

Nesting Biology, Flower Preferences,
and Larval Morphology of the Little-Known
Old World Bee *Ochreriades fasciatus*
(Apoidea: Megachilidae: Megachilinae)

JEROME G. ROZEN, JR.,¹ GIDEON PISANTY,² VINCENT TRUNZ,³ DIMITRI
BÉNON,³ ACHIK DORCHIN,⁴ AND CHRISTOPHE J. PRAZ³

ABSTRACT

Herein we present information on the nesting behavior of *Ochreriades fasciatus* (Friese) found occupying beetle galleries in dead trunks and branches of certain trees and shrubs in Israel. We also describe the pre- and postdefecating larvae thereby making known the mature larva for this uncommon Old World genus. Females of *O. fasciatus* build linear nests in existing burrows in dead wood; depending on the length of the burrow, 1-5 cells are placed in one nest. The cell partitions are made of hardened mud, while the nest plug consists of pebbles fixed together with mud. *Ochreriades fasciatus* is oligolectic on Lamiaceae and probably strongly associated with the two related genera *Ballota* and *Moluccella*. It is hoped that information concerning its nesting biology, host-plant relationships, as well as larval development and anatomy will eventually prove valuable in determining the phylogenetic position of this genus relative to other megachiline bees.

¹ Division of Invertebrate Zoology, American Museum of Natural History.

² Steinhardt Museum of Natural History and National Research Center, Faculty of Life Sciences, Tel Aviv University, Israel.

³ Institute of Biology, University of Neuchatel, Switzerland.

⁴ Department of Entomology, Cornell University.

INTRODUCTION

Ochreriades Mavromoustakis, 1956, is a rare, Old World genus of megachilid bees that has a restricted and disjunct distribution. It contains only two described species: *O. fasciatus* (Friese, 1899), known from very few locations in the Middle East (Jordan, Syria, and Israel; Müller, 2014) and *O. rozeni* Griswold, 1994, known from the single holotype female from Namibia (Griswold, 1994). In adult morphology, *Ochreriades* is unusually distinctive, as follows: (1) elongate adult body shape, more so than any other megachilid, with pronotum elevated and surrounding scutum anteriorly; (2) yellow integumental markings, unique within the osmiine and suggesting tribe Anthidiini; and (3) very long mouthparts (fig. 6), with proboscis nearly reaching tip of metasoma. The genus was originally suggested to be allied to *Chelostoma*, at that time considered closely related to *Heriades* (Mavromoustakis, 1956). Griswold (1994), however, showed that both *Chelostoma* and *Ochreriades* did not have the distinctive features of members of the *Heriades* group of osmiine genera (for details, see Michener, 2007: 448–449) and suggested that both genera may be closer to some members of the *Osmia* group of genera such as *Hoplitis* (*Alcidamea*). The phylogenetic position of *Ochreriades* has been examined in few studies and remains unsettled. A cladistic analysis of morphological characters suggested a sister relationship between *Ochreriades* and *Chelostoma*, although with weak bootstrap-support values (Gonzalez et al., 2012). Two molecular studies have assessed the position of *Ochreriades* within osmiine and megachilid bees (Praz et al., 2008; Litman et al., 2011). In both cases, *Ochreriades* was not closely related to *Chelostoma*, but its position varied within Megachilinae, as sister to all other Osmiini (*Chelostoma* included), sister to Anthidiini + Osmiini + Megachilini, or sister to Megachilini + Osmiini. In all cases, support for the position of *Ochreriades* was weak.

In the present paper, we describe the nesting biology of *O. fasciatus*, examine its host-plant relationships and pollen-collecting behavior, and provide a description of the mature larvae.

In mid-July 2013 C.J.P. contacted J.G.R. to ask whether he would like to examine the larva of the rare bee *O. fasciatus*, which had been discovered by a group of Israeli and Swiss students (V.T., D.B., and A.D.) on the Golan plateau, northern Israel. G.P. visited the site in June 2014 and collected many nest-bearing branches. From this material G.P. sent some larvae to J.G.R. and also sent nest-bearing branches to Neuchâtel University, Switzerland, where further studies were pursued by J.G.R. and C.J.P. with assistance by V.T. in late September/early October 2014. Preserved larvae were sent both from Israel and Switzerland to the AMNH to be examined by J.G.R.

METHODS

For examination, larvae and cocoons were prepared following the procedures outlined by Rozen and Hall (2011). To examine the floral preferences of *O. fasciatus*, D.B. analyzed the pollen provisions of six nests from the Golan site using light microscopy. Small quantities of the provisions were embedded in glycerol gelatin on a microscope slide. The pollen was identified to family under 400× magnification using a reference collection and the literature cited in Müller (1996a).

NESTING BIOLOGY

V.T., D.B., and A.D. originally discovered nests of *O. fasciatus* in a semiarid, open shrubland dominated by the deciduous shrub *Ziziphus lotus* (L.) Lam. (Rhamnaceae) near Kibbutz Lehavot ha-Bashan, on the slopes descending from the Golan Heights into the Hula Valley (N 33°08'32" E35°39'12", 138 m elev.; hereafter "Golan site") (figs. 1, 2). Nests were located in dead, erect cypress trees (*Cupressus sempervirens* L. (Cupressaceae)) planted along a dirt road and surrounded by several bushes of *Ballota undulata* (Fresen.) Bentham (Lamiaceae), one of the main host plants of *O. fasciatus*. Nests were distributed across all parts of the cypress trees from bottom to top, including the main trunk and side branches. Although the cypress trees were dead, the wood was very hard, and contained many beetle emergence holes (see below), in which the nests were located. Approximately 50 nests were discovered in a single dead tree in May 2013 after observing many females entering or sealing the burrows. In addition, approximately 20 nests were found in dead branches of an unknown species of deciduous tree. Around 80 more nests were discovered by G.P. in two dead trees when he visited the site in June 2014 when bee activity had almost ceased; nests were identified by the pebble-containing nest-closure plug assumed to be characteristic of the species.

In June 2014 G.P. discovered a second site in a Mediterranean shrubland located in the Judean Foothills, 1.2 km west of Kibbutz Bet Guvrin (N 31°36'51" E 34°52'50", 260 m elev.; hereafter "Judean Foothills site") (fig. 3), approximately 180 km SSW from the first site. The vegetation was dominated by multitrunk buckthorn (*Rhamnus lycioides* L. (Rhamnaceae)) and mastic (*Pistacia lentiscus* L. (Anacardiaceae)) shrubs about 2 m tall; *B. undulata* bushes grew mostly at the periphery of the shrubs, half-shaded. Each buckthorn and mastic shrub possessed dozens of thin trunks (diameter ca. 2-4 cm) growing sideways, some of them alive and bearing leaves and others dead. In four dead trunks of one of the buckthorns, close to the ground (5-50 cm above ground), he found 10 nests of *O. fasciatus*, three still active and the rest sealed. As in the previous site, the wood containing the nests was very hard.

