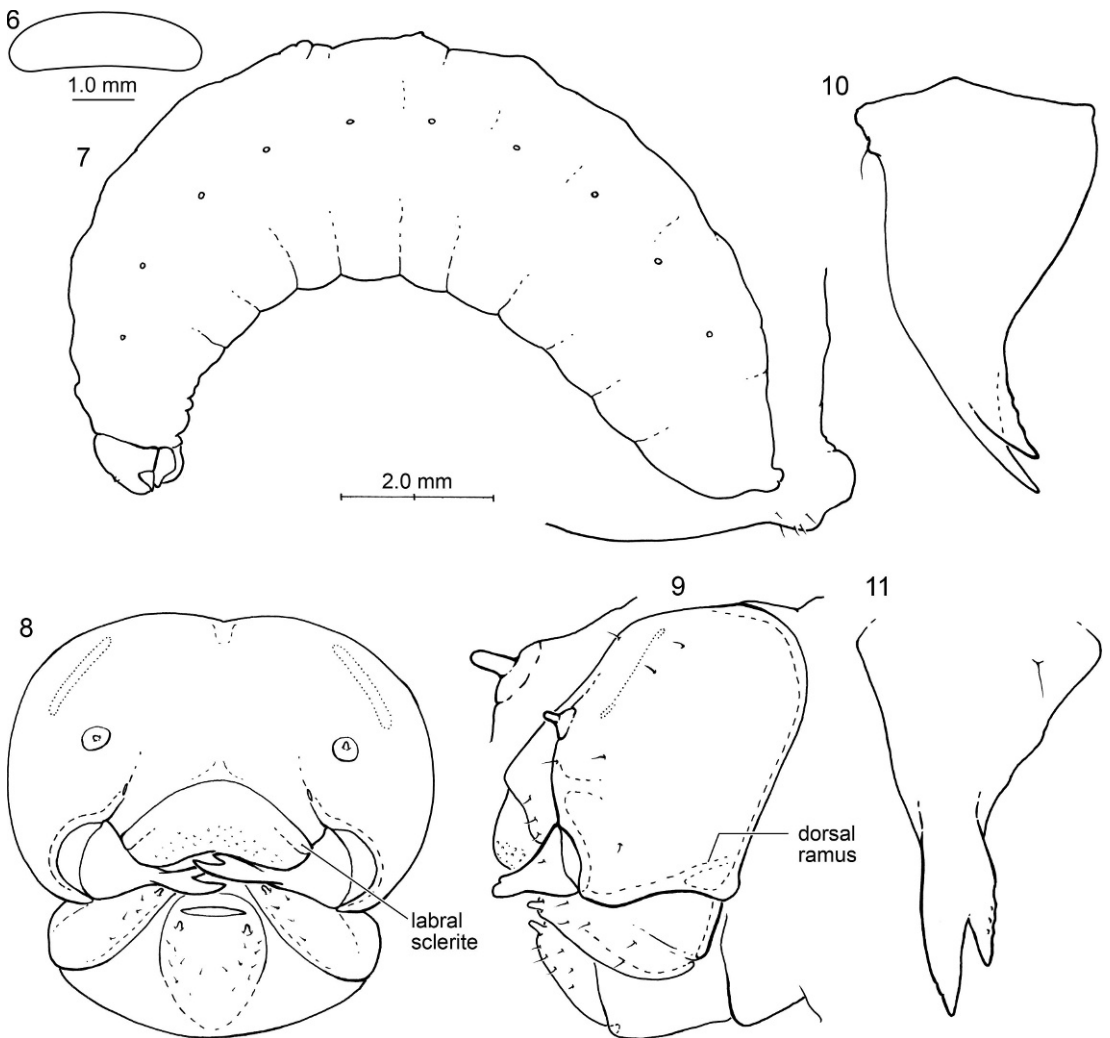
medium class in the classification of eggs/mature oocytes relative to female bee body size, as developed by Iwata and Sakagami (1966: table 2). The transparent chorionic surface viewed through a stereomicroscope was smooth and somewhat shiny.

