

Mature Larvae and Nesting Biologies of Bees Currently Assigned to the Osmiini (Apoidea: Megachilidae)

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ABSTRACT

The purpose of this study is to describe the mature larvae of all taxa of the tribe Osmiini (Megachilidae) whose postdefecating larvae have been collected and are available. The hope is that data uncovered will eventually lead to a better understanding of the interrelationships of included taxa and of their anatomies, behaviors, and ecologies (i.e., their natural histories). The species included are representatives of the following taxa: *Ashmeadiella*, *Atoposmia*, *Chelostoma*, *Heriades*, *Hoplitis*, and *Osmia* (*Hoplosmia*). We also include recently described larval representatives of *Haetosmia* and *Ochreriades*. Because of its large size and diversity, the genus *Osmia* alone (with the exception of the subgenus *Hoplosmia*) is allocated to a separate future investigation. Larvae of the tribe share many features with one another and also with other members of the Megachilidae. Anatomical structures of larval Osmiini whereby they can be differentiated from other megachilids were not identified. However, most (though not all) members of the tribe fall into one of three main subgroups on the basis of: (1) body form, (2) presence or absence of middorsal, intersegmental tubercles on basal abdominal segments 1–5, and (3) the depth of intersegmental constrictions.

In the process of gathering specimens the authors uncovered new information concerning nesting biology with respect to nest location and structure and to cocoon structure and function. These data were derived from the authors' own field studies as well as from specimens and field data collected through the years by others.

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INTRODUCTION

In his masterful volume on bees, Michener (2007) recognized 20 genera in the tribe Osmiini (Megachilidae). His studies had been based primarily on adult morphology, although choice of nesting sites was often mentioned. Shortly after its publication, Praz et al. (2008) found, through an extensive study using three nuclear genes, that most of these genera formed a well-supported, monophyletic group. However, placement of four of the included genera (*Noteriades*, *Afroheriades*, *Pseudoheriades*, and *Ochreriades*) was uncertain. Since then, the genus *Noteriades* was confirmed to belong to the tribe Megachilini (Gonzalez et al., 2012), but the placement of the three other genera remains in doubt. The purpose of the current investigation is to explore yet another source of information to illuminate the relationships of the included taxa as identified by Michener. Thus, we describe here the anatomy and behavior of the mature larvae of the Osmiini, their cocoons, and other aspects of nesting biology to the extent that such information is available. Where possible, we also would like to explore the relationships of the three problematic genera. One of the two known species of *Ochreriades* has recently been studied along these lines (Rozen et al., 2015) and thus will be further considered here. Cells of *Pseudoheriades grandiceps* Peters with partial cocoons had been preserved in the USDA laboratory in Logan, Utah, and can also be considered, but its larva remains unknown. Nests of *Afroheriades* and *Noteriades* have not been discovered, leaving their larvae, cocoons, and even nesting habitat unknown, although Griswold (1985) reported a female of *Noteriades* at a burrow entrance in wood as might be expected given the cylindrical body form of the genus.

At the start, this study was intended to treat all osmiine taxa for which information was available. However, when considering mature larvae, it quickly became apparent that the known larvae of the genus *Osmia* (with 19 subgenera totaling more than 300 species) were so diverse that they would have to be excluded even if larval representatives of all subgenera were known because the key would become unmanageable and serve no purpose. Consequently it was decided that the main effort of the paper should be to treat the tribe broadly; the larvae and nesting biology of the single genus *Osmia* should be set aside for a later, narrowly focused, in-depth review.³ We kept only descriptions of *Osmia* (*Hoplosmia*) *anceyi*, as this subgenus was regarded as a separate genus by Michener (2007); in the phylogeny of Praz et al. (2008) *Osmia* (*Hoplosmia*) was part of a clade including nonmetallic *Osmia* that was sister to all other *Osmia*.

The final part of this paper entitled “Nesting Biology” is devoted to providing new information concerning the nesting biology of the Osmiini derived from the authors’ observations either while carrying out fieldwork on these bees or during examination of specimens collected by others through the years.

³ Although the genus *Osmia* is not included in this study, the species *O. (Helicosmia) chalybea* Smith is occasionally mentioned with reference to features found in the tribe. Its larva was recently described by Rozen and Hall (2011) and both pre- and postdefecating forms are diagramed in lateral view herein (figs. 1, 2).