All the nests examined in both sites were located in existing burrows in firm wood, strongly suggesting that females do not excavate burrows. Instead, they exploit the burrows pre-made by other insects, as in many other megachilid bees such as *Heriades* and *Chelostoma* (Westrich, 1989; Müller et al., 1997). In the nests described here, most burrows were excavated by metallic wood-boring (jewel) beetles (Buprestidae), which can be identified by the distinctly oval shape of the burrows in cross section. Four buprestid larvae in total were found inside the wood, two at each site. However, D.B. and V.T.'s discovery of adult *O. fasciatus* nesting in very small (diameter ca. 1.9–2.0 mm), perfectly round holes in another kind of wood from the same area supports the conclusion that this bee will use burrows made by other insects in other kinds of wood.

Nests of *O. fasciatus* consist of a single burrow leading from a hole in the wood surface to the cell or linear series of cells inside (figs. 11, 13). As already indicated, most nests seen were built in the more oval burrows of buprestids. The entrances are approximately 3-7 mm wide (range 2.5-9 mm; $n = 8$), and burrow diameters are consistent with those of their entrances. In most nests examined, the first 1-3 cm of the burrow are oriented at an angle to the wood surface, whereas the more distal part of the burrow runs more or less parallel to the wood grain.



FIGURES 1–3. Habitat photographs of observation/collection sites of *Ochreidae fasciatus*. **1.** Golan site from a distance showing cypress trees along roadway (picture by D.B. and V.T.). **2.** Close-up of Golan site with dead cypress tree containing nests of *O. fasciatus* at left (picture by D.B. and V.T.). **3.** Judean Foothills site showing G.P. collecting at nesting site (picture by A. Gotlieb).

Behind the entrance plug there is an open space of variable length before the first cell (i.e., the last cell that was built) is reached (fig. 11). The cells are generally located in the distal, straight portion of the burrow. Most cells were 8–11 mm long and their diameters in cross section were the same as that of the burrow, i.e., cells were also oval in cross section.

Cells are arranged in a single, continuous linear series, front to rear, along the burrow, so that their long axes are more or less aligned with the wood grain (figs. 11, 13). The cell front is always the end closer to the nest entrance. In one three-celled nest, there was a 15 mm open space between the most proximal cell and the two distal ones. It is important to point out that the arrangement of cells running with the wood grain is dictated by the feeding habits of the buprestid larva to find edible tissue; it is not determined by the female bee. This cell positioning



FIGURES 4–10. Macrophotographs of adults and nest entrances of *Ochreriades fasciatus*. 4. Female on upper lip of flower of *Ballota undulata* tapping stamens with the undersurface of her metasoma and thereby collecting pollen on her metasomal scopa. 5. Male feeding on nectar from flower of *B. undulata*, showing lack of contact between dorsum of small bee and stamens above and thereby not contributing to pollen transfer. 6. Female with mouthpart extended flying toward flower of *B. undulata*. 7. Entrance covered by single large pebble. 8. Another covered by cluster of pebbles. 9. Female bringing in pebble to cover nest entrance. 10. Female with pollen-filled scopa about to enter nest. (Figs. 4, 5 by G.P., figs. 6–10 at Golan site by D.B. and V.T.)

parallels what has been reported for such megachilids as *Lithurgus chrysurus* Fonscolombe (Lithurgini) in which the behavior of the nest-making female bee determines cell orientation (Rozen, 2013).

Larvae and provisions are located in the distal part, i.e., rear, of the cell; the provisions are semiliquid, as in *Hoplitis (Hoplitis) adunca* (Panzer), and do not form a firm pollen mass. They occupy the entire rear end of the cell. Young larvae are sedentary and firmly connected to the provisions. Postdefecating larvae in cocoons have their head end at the front of the cocoon. Dissected burrows (including those from the Judean Foothills site) contained between one and five cells.

Cell partitions (figs. 12, 15) and burrow closures, i.e., nest plugs (fig. 12), are made of hardened mud and dissolve in water within a few minutes, suggesting that the mud is made with nectar and not with resin or glandular secretions. No pebbles are associated with cell partitions. The external surface of the nest plug (figs. 7, 8, 11, 12) is distinct from that of the partitions, as it incorporates relatively large pebbles (diameter 1-2 mm) that the female introduces with her mandibles (fig. 9). These pebbles are either glued together with mud, sometimes only weakly so or are inserted into moist mud. Their presence allows easy identification of completed nests even when the bees are inactive. The plug is usually located at the entrance of the burrow with pebbles extruding from the wood surface (figs. 7, 8) but can sometimes be as much as 1-2 cm inside the burrow (fig. 12), even invisible from outside. In the smallest burrows, the visible part of the plug may consist of one single pebble (fig. 7). Cell partitions are somewhat concave on both sides; their thicknesses tend to be 1.0–1.5 mm (maximally up to 2.0 mm) at the periphery but narrower toward the center.

In the Golan site, females were observed during provisioning by V.T. and D.B. Females first enter the burrow head first (fig. 10), presumably either to deliver nectar onto the provisions or to inspect the cell for parasites. After a few seconds, they come out, their metasomal scopa still filled with pollen, turn around at the nest entrance and enter the burrow, this time metasoma first. They stay in the nest slightly longer than the first time and eventually leave the nest once their scopa is empty. This observation suggests that females are not able to turn around inside the burrows (at least the narrow ones), as is also the case for many cavity- or stem-nesting bees such as *Chelostoma* and *Heriades* (this behavior may be universal in cavity-renting bees that nest in cavities whose diameters are only slightly greater than the bee using them).

COCOON STRUCTURE AND FECAL PLACEMENT: The cocoon shape of *O. fasciatus* (fig. 14) is dictated by the shape of the nest burrow and by the spacing of the partitions. Because most nests observed were in tunnels presumably made by larval Buprestidae, burrows are oval (not circular) in cross section. Furthermore, in cases where the buprestid larva is large, the cocoon may not adhere to all parts of the burrow wall.