DEVELOPMENT: Eggs and young larvae were on top of the provisions in the midline of the cells with their anterior ends (as determined by the larvae) pointed toward the cell closures. The single fifth instar, still feeding, had cast skins of the four previous instars clinging to its venter, proving that there are five larval instars. All instars possess apically bidentate mandibles, with the ventral tooth longer than the dorsal one. Only the fifth instar bears conspicuous body setae, as has previously been found for *Coelioxys* (Rozen and Kamel, 2008).

CLEPTOPARASITES: None was associated with the two nests.

COMPARISONS WITH NESTING BIOLOGY OF OTHER *HOPLITIS*

To what extent is the nesting biology of *Hoplitis monstrabilis* similar to, or different from, that of other *Hoplitis* species? In attempting to explore this question, we have relied heavily on the work of Westrich (1989) and Michener (2007) for published sources of information about the biology of the genus and on the review of our manuscript by Le Goff (see Acknowledgments), who kindly directed our attention to the papers on *Hoplitis* (*Anthocopa*) by Ferton (1891–1911) and who also supplied pictures of his own nest excavations of certain *Anthocopa* species (cited below as “Le Goff, personal commun.”). A. Müller and C. J. Praz generously shared unpublished information from their review of osmiine nesting biology (a collaboration also including Le Goff) and phylogeny. In addition to identifying *H. monstrabilis*, their assistance greatly facilitated our comparative review of its biology. We follow Michener's (ibid.) classification of the Osmiini, and subsequent updates by Praz et al.'s phylogenetic study (2008) and Ungricht et al.'s catalogue of Palearctic Osmiini (2008), and compare species of genus *Hoplitis*, especially those in subgenus *Anthocopa*, because this subgenus includes many well-known, ground-nesting species, and



Figs. 6–11. Diagrams of immatures of *Hoplitis monstrabilis*. 6. Egg, lateral view, other orientation uncertain. 7. Entire body of last larval instar, lateral view, with enlarged view of abdominal apex showing protruding anal region. 8, 9. Head of last larval instar, front and lateral views, respectively, with close-up of antenna in maximum profile. 10, 11. Right mandible of same, dorsal view, and outer view of apex in maximum profile, respectively.

to species of subgenus *Hoplitis*, which are generally surface or cavity nesters but are more closely related to *H. monstrabilis*. Nesting data for thirteen species of ground-nesting *Hoplitis* (*Anthocopa*) are available: *H. bisulca* Gerstaecker (as *Osmia lanosa* Pérez) (Ferton, 1895); Le Goff, personal commun.); *H. cristatula* Zanden (as *O. cristata* Fonscolombe) (Ferton, 1893); Le Goff, personal comm.); *H. cypriaca* *cypriaca* (Mavromoustakis) (Mavromoustakis,

1954); *H. idalia* (Mavromoustakis) (Le Goff, personal commun.); *H. jakovlevi* (Radoszkowski) (as *serrilabris* (Morawitz) (Banaszak and Romasenko, 2001; Le Goff, personal commun.); *H. longispina* (Pérez) (Cros, 1937); *H. mocsaryi* (Friese) (Westrich, 1989); *H. papaveris* (Latreille) (Ferton, 1896 [as *O. papaveris* Latreille]; Müller, 1907; Friese, 1923); *H. perezi* Ferton (as *O. perezi* Ferton) (Ferton 1895; Le Goff, personal commun.);

H. saundersi Vachal (as *O. annulata* Latreille and *O. saundersi* Vachal) (Ferton, 1891, 1911); *H. similis* (Friese) (Brauns, 1926; Michener, 1968, as *H. anthodemnion* Michener); *H. singularis* (Morawitz) (Marikovskaya, 1995); *H. villosa* (Schenck) (Friese, 1923; Müller, 1907; Petit, 1970, 1977; Westrich, 1989).⁵