METHODS

Most descriptions of bee larvae have been based on the last larval instar after it has voided the contents of its alimentary tract—the postdefecating form. In univoltine bees this is mostly the diapausing larva, the stage with the most extended duration and therefore the one that has the greatest chance of being collected, although in several early-flying osmiine bees the pupa or even the adult overwinters (Westrich, 1989). Furthermore, the postdefecating form is the one with the most consistent shape over long stretches of time since its body form is not affected by food ingestion and growth, as is the case with the predefecating, last larval instar. However, it has been customary to describe predefecating forms if postdefecating larvae are not available because head structures and spiracular anatomy modify little during the entire stadium. If both pre- and postdefecating forms are on hand, predefecating forms should also be illustrated and included in descriptions to contrast with the anatomy of the postdefecating larva and to explore the possible adaptive functions of the predefecating anatomy particularly with respect to mobility. Several times during the course of this study, larvae were encountered that had been preserved before they had completely voided their feces and entered diapause. Although they are termed “defecating forms” for the sake of accuracy, they have in most respects the physical attributes of predefecating larvae in that the cuticle is thin and easily torn in the clearing process. One aspect not examined in the present paper but that deserves further work is whether there are anatomical differences between postdefecating larvae of the warm-weather generations and those of the long-diapausing cold-weather generation in multivoltine species.

To be thoroughly studied, a postdefecating bee larva must be examined in three different ways. The first involves no preparation; the specimen is removed from its storage vial and examined stereoscopically. This inspection provides the viewer with the shape and contour of the animal, and its natural pigmentation. Either of the following two ways (order not important) can then be taken provided that more than one specimen is available: (1) clearing and staining for examination by stereomicroscope and compound microscope, and (2) critical-point drying followed by coating with gold/palladium for SEM viewing. Each procedure renders a single specimen unsatisfactory for the other procedure.

For clearing, the head is removed from the body, and both parts are boiled in an aqueous solution of sodium hydroxide until all opaque tissue is removed. They are then transferred to 75% ethanol, stained with Chlorazol Black E, and finally placed in glycerin on a well slide for study and eventual storage. A specimen so treated will reveal: (1) thickness, length, and direction of internal head ridges, (2) tentorial and spiracular anatomy, and (3) surface vestiture (i.e., setae and spicules). Although, this procedure alone is satisfactory for freshly preserved specimens, specimens collected in earlier decades often remain spotted after clearing and staining and therefore are difficult to analyze. Such specimens can be submerged in a solution of liquid Oxi Clean™ Laundry Stain Remover with more than equal quantity of water, heated for some minutes on a hot plate, and the coloring will gradually even out.

For SEM examination the entire (non-dissected) larval specimen is first critical-point dried and then coated with gold/palladium. At the AMNH, we currently use a Hitachi S-5700 scanning electron microscope. Resulting micrographs of high resolution reveal information con-

TABLE 1. Osmiine larvae (exclusive of *Osmia*) described by others; specimens unavailable for reexamination.

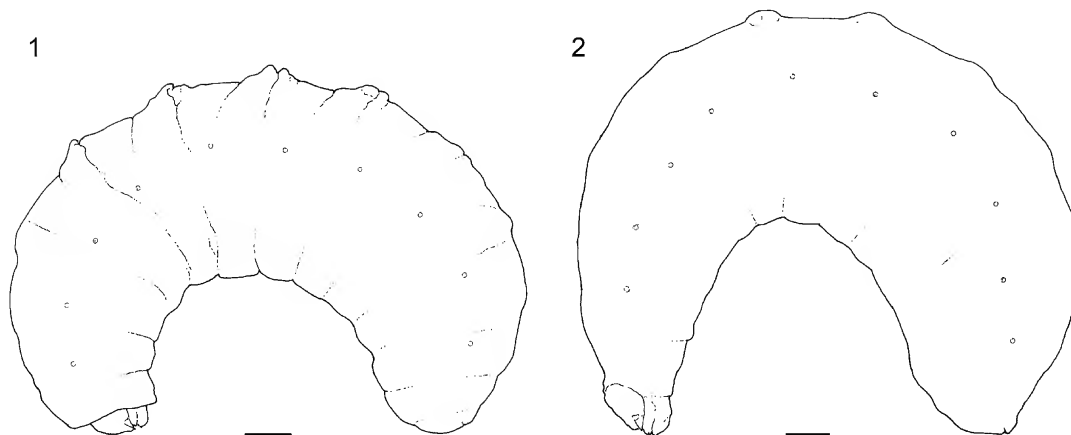
Current Name	Name Used in Reference Cited	Reference
<i>Ashmeadiella</i> sp.	<i>Ashmeadiella</i> sp.	Michener, 1953
<i>Heriades</i> (<i>Heriades</i>) <i>crenulatus</i> Nylander	<i>Eriades crenulatus</i> Nylander	Grandi, 1961
<i>Hoplitis</i> (<i>Alcidamea</i>) <i>leucomelana</i> (Kirby)	<i>Osmia leucomelana</i> (Kirby) <i>Osmia parvula</i>	Micheli, 1930 Dufour and Perris, 1840
<i>Hoplitis</i> (<i>Pentadentostmia</i>) <i>nitidula</i> (Morawitz)	<i>Hoplitis</i> (<i>Tridentostmia</i>) <i>nitidula</i> (Morawitz)	Torres et al., 1997
<i>Hoplitis</i> (<i>Alcidamea</i>) <i>tridentata</i> (Dufour and Perris)	<i>Osmia tridentata</i> Dufour et Perris	Enslin, 1925
<i>Hoplitis</i> (<i>Anthocopa</i>) <i>similis</i> (Friese)	<i>Hoplitis</i> (<i>Anthocopa</i>) <i>anthodeminon</i> Michener	Torres et al., 1997
<i>Hoplitis</i> (<i>Proteriades</i>) <i>bunocephala</i> Michener	<i>Proteriades</i> (<i>Hoplitina</i>) <i>bunocephala</i> (Michener)	Thorp, 1968
<i>Hoplitis</i> (<i>Hoplitis</i>) <i>adunca</i> (Panzer)	<i>Osmia adunca</i> Panzer	Grandi, 1961
<i>Hoplitis</i> (<i>Hoplitis</i>) <i>anthocopoides</i> (Schenck)	<i>Hoplitis</i> (<i>Hoplitis</i>) <i>anthocopoides</i> (Schenck)	Eickwort, 1973
<i>Hoplitis</i> (<i>Hoplitis</i>) <i>lepeletieri</i> (Pérez)	<i>Osmia lepeletieri</i> Pérez	Enslin, 1925 Micheli, 1933
<i>Hoplitis</i> /(<i>Hoplitis</i>) <i>loti</i> (Morawitz)	<i>Osmia loti</i> Morawitz	Micheli, 1931
<i>Hoplitis</i> (<i>Alcidamia</i>) <i>spoliata</i> (Provancher)	<i>Hoplitis</i> (<i>Andronicus</i>) <i>cylindrica</i> Cresson	Baker et al., 1985