In general the cocoon is elongate, semitransparent, pale, more or less cylindrical in shape, and rounded at both ends (fig. 14). It is approximately 10 mm long and has a diameter dictated by and therefore slightly less than the burrow diameter. As a comparison, the body lengths of female bees are on average 8 mm (range 7–10 mm). About halfway to the rear, the surface gradually darkens with smears of black feces that farther toward the rear darken to a completely black, shiny, but opaque surface. The inner surface of the cocoon front is white, smooth, evenly

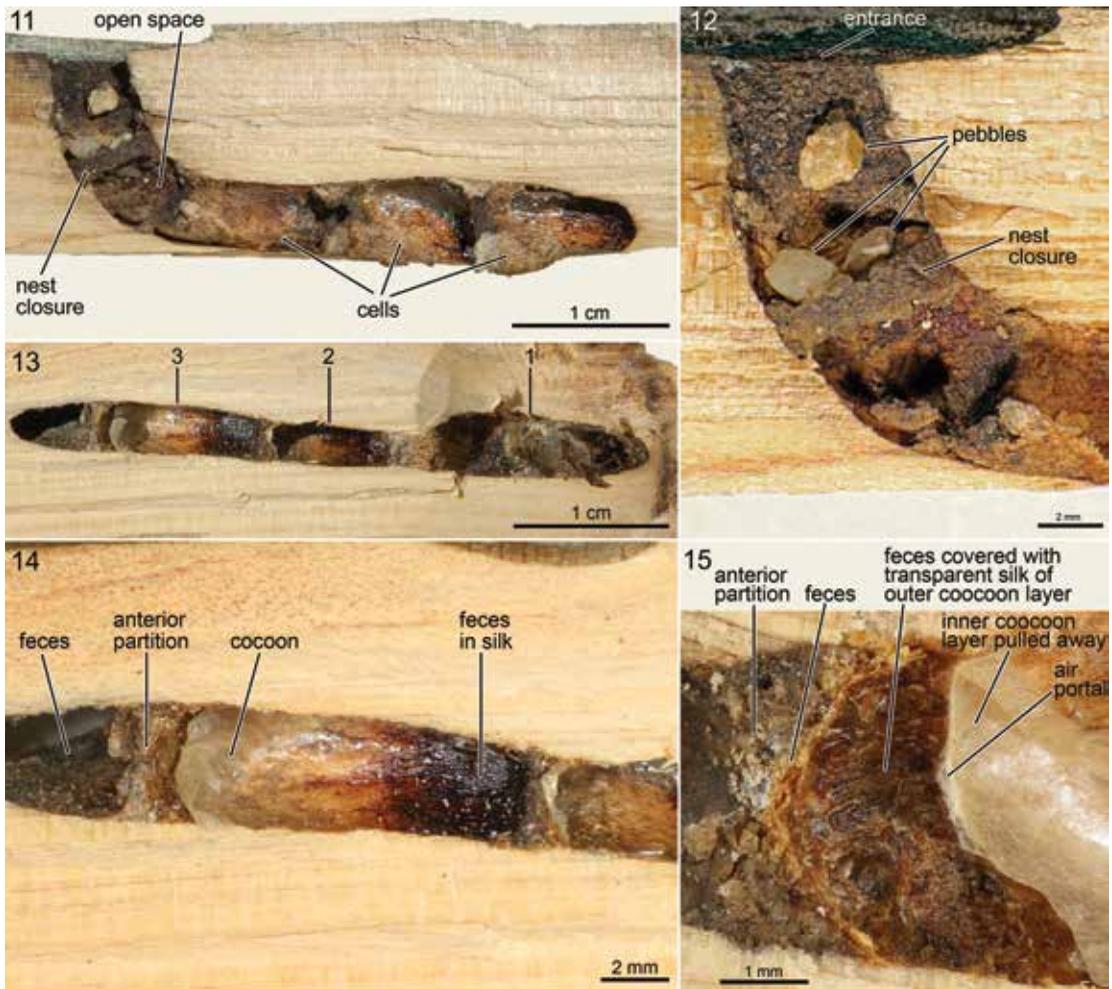
curved, rather opaque, and composed of a fine webbed silk. In cross section the fabric at the front consists of an inner layer separate from but lying immediately next to the outer layer.

By examining completed cocoons of *O. fasciatus*, we recognized that cocoon spinning and defecation are interrelated, overlapping activities of the last larval instar. Before silk production starts, the larva deposits light brown feces with a faintly greenish cast against the anterior cell partition (figs. 14, 15). The pellets tend to be moist and blend together to form a mottled brown band immediately behind the darker grayish-brown partition of soil made by the female (fig. 15). Although the thickness of the two bands at their peripheries is sometimes similar, the fecal mass thins in some cases toward its center, creating in these cases a concave posterior surface to the fecal mass, at times allowing small pebbles of the soil partition in front to be exposed. Other times, as in figure 15, the fecal layer is far less concave.

The larva then spreads a very thin transparent sheet of silk over the inner surface of the fecal layer and along the wooden surface of the anterior cell wall. Thus is formed the outer layer of the front of the cocoon. The silk adhering to the mottled feces (figs. 15, 16) is so transparent that it was only first detected along a torn edge. However, widely scattered fine silk fibers attach it to the more substantial cocoon fabric that later will become the inner layer of the anterior part of the cocoon. Thus, the inner wall of the cocoon can rather easily be torn from the anterior part of the cocoon (figs. 14, 15). However, toward the rear of the cocoon the inner and outer cocoon layers more closely fuse to one another and incorporate the subsequent fecal deposits, accounting for the darkening of the cocoon rear. These feces are now black and smeared between layers of silk (fig. 14). Toward the cell rear, the cocoon fabric clings more tightly to the cell wall. Where the feces are the thickest the cocoon's texture becomes almost leathery.

These observations indicate that fecal production starts shortly before cocoon spinning and is completed while silk production continues. Furthermore, fecal coloration darkens as defecation continues, as has also been reported for some other Megachilidae (Rozen and Hall, 2011).