Our limited sample of nests of *Hoplitis monstrabilis* was on an essentially horizontal surface of hard soil. However, Michener (1968) found numerous nest entrances of *H. (Anthocopa) similis* in vertical clay banks, whereas Brauns (1926) apparently retrieved them from a horizontal nesting site. This suggests that inclination of the nesting surface is not important for that species, and according to Le Goff (personal commun.) that is true for most *Anthocopa* species that he studied. Furthermore, degree of compactness of nesting soil may be of little importance since *H. papaveris* nests in both situations (Friese, 1923). By contrast, known species of subgenus *Hoplitis*, which are more closely related to *H. monstrabilis* than the ground-nesting species discussed above, are not ground nesting but instead make mortar and pebble nests adhering to the exposed surfaces of rocks or within stems or various cavities (Westrich, 1989). Nesting data are available for many species in Westrich (1989, and references cited therein) including: *Hoplitis adunca* (Panzer) (Westrich, 1989); *H. anthocopoides* (Schenck) (see in particular Eickwort, 1973), *H. ravouxi* (Pérez) (Westrich, 1989). Among known species of subgenus *Hoplitis*, the majority, including the well known *H. anthocopoides*, make mortar and pebble nests adhering to exposed rock surfaces, and initiated in a rock crevice, whereas others are more flexible, building nests within various cavities such as holes in wood or stems or in the soil as does *H. adunca*. *Hoplitis fertoni* (Pérez) is exceptional as it nests in snail shells (Le Goff, 2003). Additional Palearctic subgenera of *Hoplitis* including *Annosmia* and *Pentadentosmia* (involving numerous desert-inhabiting species) are ground nesting (Praz et al., 2008),

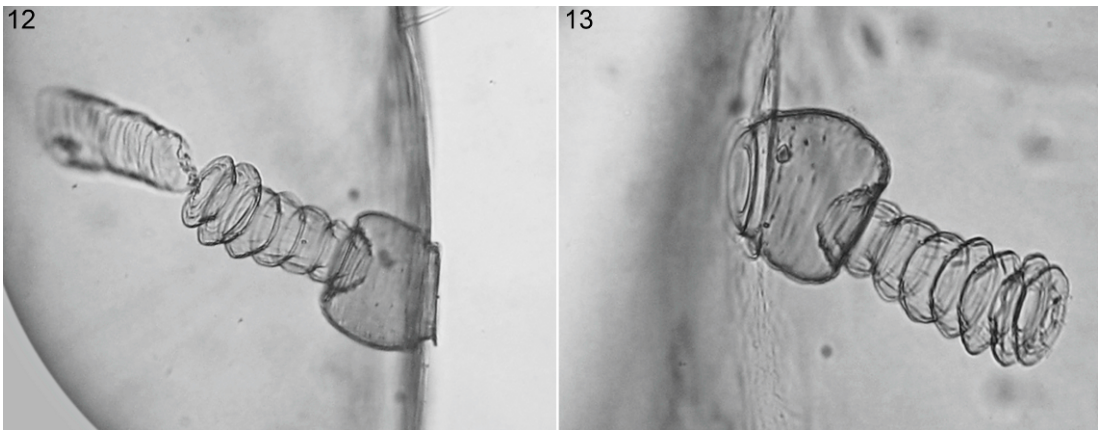
⁵ In addition, Marikovskaya (1995) has published biological information on *Hoplitis (Anthocopa) singularis* (Morawitz), the type species of the formerly recognized subgenus *Glossosmia*, but we have been unable to secure a copy of the paper.

and some Nearctic *Hoplitis (Proteriades)* nest in holes in the ground (Michener, 2007). *Hoplitis monstrabilis* is the first report of a *Hoplitis (Hoplitis)* nesting in the ground (A. Müller, C. J. Praz, and G. Le Goff, review of Osmiini nesting biology in prep.), but this behavior may be more widespread in the subgenus; the nesting biology of many species, including the two other species in the *lapidaria* species group, remain unknown.