cerning structure, identification, and distribution of vestiture (setae and spicules) and surface texture. Overall body form and contour can also be well represented.

Cocoons to be examined with an SEM require no critical-point drying. After being cut open to remove contents, sections to be examined can simply be mounted on stubs and coated. SEM examination usually clearly reveals the position and size of the air-exchange portal, a fenestrated area on the inner surface that elsewhere is nonporous. The portal is the entrance to a pathway allowing air exchange through the layers of cocoon fabric.

In paragraphs entitled Material Studied, F.D. Parker (personal commun. with J.G.R.) reports the following with respect to specimens he collected: They came from trap stems made from elderberry and placed upright in the ground. Stems were put out before the active season, usually in March, and collected in the fall, usually around November. They were opened in the laboratory and contents placed in individual gelatin capsules and reared in the spring in temperature controlled cabinets. Consequently only the year is recorded for his specimens. Parker provided the following GPS readings for two of his Utah collection localities: Bear Lake: 41 52 41.21 N 111 21 57.78 W and Willard Peak: 41 24 27.37 N 111 58 03.22 W.

Scale bars on larval diagrams = 1.0 mm. Table 1 lists the names of osmiine larvae that have been described by others but specimens of which were not available for study here. Complete scientific species names including authorship are presented in the key and in titles of treated taxa. Only mature larvae (i.e., fifth larval instar) are treated here. Unless stated otherwise, they are the postdefecating form.



FIGURES 1, 2. Last larval instar of *Osmia chalybea*, lateral view, postdefecating form and predefecating form, respectively.