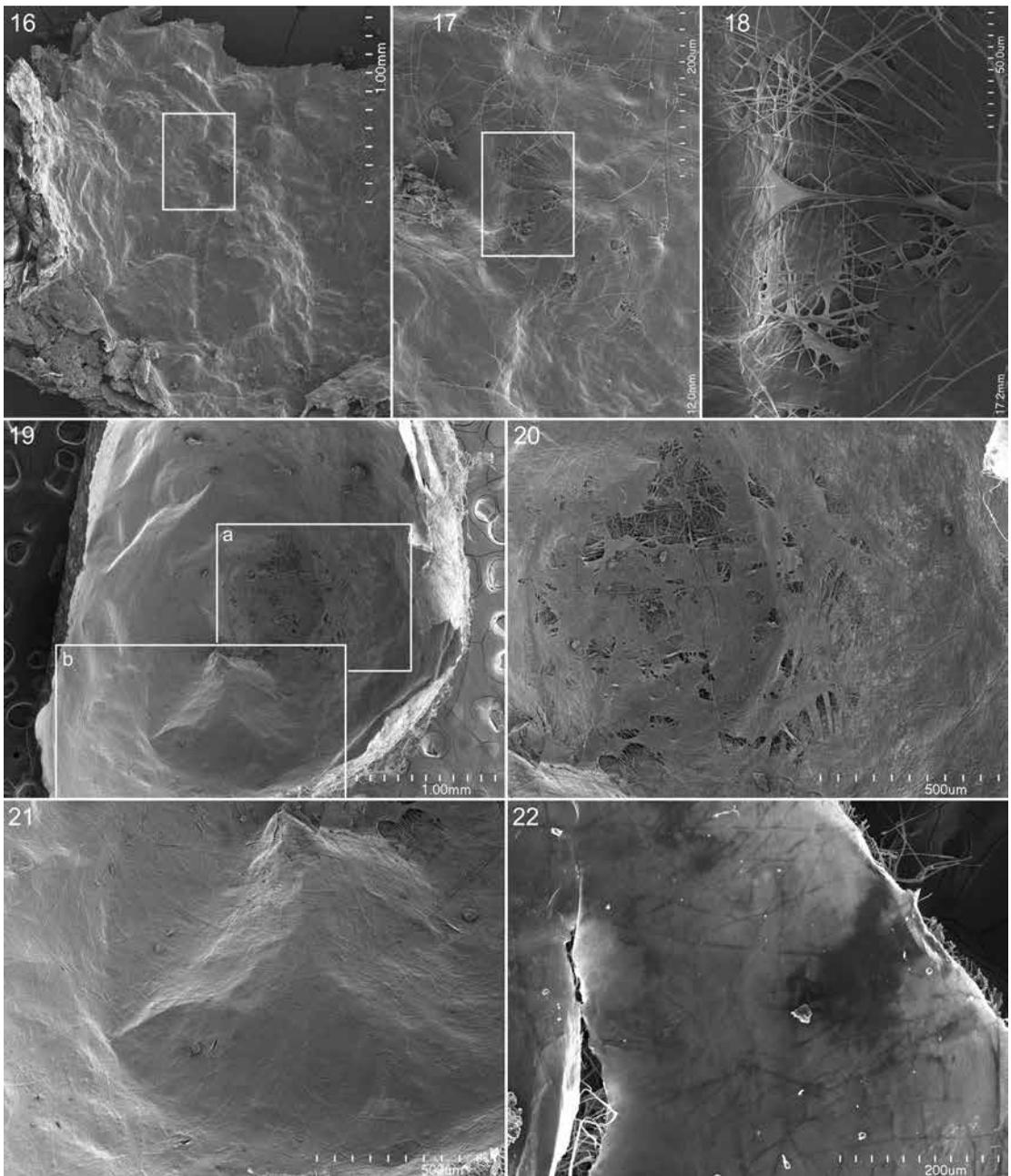
Several recent studies (Rozen and Hall, 2011; Rozen et al., 2011; Rozen and Mello, 2014) have pointed out that cocoons appear to serve several functions, among which are: exclusion of parasites and regulation of cell humidity over long periods. These studies also point out that air exchange between the interior of the cocoon and the surrounding environment is affected by a heavily screened air portal usually at the front end of the cocoon, sometimes referred to as the filter area or cocoon nipple. In the case of the cocoon of *O. fasciatus*, the air exchange portal indeed appears to be at the front end of the cocoon, identified by an irregular cluster of holes in the inner, sheetlike silk lining (figs. 19, 20), in front of which is a dense mass of fibrous white silk (fig. 15). The portal presumably functions to exclude parasites while permitting air exchange between the inside and outside atmospheres. Elsewhere, the inner surface of the inner layer of the cocoon is covered with a thin, clear, cellophanelike sheet of silk (figs. 19, 21, 22) providing a moisture-proof barrier. What is not certainly understood is the route of air exchange through the thin outer layer of silk that covers the feces deposited at the front end of the cell. Perhaps that silk is fenestrated. Alternatively air may be exchanged further back along the cell wall where the outer and inner layers meet and fuse. However, it should be noted that recent investigations on the cocoon of a larval *Hoplitis* demonstrates that the air passageway in that



FIGURES 11–15. Macrophotographs of nests of *Ochreirades fasciatus* in firm cypress wood, side view. **11.** Entire nest of three cells, which had been opened to remove contents. **12.** Close-up of entrance, showing recessed cell closure with pebbles above. **13.** Another nest with three cells, entrance to the left but not visible. **14.** Cell 3 from that nest with partial cocoon; front end of cocoon intact but partly pulled away from anterior partition; rear end of cocoon partly removed to reveal texture of inner surface with black feces imbedded in silk. **15.** Front end of cell from yet another nest, with inner layer of cocoon farther removed from outer transparent layer of cocoon appressed to mottled feces.

genus opens to the exterior by a ring of openings that circle the front of the cocoon where the outer cocoon layer attaches to the inner layer (to be fully described in a forthcoming paper).

PARASITISM AND PREDATION: No cleptoparasitic bees were associated with nests of *O. fasciatus*. However, five larvae of at least two species of predatory checkered beetles (Cleridae) were found inside the logs harvested from the Golan site. At least two of these larvae were found inside *O. fasciatus* nests, one of which was in the middle of a four-celled nest whose remaining cells on both sides contained uninjured bee larvae. Several specimens of *Leucospis dorsigera* Fabricius, 1775 (Hymenoptera: Chalcidoidea: Leucospidae), were observed flying



FIGURES 16–18. SEM micrographs of central part of anterior cell partition of *Ochreriades fasciatus* with surface covered by transparent layer of silk of front end of cocoon now made visible by reflected electrons. Note feces and part of anterior cell partition, upper left. **17, 18.** Sequential close-ups of rectangle in **16.** showing silk surface. FIGURES 19–21. SEM micrographs of inner surface of front end of cocoon showing fenestrations of central air portal. **19.** Entire front end. **20.** Close-up of central part identified by rectangle **a**, figure 19. **21.** Close-up of central part identified by rectangle **b**, figure 19. FIGURE 22. SEM micrograph of piece of inner surface of cocoon wall with bits of debris on glassy smooth, transparent inner surface of silk that had been applied over fibrous silk.

around the dead tree containing the nests of *O. fasciatus* in the Golan site. Three dead adults of the same species were found in occupied nests of *O. fasciatus*.