Evidence is clear that the two females of *Hoplitis monstrabilis* excavated their own nests since there were no remnants such as old nest tunnels or cells at the site. However, we also know that within the Megachilinae, some taxa nest in preexisting cavities including abandoned nests from previous generations of both other taxa and conspecific taxa. Our sample of two nests was too limited to ascertain if this species might also use pre-existing cavities. Among the other species of ground-nesting *Hoplitis*, many species probably avail themselves to preexisting cavities, but if none is available, females perform their own excavations. *Hoplitis anthocopoides* partly reuse previous years mortar and pebble nests after cleaning them of debris (Eickwort, 1973).

A consistent feature of known nests of ground-nesting *Hoplitis*, including those of *Hoplitis monstrabilis* and all species of subgenus *Anthocopa*, is their shallow depth, whether the nesting surface is horizontal or vertical. This seems a remarkable feature since such surfaces lose moisture readily and are subjected to excessive heat and cold; bees hibernating and/or aestivating under these conditions for many months would seem to be at risk from desiccation or extreme temperatures. However, this is not a feature unique to *Hoplitis*: many groups of megachilid bees cope well under these circumstances, for example, *Megachile* in trap nests (Rozen and Kamel, 2008: figs. 1–3), and *Hoplitis (Hoplitis)* in mud nests adhering to rocks.

In common with other species of *Hoplitis (Hoplitis)*, but in contrast to most known species of subgenus *Anthocopa*, *H. monstrabilis* do not line its brood cells and nest tunnels with blossom petals or other vegetative tissue (Westrich, 1989). Cells of *H. monstrabilis* need further study to determine the nature of the



Figs. 12, 13. Photographs of spiracle on cleared larva of *Hoplitis monstrabilis*. **12.** Side view, showing elevation of rim and globular shape. **13.** Oblique lateral view, showing peritreme and faint atrial ridges.

thin cell wall of soil: is it a special clay coating transported into the cell and applied by the female, or is it merely the result of the female smoothing the inner surface of the newly excavated cell? A chance recovery of a cell in construction might provide the answer.

Both nests of *Hoplitis monstrabilis* were actively being provisioned when found and excavated, so we can offer no information concerning its nest closure. With respect to ground-nesting *Anthocopa* species, Westrich (1989) states that nest entrances of *H. mocsaryi* are left open after the female departs. Nests of *H. papaveris* are closed with sand (Friese, 1923); the nest tunnel of *H. similis* is filled with soil to the ground surface (Michener, 1968), which is apparently also the case with *H. papaveris* (Müller, 1907). Nest closures and cell partitions of *H. singularis* are formed from masticated green leaves (Marikovskaya, 1995).

Although some *Hoplitis* nests consist of only single cells, other species including *H. monstrabilis* construct nests of more than one cell. The nest of *H. monstrabilis* with eight cells might have become larger had we not excavated it and collected the female. (Eickwort, 1973, cited a mean number of cells in new *H. anthocopoides* nests of 7.2, SE = 0.86, n = 29). Small nests imply that many species of ground-nesting *Hoplitis* (*Anthocopa*) normally make more than one nest, as was also concluded by Le Goff (personal comm.). Although the cells

of *H. monstrabilis* were almost horizontal, those of *H. (Anthocopa) similis* ranged in inclination from 20°–60° from horizontal (Michener, 1968). The illustrations of Ferton (1895: figs. 7, 12, 13) and photographs of Le Goff (personal commun.) would seem to suggest that within the subgenus cell inclination and arrangement relative to one another may be significantly variable.

In studies of solitary bees, we tend to consider whether some species mate at the flowers where females gather pollen and nectar and/or at the nesting site where females are emerging and returning. In the case of *Hoplitis monstrabilis* we saw no males at the nesting site, and collected only a single male in the general area. This hints that mating may take place earlier in the season in the vicinity of flowers. *Hoplitis* (*Hoplitis*) species such as *anthocopoides* patrol and defend territories consisting of blooming host plants and rock or bare soil resting perches; females mate a single time when visiting flowers (Eickwort, 1977).