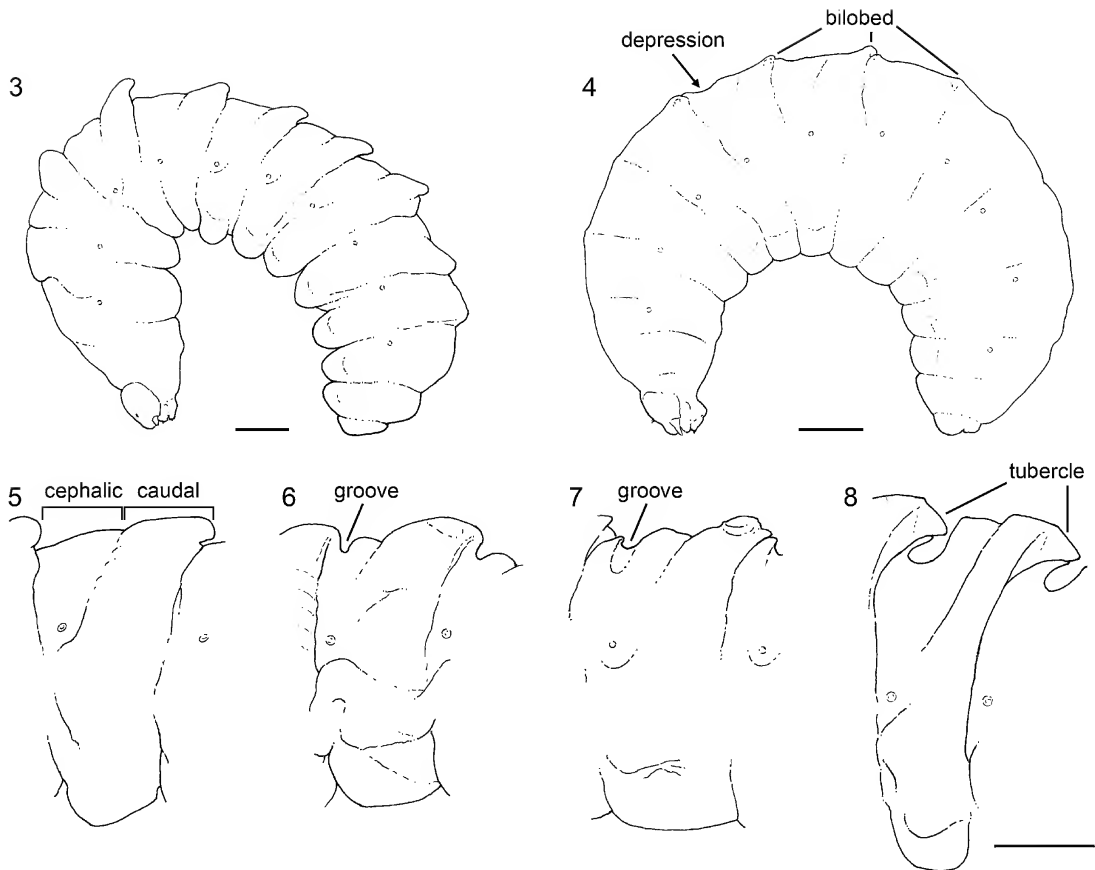
LARVAE

SPECIAL ANATOMICAL FEATURES AND THEIR FUNCTIONS

Herein, we describe and interpret the function of certain unusual anatomical features encountered when examining larvae of this tribe.

Retracted head capsules of *Atoposmia hypostomalis* (fig. 20), *Osmia anceyi* (fig. 28), and presumably *Osmia chalybea* (fig. 1) are features of only postdefecating larvae. Although these larvae seem dramatically different from larvae with exerted heads, the functional importance of head retraction may not be as significant or meaningful as its visual effect. This is demonstrated by the appearance of a predefecating larva of *O. chalybea* (fig. 2) with its head normally exerted for feeding and cocoon spinning. The adaptive function of a retracted head for the long hibernation of the larva wrapped in a protective cocoon is obscure. The poorly preserved single specimen of *Atoposmia copelandica* did not exhibit a retracted head capsule, possibly an accident of preservation. This is suggested by the extent of integument devoid of setae immediately posterior to the head, which might accommodate the folding of the neck region into the conspicuously setose integument of the posterior part of the pronotum.

Many but not all taxa treated here exhibit apically rounded tubercles along the dorsal midline of the first four or five abdominal segments, with some species having a dorsal metathoracic tubercle as well. Depending on the species, the tubercle may be a single median apical lobe or may be transversely bilobed (i.e., two lobes close to one another, side by side, too close to be confused with paired, dorsal tubercles of many groups of bees, such as found in Calliopsini (Andrenidae), e.g., Rozen, 2013b: figs. 7, 9). Each tubercle arises from the posterior edge of the caudal annulet of the abdominal segment. In some species the anterior edge of the following cephalic annulet is modified and participates in the structure of the tubercle, as most notably exemplified by *Hoplitis biscutellae* (fig. 8). Whether with a single lobe or bilobed, apical surfaces of tubercles lack setae and spicules. Possible functions of the tubercles are discussed below.



FIGURES 3–8. Postdefecating larvae of *Hoplitis*, lateral views. 3. Entire larva of *H. hypocrita*. 4. Entire larva of *H. xerophila*. 5–8. Abdominal segment 3, enlarged showing contrasting anatomies of: 5. *H. hypocrita* (with caudal and cephalic annulets identified), 6. *H. sambuci*, 7. *H. uvulalis*, and 8. *H. biscutellae*.

An interesting feature first noted in the larva of *Hoplitis hypocrita* is the extensive thickening and stiffening of its cuticle, so that after clearing, the cuticle tends to maintain its shape to a greater degree than is characteristic of most postdefecating bee larvae. Furthermore, there is more extensive pigmentation of its mouthparts including the lobes of the hypopharynx. Because the predefecating larva is unknown, it is uncertain to what if any degree its cuticle is also uncommonly stiff.