FLORAL PREFERENCES AND FORAGING BEHAVIOR

Ochreriades fasciatus appears to be strictly oligolectic on Lamiaceae. Females were observed collecting pollen from *Ballota undulata* at both nesting sites, as well as at several other locations in Israel and Jordan (Golan Heights, 2 km NW Hamat Gader, 3 May 2010, leg. C. Sedivy and C. Praz; Golan Heights, 7 km N Ein Gev, 2 May 2010, leg. C. Sedivy and C. Praz; Jordan, Wadi Shu'ayb, 20 km W Amman, 22 April 2007, leg. C. Sedivy and C. Praz. In addition, females were also observed collecting pollen from *Moluccella laevis* L. (Israel, Judean Foothills, Nahshon, leg. G. Pisanty; 1 km SE Beit Nir, leg. G. Pisanty). The analysis of the pollen provision from the nests of *O. fasciatus* reveals that all six nests sampled contained only tricolpate Lamiaceae pollen, probably belonging to *Ballota undulata* (although pollen identification was possible only to the family level). In addition, Andreas Müller kindly made available analyses of the pollen contained in the scopa of 14 museum specimens of *O. fasciatus*. The pollen loads from these females originating from five localities in Syria (8 females), Jordan (1 female) and Israel (5 females) consisted entirely of tricolpate Lamiaceae pollen (Müller, 2014), further suggesting that *Ochreriades* is oligolectic on Lamiaceae, probably with a strong or exclusive preference for *Ballota* and *Moluccella*. Males also actively patrol the host plants, often hovering at 10-20 cm from the host plant in search of females. Flowers from other families are occasionally visited but probably for nectar only, including *Citrullus lanatus* (Thunb.) Matsum. and Nakai (Cucurbitaceae; 1 male), *Heliotropium* spp. (Boraginaceae; 1 male), and *Lavatera punctata* All. (Malvaceae; 1 female) (G.P., personal obs.).

The method of pollen collection by *O. fasciatus* females is noteworthy. The Lamiaceae are strongly nototribic, i.e., the flower is bilaterally symmetrical, the anthers are placed in the upper corolla, and pollen is deposited onto the dorsal surface of the floral visitor when it forages for nectar. Many bees specializing on the Lamiaceae, or on other nototribic flowers, possess modified hairs on the clypeus or frons; these hairs are short, nonplumose, usually thickened basally, and often slightly bent downward or wavy apically (Müller, 1996b). They form a short comb or brush that is used for extracting the pollen from the upper lip. However, *O. fasciatus* entirely lacks modified pilosity on the clypeus. Rather, the females climb the upper lip of the flower and repeatedly tap their metasomal scopa directly against the anthers (fig. 4). The presumably unrelated bee *Protosmia* (*Nanosmia*) *minutula* (Pérez) shows similar behavior on other Lamiaceae (e.g., *Teucrium montanum* L. (Müller, 1996b; Müller et al., 1997: 321), and one unidentified species of *Protosmia* (*Protosmia*) was also observed to collect pollen in a similar way at the Golan site (V.T., D.B.). *Ochreriades fasciatus* females alternate these pollen-collecting visits with nectar visits, in which they land on the lower lip of the flower and insert their proboscises into the corolla. The corolla of both *Ballota* and *Moluccella* is moderately deep and adapted to large, long-tongued bees such as *Anthophora*. This suggests that the particularly long mouthparts of *O. fasciatus* (and *O. rozeni*, whose host plant is unknown) that nearly reach the tip of the meta-

soma are an adaptation to reach the nectar of their host plants. Müller (1996b) stated that pollination of Lamiaceae by bees was likely achieved mostly during nectar visits, as pollen-collecting females restrict their pollen visits to flowers in the male phase (many Lamiaceae are strongly protandrous; Müller, 1996b, and references therein). Interestingly, it appears that both sexes of *O. fasciatus* are too small to come in contact with the anthers during nectar visits on their host plants (fig. 5), and the overall contribution of *O. fasciatus* to pollination of their host plants may be very limited.

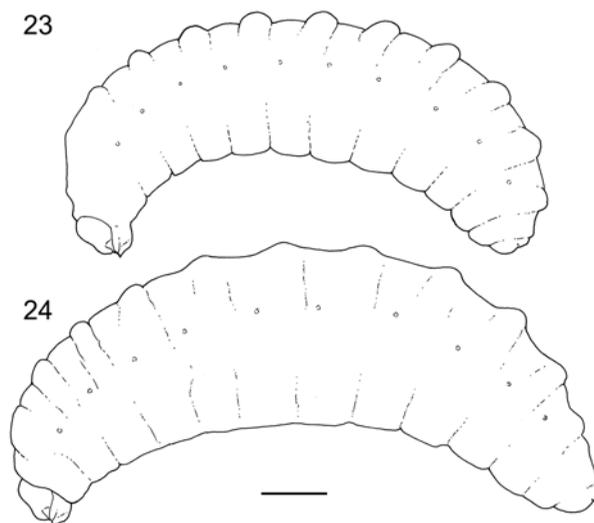
DESCRIPTION OF THE MATURE LARVAE OF *OCHRERIADES FASCIATUS*

Figures 23–37

DIAGNOSIS: The mature larva of *O. fasciatus* (figs. 23, 34) closely resembles other known larvae of the Megachilinae. The moderate body form between robust and slender is more slender than those of Anthidiini (Michener, 1953: figs. 109, 114, 119, 120; Rozen and Hall, 2012: fig. 52; Rozen, 2015), but the apically bidentate mandible (figs. 33–36) is typical for the family (except for certain *Stelis*), even though the apically rounded teeth are less common. Body vestiture on fifth instars (figs. 27–29) is also a family feature, but is substantially reduced in *O. fasciatus* compared with many family members and seems to consist of only setae, not spicules. The dense cluster of curved setae below the anus on abdominal segment 10 seems unusual (fig. 30). The dentate atrial wall of the spiracle (fig. 37) is a common, though not unique, feature of the family; the elongate, parallel-sided subatrium may be less common. As in all megachilids, paired dorsal tubercles are absent, but many larval megachilids exhibit more or less developed, middorsal intersegmental tubercles on midbody segments (Michener, 1953: fig. 114; Rozen and Hall, 2012: figs. 18, 52) (such tubercles seem to arise from the posterior edge of the caudal annulet and involve the partly surrounding extreme anterior edge of the following cephalic annulet). In some cases such tubercles are small and obscure and therefore easily overlooked. However, in *O. fasciatus* there is no hint of these tubercles.