Although we found no cleptoparasites associated with *Hoplitis monstrabilis*, other species of *Hoplitis* are reportedly parasitized by species of *Coelioxys*, *Stelis*, and *Dioxys* (Westrich, 1989; Banaszak and Romasenko, 2001). Because our nest sample was so small, we would not be surprised if future studies were to reveal that cleptoparasitic bees are associated with *H. monstrabilis*.

DESCRIPTION OF LAST LARVAL INSTAR

Figures 7–19

The following description, the first for any ground-nesting *Hoplitis* (*Hoplitis*) and for the *lapidaria* species group, is based on a single last-stage larva that was still feeding on provisions when preserved. Because last instars gradually develop head pigmentation and grow robust as they ingest provisions, neither the pigmentation nor body form described here can reliably predict head pigmentation and body shape of a postdefecating larva. This specimen agrees with the preliminary description of mature larvae of the Megachilini in Rozen and Kamel (2007: 19) unless stated otherwise. See that description for details not presented below.

In studying the specimens, we first drew it for the larval diagrams and then cleared the specimens in a hot aqueous solution of sodium hydroxide. After lightly staining the cleared specimen with Chlorazol Black E and transferring it to a glycerin-filled well slide, we added details to the illustrations. We then prepared the head capsule for SEM examination by critical-point drying and coating it with gold-palladium alloy.

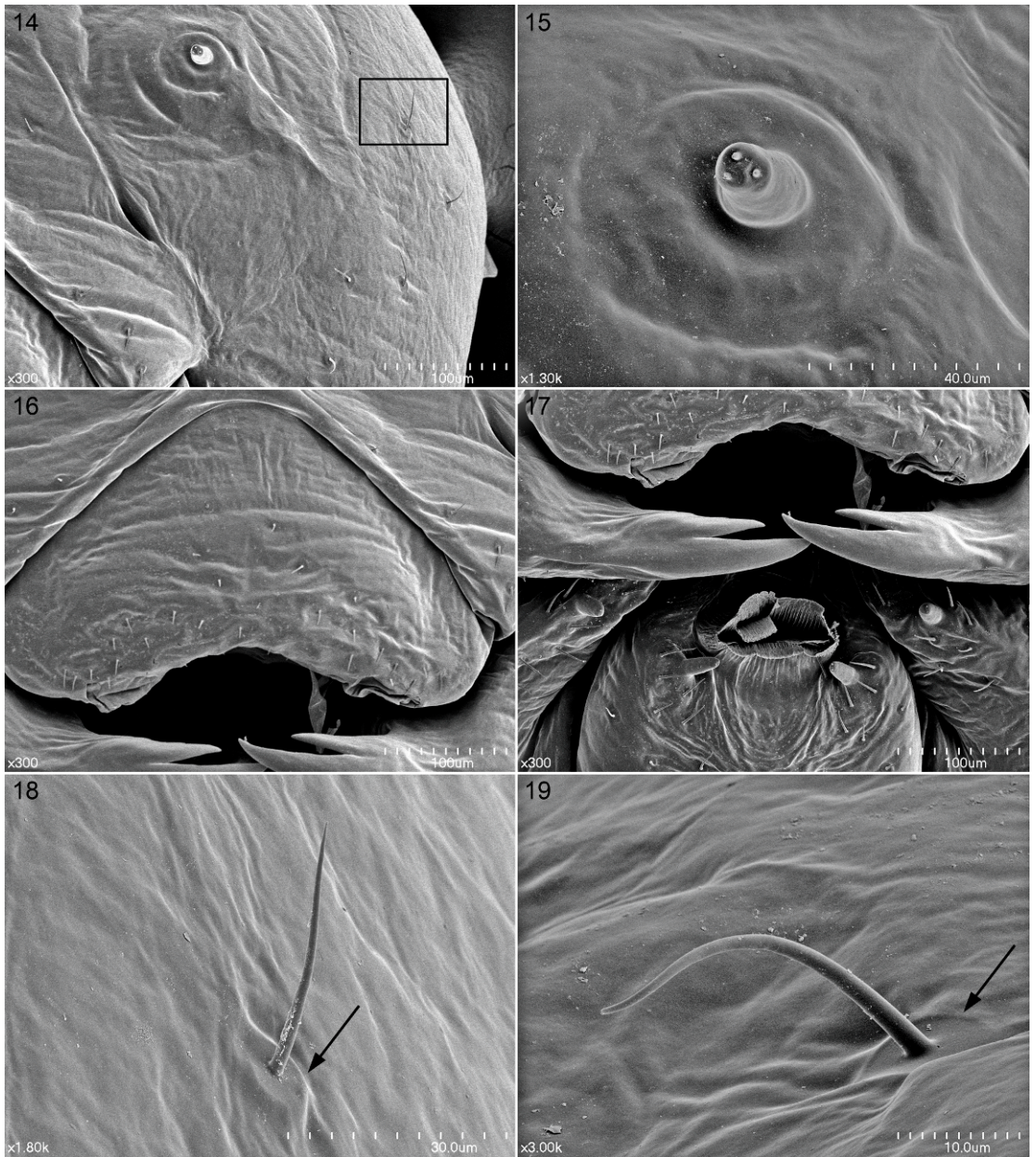
DIAGNOSIS: Although the apically attenuate mandibles (figs. 11, 17) of this specimen appear distinctive from those of most other described megachilids, this condition might be ephemeral, disappearing as the mandibles wear. In other respects, this larva seems almost indistinguishable from other known nonparasitic members of the Megachilinae, including previously described species of *Hoplitis* (*Hoplitis*) (Eickwort, 1973, and refs. therein), and emphasizes the overall homogeneity of last larval instars of the subfamily Megachilinae.