Close examination of the head of the postdefecating larva of *Hoplitis hypocrita* reveals that the cuticle of the prementum and postmentum is faintly dark and stiff except for a clear membranous band of flexibility at the junction of these two areas. This band permits the prementum to retract and to extend during cocoon spinning and perhaps food ingestion. While this demarcation is visible because its colorless transparency contrasts with the ever so slight darkening of the surrounding stiffer cuticle, it accounts for the distinct line of separation between the prementum and postmentum, a feature held in common by larvae of all Osmiini. Thus, it should be realized that with bee larvae, dark pigmentation alone does not define areas of

reduced flexibility; conversely, lack of pigmentation does not always imply flexibility. Although the postmentum of the cleared postdefecating larva of *H. hypocrita* appears to be completely clear and membranous, it is in fact firmly attached to the parietals and functions as a stable base with which the prementum flexes.⁴

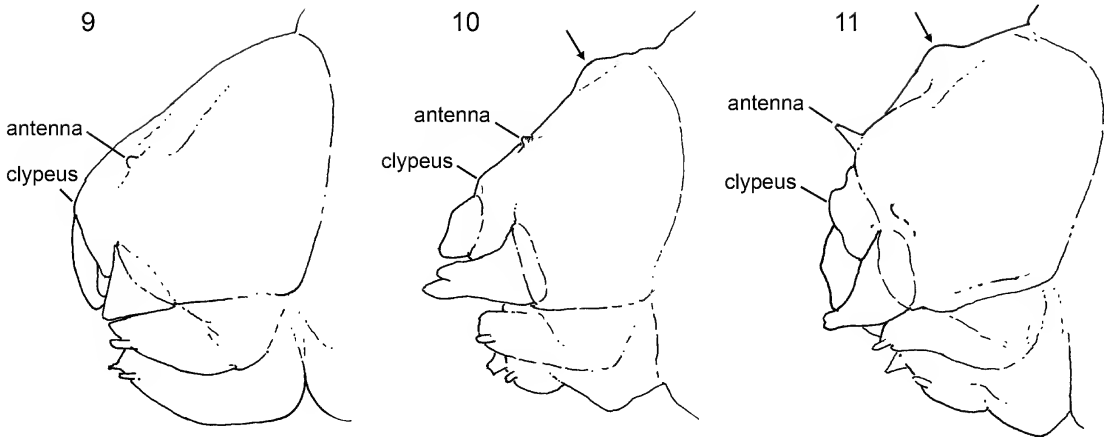
The differential thickening of presumably clear membranous larval cuticle described for the labial region, above, is also observed in the relatively transparent and unpigmented dorsal cuticle of the larval body. Taking abdominal segment 3 as an example for various species of *Hoplitis*, the cephalic annulet is immovably fused with the caudal annulet, but a line of flexibility exists between this body segment and the one in front and the one behind, permitting the body to both bend and unbend and to swing to a lesser extent from side to side as the larva moves to feed, defecate, and spin its cocoon. The difference between some species of *Hoplitis* with respect to the contour of thick dorsal integument is remarkable in some cases, as identified in the descriptions. Although it is not clear why this variation exists, we hypothesize that the division of segments into dorsal caudal and cephalic annulets with many species having dorsal midline tubercles at the rear of the caudal annulet functions to enable the larva to crawl around the cell while bracing its dorsum against the cell wall. The vestiture of the larva, which is found mostly on the dorsal and lateral surfaces of the body, presumably assists by providing traction through waves of contraction and expansion of body segments as the larva moves forward. The midline dorsal tubercles of those species having them presumably assist in this ambulation, perhaps by pushing against the cell wall either to enhance bracing against the cell or, conversely, by lowering the setose body surface from the wall so the surrounding surface can be slipped forward. Careful analyses of live, moving larvae, perhaps in a celllike artificial chamber, will probably enable a test of these ideas.

TRIBAL DESCRIPTION OF OSMIINI BASED ON AVAILABLE LAST LARVAL INSTARS

The purposes of the following are (1) to provide a coherent understanding of the important features of osmiine last larval instars by which they might be recognized and distinguished from those of other bees, and (2) to identify larval features that are variable within the tribe and that thereby might provide insight into intratribal relationships. The description also includes larval features held in common by all taxa treated herein to avoid needless repetition in their individual descriptions.

As long known, last larval instars of Megachilidae can be recognized because of the presence of body vestiture (setae and/or spicules) (Michener, 1953), which have also been reported for the Allodapini (Michener, 2007). Recently it has been suggested that this feature in megachilids appears to be restricted to the last larval instar, for earlier instars rarely exhibit any vestiture (Rozen et al., 2010a; Rozen and Hall, 2012) (with a few well-documented exceptions, e.g., Rozen et al., 1978). Limited displays of body setae, however, have also been reported in

⁴ Some species of the anthidiine genus *Stelis* bear distinct, paired, well-defined sclerites on the postmentum (Rozen and Hall, 2011: figs. 83, 84). The fact that the sclerites are not fused to the parietals suggests that they function differently from the thickening of the postmental integument of *Hoplitis hypocrita*.