The following description is based on both pre- and postdefecating larvae.

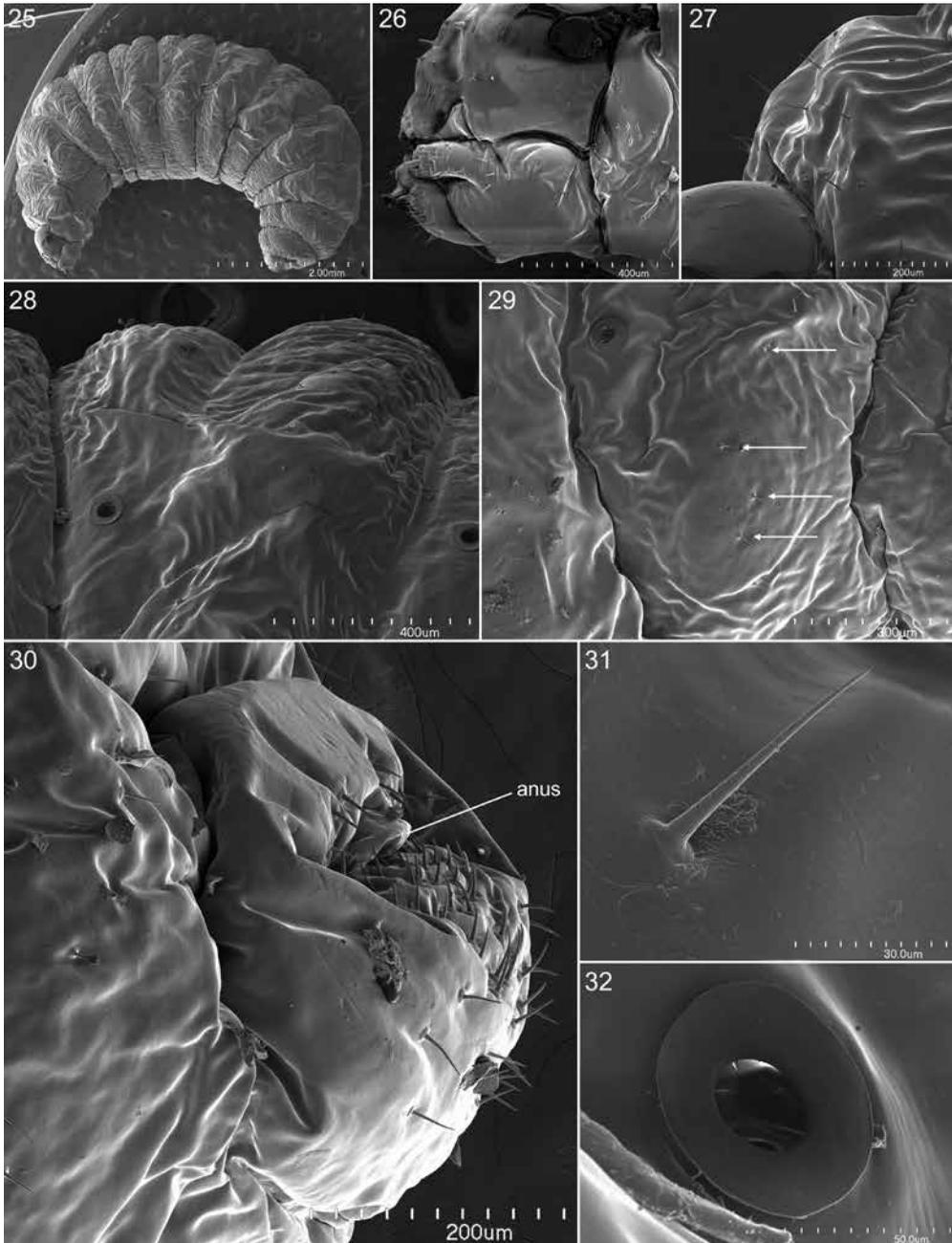
DESCRIPTION: Head: Head moderately small in relation to body size (figs. 23–25); oriented in normal, hypognathous position relative to thorax. Setae moderately long but sparse to non-existent on upper part of head capsule; those of maxillary and labial apices large, curved, moderately abundant, and conspicuous. Head capsule unpigmented except at points of articulations with mandibles; labrum faintly pigmented except transverse labral sclerite slightly darker; mandibles moderately pigmented except mandibular apices and areas of articulation with head capsule strongly pigmented; maxillary sclerites faintly pigmented; salivary lips strongly projecting, deeply pigmented; antennal papilla, maxillary and labial palpi all uniformly moderately pigmented. Spiculation apparently absent even on hypopharynx, not on maxilla. Coronal ridge present for less than one-third distance from postoccipital ridge toward level of antennae in frontal view; postoccipital ridge well developed, bending forward somewhat toward median line on top of head; hypostomal ridge well developed, giving rise to pronounced dorsal ramus that extends posteriorly for short distance before ending abruptly in front of postocci-