DESCRIPTION: Head (figs. 8, 9, 14–19): Setae long; those of parietals widely and sparsely scattered, erect, more or less curved, and with large, slightly elevated alveoli at base (figs. 18, 19); those of maxillary and labial apices straight, forward projecting and those of labral apex decumbent, downward directed. Following areas moderately to faintly pigmented: mandibles especially at apices, internal mandibular ridges (especially at points of

articulation), internal head ridges at articulation with mandibles, articulating arms of stipites, points of articulation of cardines with stipites, dorsal surface of premental sclerite between attachment of articulating arms of stipites; other areas scarcely pigmented; fine spiculation apparently restricted to dorsal surface of maxilla at its base and to lateral lobes of hypopharynx. Area immediately above hypostomal ridge and just behind posterior mandibular articulation not produced as downward-directed tubercle as present in many *Coelioxys* (Rozen and Kamel, 2007: fig. 47). Hypostomal ridge giving rise to dorsal ramus that extends posteriorly from middle of ridge nearly to postoccipital ridge (fig. 9) in association with inflection of parietal at deeply set posterior tentorial pit; anterior tentorial pit distinctly closer to anterior mandibular articulation than distance between it and basal ring of antenna; epistomal ridge extending dorsally for short distance mesad of anterior tentorial pit. Parietal bands clearly evident. Diameter of basal ring of antenna small, somewhat less than twice distance from ring to center of anterior tentorial pit; antennal papilla (figs. 9, 14, 15) small, slender, gradually, evenly tapering apically, about three times as long as basal diameter, bearing three sensilla. Apical margin of clypeus strongly angled upward at midline (fig. 16), so that at midpoint margin at to slightly above level of anterior tentorial pits.⁶ Labral sclerite unpigmented, with lower margin poorly defined, but sclerite obviously transverse (fig. 8); labrum unpigmented, without pigmented median spot extending from labral sclerite to apical labral margin as in *Coelioxys* (Rozen and Kamel: 2007: figs. 44, 45); apical labral margin broad, weakly concave (fig. 16).