FIGURES 9–11. Larval heads of *Hoplitis* in lateral profile, with arrow pointing to projection, if present, on vertex. 9. *H. hypocrita*. 10. *H. producta*. 11. *H. biscutellae*.

last larval instars of a few nonmegachilid taxa such as *Eremapis* (Exomalpsini) (Rozen, 2011a) and Emphorini (Rozen, 2011b), both Apidae.

DESCRIPTION: Head: Head size moderate to very small in relation to body size (figs. 1–4, 12–28); most are oriented in normal, hypognathous position relative to thorax. Setae moderately long but sparser on upper part of head capsule; overall setal abundance varying among species; those of maxillary and labial apices tending to be large, curved, abundant, and conspicuous. Head capsule pigmentation tending to be at points of articulation with mandibles; labral pigmentation present but variable, mostly involved with transverse labral sclerite; mandibular apices always pigmented; maxillary sclerites often lightly pigmented, never strongly so; salivary lips always strongly projecting, pigmented or not; antennal papilla and maxillary and labial palpi sometimes lightly pigmented. Integumental spiculation always absent, possibly except for outer surfaces of hypopharyngeal lobes. Internal head ridges: coronal ridge absent or present only near top of head, never extending beyond halfway to 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 either for short distance or for meeting postoccipital ridge; both hypostomal ridge and ramus staining darkly, indicating strong development; posterior part of ridge bending strongly mesad, forming deeply recessed posterior tentorial pit at junction with posterior tentorial bridge; pleurostomal ridge always more or less present; 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; hence ridge never extending across to opposite side of head. Tentorium of postdefecating larva usually partly absent because of impending ecdysis, hence details not provided. Parietal band always more or less evident. In lateral view, clypeus usually not projecting much beyond frons, antenna in most cases arising from faint prominence, and labrum normally not extending much beyond clypeus. Lower margin of clypeus angled dorsally at midline, so that at midpoint margin nearly at level of anterior tentorial pits. Labrum broadly emarginated apically; labral sclerite transverse, often well defined because of pigmentation.

Mandible moderately robust; apex bidentate with ventral tooth longer than dorsal tooth; shape of teeth variable; apical concavity defined; cuspal area not projecting; outer surface of mandible usually with one conspicuous seta, occasionally with two setae, near base.⁵ Maxillary apex strongly bent mesad in frontal view, so that maxillary palpus subapical in position; cardo distinct; stipes consisting of conspicuously long stipital rod that is sometimes pigmented and is darkly stained by dye; at posterior end, rod articulating with cardo, and, at anterior end, rod broadening and branching to form often pigmented articulating arm of stipes; other arm of branch circling orally around outer side of mound of hypopharynx; maxillary and labial palpi elongate, probably usually more than two times basal diameters. Labium always clearly divided into prementum and postmentum; apex usually moderately narrow in frontal view; premental sclerite rarely visible as pigmented sclerite, but border between pre- and postmentum distinctly incised (see Special Anatomical Features, above); prementum projecting dorsally at midline and sclerotized, often pigmented, forming dorsal bridge of prementum that extends between apices of articulating arms of stipes; when premental sclerite pigmented (e.g., in some *Osmia*), bridge and sclerite encircle prementum; postmentum seemingly nonsclerotized but see Special Anatomical Features (above). Salivary lips strongly projecting, transverse, with inner surface usually bearing parallel, longitudinal grooves; lips variable in width. Hypopharynx consisting of transverse pair of dorsally projecting mounds.

Body: Depending on species, body vestiture consisting of only setae or of setae and spicules, either of which may be more or less abundant; vestiture tending to be most abundant on sides and dorsum of body, usually far less abundant on ventral surface; vestiture of lateral lobe of abdominal segment 8 (i.e., area below level of spiracle) employed in following descriptions as index of abundance. Body form of postdefecating larva tending to be of three types in lateral outline: (1) Larger toward rear of body with distinction of cephalic and caudal annulets becoming less apparent at posterior end of body than at anterior end of body (figs. 20, 24–26, 28). (2) Midbody segments thickest and lacking middorsal tubercles, with anterior and posterior ends of body tapering and with distinction of cephalic and caudal annulets maintained at posterior end, imparting more uniform appearance along length of body (figs. 12–19, 22, 23, 27). (3) Body elongate with deep constrictions between segments, so that anterior segment tending to override following (figs. 3, 5–8). Exceptions to three body types described above include *Haetosmia vechti* (fig. 21) and perhaps *Hoplitis xerophila* (fig. 4). Paired, widely spaced, dorsal body tubercles (i.e., paired sublateral dorsal body tubercles) as in Panurginae (Rozen, 2013b, 2014) absent; midbody tubercles often present on metathorax and abdominal segments 1–4 to 1–6 on some species. On pre- and postdefecating larvae (figs. 1–4, 12–28), venter of abdominal segment 9 not produced, in contrast to all known larval Megachilidae; abdominal segment 10 attached to approximate middle of segment 9 in lateral view; anus positioned toward top of segment 10. Abdominal segment 10 often with posteriorly projecting unpigmented ridge ring-ing anus except for ventral one-quarter; this ring staining readily to treatment with Chlorazol