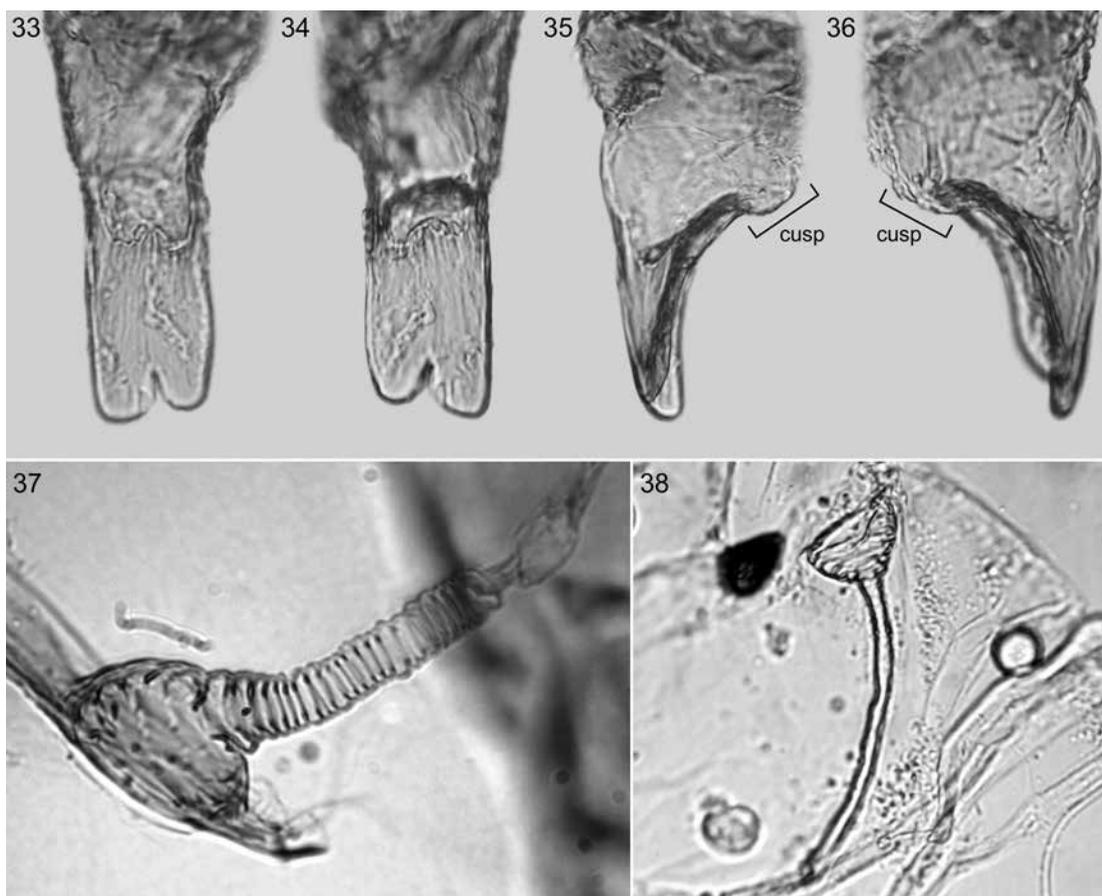
FIGURES 23, 24. Diagrams of post- and predefecating larvae of *Ochreriades fasciatus*, lateral views, to same scale, respectively. Setae not depicted.

tal ridge; both hypostomal ridge and ramus staining darkly; posterior part of ridge bending strongly mesad, forming deeply recessed posterior tentorial pit at junction with posterior tentorial bridge; posterior bridge absent in postdefecating larva because specimen preparing to molt; internal pleurostomal ridge obviously present but not well defined; epistomal ridge moderately well developed from anterior mandibular articulation to anterior tentorial pit; from pit, ridge extending vertically until fading out above level of antennal papilla (as in *Haetosmia*); hence ridge not extending across to opposite side of head. Tentorium mostly absent because of impending ecdysis. Parietal bands deeply incised. In lateral view, clypeus not projecting much beyond frons, antenna arising from faint prominence, and labrum not extending much beyond clypeus. Diameter of basal ring of antenna about two-thirds distance from closest point on ring to center of anterior tentorial pit; antennal papilla distinctly but not strongly pigmented, moderately large and elongate, longer than twice basal diameter, apically rounded, bearing perhaps three sensilla apically. Lower margin of clypeus angled upward at midline, so that at midpoint margin nearly at level of anterior tentorial pits. Labrum deeply emarginated apically; labral sclerite transverse but poorly defined, unevenly pigmented.

Mandible (figs. 33–36) moderately robust; apex darkly pigmented, bidentate with ventral tooth longer than dorsal tooth; mandibular apex approximately parallel sided in inner and outer views (figs. 33, 34); both teeth on postdefecating larva broadly rounded apically; dorsal apical edge of dorsal tooth faintly, irregularly uneven; ventral apical edge of ventral tooth also faintly uneven; apical concavity defined; cuspal area (fig. 36) developed, projecting, with surface irregularly uneven; outer mandibular surface with single conspicuous long curved seta near base. Maxillary apex strongly bent mesad in frontal view, so that maxillary palpus subapical in position; cardo distinct, posterior end directed toward posterior tentorial pit; stipes weakly sclerotized except for conspicuously long stipital rod that is darkly stained by dye, at posterior end articulat-



FIGURES 25–32. SEM micrographs of postdefecating larva of *Ochreriades fasciatus*, all lateral views or approximate lateral views. 25. Entire larva, near lateral view. Note that SEM image accentuate texture of surfaces that have been modified by critical-point drying in contrast to outline shape defined by camera lucida illustration (fig. 23). 26. Close-up of lower part of head and prothorax. 27. Pronotum, showing scattered, elongate, tapering setae. 28. Dorsal part of abdominal segment 3, showing short setae and division of cephalic and caudal annulets. 29. Lateral lobe of abdominal segment 8, showing paucity of setae (arrows). 30. Abdominal segment 10, close-up, showing abundant curved sharp setae below anus. 31. Dorsal pronotal seta, close-up. 32. Close-up of spiracle, outer view.



FIGURES 33–36. Microphotographs of cleared right mandible of postdefecating larva of *Ochreariades fasciatus*. **33.** Outer view with position of seta (removed during dissection) near base indicated by arrow. **34.** Inner view. **35.** Dorsal view. **36.** Ventral view. **FIGURE 37.** Microphotograph of spiracle, side view, showing elevated atrial rim, dentate atrial wall, and long, multichambered subatrium. **FIGURE 38.** Microphotograph of spiracle of fourth instar, side view, showing long subatrium without chambers.

ing with cardo, at anterior end broadening and branching to form weakly pigmented articulating arm of stipes; maxillary and labial palpi elongate, probably more than two times basal diameters, both pigmented like antennal papilla but slightly thinner than papilla. Labium clearly divided into prementum and postmentum; apex moderately narrow in frontal view; premental sclerite apparently absent but border between pre- and postmentum distinctly incised; prementum projecting dorsally at midline and sclerotized, pigmented on some specimens, forming dorsal bridge of premental sclerite that extends between apices of articulating arms of stipes; postmentum non-sclerotized. Salivary lips strongly projecting, transverse, with inner surface bearing parallel longitudinal grooves; width of lips slightly less than distance between bases of labial palpi. Hypopharynx distinctly separated pair of nonspiculate mounds.