Mandible (figs. 10, 11, 17) moderately elongate, apically attenuate, curved, and slender; apex bidentate with ventral tooth considerably larger and longer than dorsal tooth; both teeth acutely pointed; dorsal

⁶ The apparent clypeal/labral discrepancy between figs. 8 and 16 is presumably due to the retraction of the labrum resulting from critical-point drying for SEM examination. The soft conjunctive connecting the lower end of the clypeus to the labrum folded in, causing the retreat of the labrum. Thus the strong angling of the lower clypeal margin is revealed in fig. 16.



Figs. 14–19. SEM micrographs of mature larva of *Hoplitis monstrabilis*. **14.** Right side of head showing antenna, anterior tentorial pit, part of labrum, and cranial setae, frontal view; rectangle identifying seta enlarged in fig. 18. **15.** Close-up of antenna, showing three apical sensilla. **16.** Apex of clypeus and labrum, frontal view. **17.** Mouthparts, including salivary opening, frontal view. **18, 19.** Two long cranial setae, showing large, elevated alveoli identified by arrows; fig. 18, from side of parietal at level of lower edge of parietal band, identified by rectangle in fig. 14; fig. 19 from upper area of parietal band.

apical edge of dorsal tooth finely, irregularly serrate when viewed with compound microscope (not clearly visible with stereomicroscope); ventral apical edge of lower tooth less distinctly serrate; inner apical surface shallowly concave; cuspal area not developed; outer surface with single seta not borne on tubercle. Cardio and stipes well-developed sclerites but not pigmented except for articulating arm of stipes; maxillary palpus small, about as long as surrounding setae, perhaps slightly larger than antennal papilla. Apex of labium normally wide (figs. 8, 17); premental sclerite not evident laterad of attachments of articulating arms of stipes because of lack of pigmentation, but probably well represented on post-defecating form since labium clearly divided into prementum and postmentum; maxillary and labial palpi subequal in length. Salivary lips projecting, broadly transverse, width about equal to distance between bases of labial palpi; inner surface of lips, visible only after specimen subjected to critical-point drying process, with numerous parallel, raised ridges extending outward. Hypopharynx consisting of widely separated lateral lobes that are spiculate; area between them irregular but nonspiculate.

Body (fig. 7): Body setae rather short and inconspicuous compared with last larval instars of many other megachilids, but still quite visible, and with distinct alveoli compared with last larval instars of other families; pleural area of abdominal segment 8 with approximately 5 setae; integument with scattered patches of fine spicules. Body form robust; intersegmental line weakly incised because of bloated body shape; intrasegmental lines not evident but possibly visible on postdefecating form; paired body tubercles absent; middorsal body tubercles more or less evident on abdominal segments 2 and 3 and possibly elsewhere; pleural swellings poorly developed in early fifth instar; abdominal segment 10 attached to approximate middle of segment 9; anus apparently positioned toward top of segment 10 on projection, which may be eversible, as perhaps characteristic of many cocoon-spinning bees. Spiracles well sclerotized, unpigmented, subequal in size; globular atrium projecting well above body wall, with rim (fig. 12); peritreme mod-

erately narrow, so that atrial opening distinctly wider than peritreme width; atrial inner surface with faint rows (fig. 13) concentric with primary tracheal opening; these rows with fine ridges which may have occasional sharp, fine projections (alternatively, fine ridges may occasionally trap and hold fine debris); primary tracheal opening with collar; subatrium moderately robust; subatrium moderately short, with 7–10 chambers. Male sex characters unknown; female with paired, ventral, paramedian integumental scars on abdominal segments 7–9, with those of segment 7 farthest apart and those of segment 9 closest together.

MATERIAL EXAMINED: One fifth instar, Turkey: Erzurum, VII-11-2007, J.G. Rozen, H. Özbek, M.G. Rightmyer, J.S. Ascher.

REMARKS: The moderately elongate, apically curved and attenuate mandibles of this species suggest that they might serve as a defensive weapon against larval cleptoparasites, although no cleptoparasite has yet been associated with this species. However, their length may wear down with use, as seems to be the case with last instars of other megachilid taxa.

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