⁵ The number of setae on the outer mandibular surface, i.e., whether one or two, may not be a significant feature among larvae of this tribe since among several sampled taxa (e.g., *Heriades truncorum*) opposing mandibles of a single specimen have different numbers.

Black E. Spiracles usually unpigmented to lightly pigmented, subequal in diameter; atrium globular with width usually greater than depth, projecting above body wall, with rim; atrial inner surface smooth to ringed with ridges concentric with primary spiracle opening, often with 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 variable in length. Sex characters unknown.

COMPARISON WITH MEGACHILINI

The description of the larvae of the Osmiini, above, is based on the material treated in the following key. However, this description cannot be relied upon to distinguish osmiine larvae from those of other nonparasitic⁶ members of the entire Megachilinae because of the large size of the subfamily and lack of information concerning mature larvae of so many included taxa. It was therefore decided to undertake an exploratory character comparison between the description of the Osmiini, above, and the description of the Megachilini as presented by Rozen and Kamel (2007), augmented by the more complete evaluation of the genus *Megachile* in Rozen et al. (2016). Such a comparison might be useful in two ways: it might test the usefulness of larval characters in evaluating phylogenetic relationships in the subfamily in general, and specifically it might test the hypothesis that *Ochreriades* is the sister to the lineage that gave rise to the Osmiini and Megachilini, one of the topologies recovered in Praz et al. (2008).

No consistent differences were detected regarding larval head features between the two tribes. In body shape, Megachilini were consistently linear in lateral view with the largest segments toward the rear. With Osmiini body shape was highly variable, with one group (*Ashmeadiella*, *Chelostoma*, and *Ochreriades*) having more slender bodies, widest at midbody and tapering toward both ends (figs. 12–18, 22, 23, 27). With other osmiines, the posterior end of the abdomen was extensively enlarged (figs. 1, 20, 24, 26, 28) or in other ways (figs. 3, 4, 20, 21) distinguishable from the three genera identified above.

One feature dealing with body vestiture may shed light on the relationship between *Ochreriades* on one hand with the Osmiini and Megachilini on the other hand. Rozen et al. (2016) pointed out that in Megachilini body vestiture consists of only setae and no spicules. However, in the Osmiini, mature larvae of some taxa have a body vestiture of both setae and spicules while others have setae alone. Larval *Ochreriades* has only body setae (Rozen et al., 2015). Among the various branches of the Megachilidae, larvae of Pararhophitini are known to have both types of body vestiture (McGinley and Rozen, 1987). In the Fideliini both types of vestiture are found in *Fidelia* (Rozen, 1970) and *Parafidelia* (Rozen, 1977), but in *Neofidelia*, only body setae are found (Rozen, 1973a). Among the Lithurgini both types of body vestiture have been reported for *Lithurgus*, *Lithurgopsis*, and *Trichothurgus* (Rozen, 1973b; Rozen and Hall, 2014). If it is assumed that the widespread occurrence of two types of body vestiture in all the

⁶ Cleptoparasitism has evolved a good many times in the Megachilidae, possibly resulting in a number of de novo appearances of parallel anatomical features. Furthermore, larvae of presumed cleptoparasitic osmiines have not yet been studied. To simplify analysis, only nonparasitic groups have been considered here but are referenced in other places in the paper.

basal branches of the family is evidence that it is the primitive condition in the Megachilidae, then the occurrence of setae alone is derived.

However, the presence or absence of body spicules may be a labile feature in megachilid bees, as evidenced by absence of spicules in *Neofidelia* mentioned above, as well as the following: in the Anthidiini *Trachusa larreae* (Cockerell) (Rozen and Hall, 2012), *Anthidium chilense* (Urban) (as *Notanathidium (Allanthidium) chilense*, Rozen, 2015), and *Stelis (S.) elongativentris* Parker (Rozen, 1987) are reported to have setae and spicules, whereas *Stelis (S.) phaeoptera murina* Pérez (Rozen and Kamel, 2009) and *Stelis (S.) ater* Mitchell (Rozen and Hall, 2011) have only setae.