Body (figs. 23–25, 27–32): Body vestiture without spicules, consisting only of slender, pale setae, tapering to fine points, arising from small but distinct alveoli; these setae inconspicuous

but moderately elongate and tapering (figs. 27, 31); setae moderately abundant on elevated dorsal surfaces of thorax and widely scattered on anterior ventral surface of thorax; some setae present on dorsal surfaces of caudal annulets of abdominal segment 8, 9, and 10, on ventral surface of abdominal segments 8 and 9, and especially abundant on abdominal segment 10 below anus (fig. 30); dorsal surface elsewhere with scattered short inconspicuous setae (fig. 28); lateral lobe of abdominal segment 8 (i.e., area below level of spiracle) with approximately 2–4 setae (fig. 28). Body form of postdefecating larva moderate in lateral outline between robust and slender (figs. 23, 25); body segments gradually increasing in height with abdominal segments 4 to 6 having greatest diameters; paired body tubercles absent, but caudal annulets of most body segments projecting farther than cephalic annulets and surprisingly uniform in appearance; middorsal intersegmental tubercles totally absent; lateral lobes of most body segments uniformly moderately developed. Body form of predefecating larva in lateral outline (fig. 24) with midbody segments having greatest diameter and outline tapering forward and backward from there. On pre- and postdefecating larvae (figs. 23, 24), venter of abdominal segment 9 not produced, as is true for all known larval Megachilidae; abdominal segment 10 attached to middle of segment 9 in lateral view; anus positioned toward top of segment 10. Spiracles (figs. 32, 37) unpigmented, subequal in diameter; atrium globular with width not much greater than depth, projecting little above body wall, with rim; diameter of atrial opening about 1.5 times radial width of peritreme (as measured on SEM micrograph, fig. 32); atrial inner surface with rows of wrinkles concentric with primary tracheal opening; some wrinkles giving rise to rows of concentrically directed spicules; primary tracheal opening with collar (i.e., integument of first chamber of subatrium tending to be more robust than that of subsequent chambers); subatrium long, with about 20 or more chambers of approximately equal size except one or two next to atrium slightly larger in diameter. Sex characters unknown.

MATERIAL EXAMINED: Two postdefecating larvae: Israel: Lehavot ha-Bashan (Hula Valley), coordinates: N 33°08'32" E 35°39'12", 138 m elev., May 5, 2013 (V. Trunz, D. Bénon) within dead cypress wood (*Cupressus sempervirens* L.). The following were collected as nests in the field at N 33°08'28" E 35°39'27", 170 m elev., on June 13, 2014, (G. Pisanty) and nests were opened on dates indicated: 1 predefecating larva, VI-16-2014; 6 predefecating and 2 postdefecating larvae, VI-18-2014. From nests collected by G. Pisanty, June 13, 2014, and sent to Neuchatel: 2 postdefecating larvae IX-30-2014 (C. Praz); 2 postdefecating larvae, IX-31-2014 (C. Praz).

REMARKS: One of the larvae sent by G.P. was a young fifth instar as judged by its substantially smaller size than any other predefecating specimen. Loosely attached to the body was a bundle of its cast exoskeletons, a condition frequently encountered in the Megachilidae, probably promoted by the earlier instars' inability to move from where they had been deposited as an egg. The small fifth clearly exhibited its distinctive long body vestiture as well as well-developed salivary lips. Among the cast exoskeletons, paired mandibles and some other head parts of the third and fourth instars were clearly visible. Not surprisingly both sets of mandibles were apically bifid and body exuviae lacked setae. Although spiracles of the third instar were difficult to evaluate, those of the fourth instar (fig. 38) showed a funnel-shaped, heavily sculptured atrium and a long, parallel-sided, faintly curved subatrium not divided into chambers.

CONCLUDING REMARKS

The present paper introduces many hitherto unknown aspects of the nesting and foraging biology of the rare bee *O. fasciatus*. An important question is whether these biological aspects, as well as larval morphology and cocoon structure, may provide useful phylogenetic information to settle the hitherto unclear phylogenetic placement of *Ochreriades* within Megachilidae. With respect to larval anatomy, larval *O. fasciatus* has no middorsal intersegmental tubercles whereas they have been illustrated for a number of species of *Hoplitis* (Enslin, 1925: figs. 3, 4), but larvae of other important taxa are still uncollected and unknown. We therefore do not expand further here on the comparative anatomy of osmiine larvae. This will be the subject of a subsequent paper. Regarding the nest architecture, the nest construction in *O. fasciatus* is somehow similar to what is observed in the genus *Chelostoma*, especially in the fact that partitions are made of mud (without incorporated pebbles) while the nest plug includes both mud and pebbles (Westrich, 1989; Müller et al., 1997). The pebbles included in the nest plug are comparatively larger and the proportion of mud in the plug is lower in *O. fasciatus* than in *Chelostoma*. In spite of these differences, the inclusion of pebbles into the nest plug is a noteworthy similarity between *O. fasciatus* and *Chelostoma*. However, other osmiine lineages are known to include pebbles into the nest plug but not into the cell partitions. Bees of the genus *Heriades* use resin as nesting material (Matthews, 1963; Westrich, 1989; Müller et al., 1997). While the cell partitions are made of pure resin, the nest plug consists of resin into which small pebbles, sand grains, dirt, slivers of wood, dry plant fragments, and other miscellaneous detritus are added (Matthews, 1963; Westrich, 1989; Müller et al., 1997). Use of stones and other detritus is most probably a barrier to nest enemies such as birds, parasites, or parasitoids, a likely underestimated mortality factor in solitary bees (Elz et al., 2015). Based on these observations, one wonders whether the incorporation of pebbles into the nest plug is homologous among the various osmiine lineages discussed above or the result of convergent evolution due to high predator or parasite pressure in cavity-nesting bees. Lastly, although floral preferences may not constitute a phylogenetically reliable character, one comparison between host specialization in *Ochreriades* and *Chelostoma* is noteworthy. Sedivy et al. (2008) studied the floral preferences of *Chelostoma* in detail. They found that most species of *Chelostoma* were oligolectic on various hosts, as is *Ochreriades*, yet a striking difference with *Ochreriades* is the fact that zygomorphic (or bilateral) flowers were entirely absent from the host plants of *Chelostoma*. In conclusion, although information on the nesting biology, mature larva, and floral preferences presented herein does not currently shed light on the phylogenetic relationships of *Ochreriades* to other osmiines taxa, it does provide new information that can be compared when more complete studies of the other taxa are forthcoming.

Another consideration: Although phylogenetic information is important and interesting, it is not the only goal of natural history. Understanding and knowledge of the whole organism (all life stages plus the respective anatomy and behavior during those stages) and determining how the organism is adapted to its environment are other goals. With respect to *O. fasciatus*, the study is far from complete. Among questions yet to be answered: What is the anatomy of

its egg? Where and in what position is it deposited? How many larval instars are there? It has been hypothesized that megachilid larvae do not crawl until they reach the fifth stadium (Rozen and Hall, 2011). Is that true for *O. fasciatus*? In what developmental stage does the species overwinter? Are we certain where adults mate?

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