And yet another matter remains obscure. It has been postulated that body vestiture in megachilid bees enables the mature larva to move around in its cell to finish feeding, to position its fecal deposits, and to manufacture its cocoon (Rozen and Hall, 2011, 2012, 2014; Rozen, 2013a). In most of these cases two types of vestitures are involved: spicules and setae. We also know that with some taxa setae alone are involved (e.g., *Ochreriades*, *Megachile*). We do not understand the differences in the function of these two mechanical systems that accomplish the same thing. There is more work to be done.

KEY TO MATURE LARVAE OF OSMIINE SPECIES DESCRIBED HEREIN
EXCLUSIVE OF OSMIA

The preparation of this key was an attempt to analyze larval features that might be employed to distinguish between the various genera of osmiines. As indicated in the introduction, mature larvae of *Osmia* are too poorly known at this time to be generically characterized. Furthermore, larval representatives of only two of the subgenera of *Hoplitis* are known. All other osmiine taxa whose larvae are treated in the paper can be found below except for *Atoposmia copelandica*, the single specimen of which was poorly preserved. Unknown is whether the head of the postdefecating form of this species normally retracts into the prothorax, as does the head of *Atoposmia hypostomalis*, as mentioned above in the section on Special Anatomical Features.

- 1. Intersegmental lines deeply incised with caudal annulets of anterior abdominal segments tending to override anterior part of following cephalic annulets (fig. 3); body integument of postdefecating larva relatively stiff, so that body shape retained even after clearing (all species of *Hoplitis* dealt with herein except for *H. xerophila*) 2
- Intersegmental lines normally to weakly incised, so that segments not overriding one another as described above (figs. 4, 12–28); integument of postdefecating larva relatively soft, so that body of cleared specimen tending to flatten when not submerged in glycerin 5
- 2(1). Antenna projecting as far as clypeus in lateral profile (fig. 11); cephalic annulet of abdominal segments 3 and 4 each with deep transverse groove resulting in formation of median, strong, posteriorly directed intersegmental tubercle (fig. 8)
..... *Hoplitis (Alcidamea) biscutellae* (Cockerell)
- Clypeus projecting farther than antenna in lateral profile (figs. 9, 10); cephalic annulet of abdominal segments 3 and 4 with (figs. 6, 7) or without (fig. 5) transverse groove, but if with groove never forming posteriorly directed intersegmental tubercle 3

- 3(2). Mandibular teeth, at least usually, apically rounded; vestiture of lateral lobe of abdominal segment 8 without pigmented spicules, consisting of only fine setae (although if broken, setae might be confused with spicules) *Hoplitis (Alcidamea) fulgida* (Cresson)
- Mandibular teeth apically acute, short to elongate; vestiture of lateral lobe of abdominal segment 8 consisting of both setae and pigmented spicules. 4
- 4(3). Vertex in lateral profile slightly curved (fig. 9), without angle or protrusion; cephalic annulet of abdominal segment 3 without transverse groove (fig. 5)
. *Hoplitis (Alcidamea) hypocrita* (Cockerell)
- Vertex in lateral profile either bent (as in fig. 11) or bearing low protuberance (fig. 10); cephalic annulet of abdominal segment 3 with distinct, small to large transverse groove
. *Hoplitis (Alcidamea) producta* (Cresson)
. *Hoplitis (Alcidamea) sambuci* Titus
. *Hoplitis (Alcidamea) uvulalis* (Cockerell)
- 5(1). Postdefecating larva in lateral view with thickest part of body near midbody and posterior part of body gradually tapering (figs. 12–18, 21–23, 27); elevation of caudal annulets tending to persist posteriorly at least to abdominal segment 7; head size except for *Haetosmia vechti* (fig. 21) tending to be small to very small relative to body size (figs. 12–19, 22, 23) 6
- Postdefecating larva in lateral view with thickest part of body well posterior to midbody and posterior part of body ending more abruptly (figs. 20, 24–26, 28); elevation of caudal annulets tending to be lost beyond abdominal segment 5; head size tending to be moderate relative to body size (figs. 4, 20, 24–27) 10
- 6(5). Caudal annulets without midline dorsal tubercle, so that caudal annulet uniformly setose; head size relative to body size small (figs. 12–16, 18) to very small (figs. 17, 22, 23) 7
- Caudal annulets of abdominal segments 1–4 with elevated midline tubercles that lack setae (fig. 21, arrows); head size relative to body size moderate (fig. 21) *Haetosmia vechti* Peters
- 7 (6). Head size very small relative to body size (figs. 17, 22) 8
- Head size relative to body size larger (figs. 12–16, 18) than that of *Chelostoma*
. *Ashmeadiella* (all species treated herein except for *A. opuntiae*)
. *Ochreriades fasciatus* (Friese)
- 8(7). Antennal papilla longer, length about 3 times basal diameter
. *Ashmeadiella (A.) opuntiae* Cockerell
- Antennal papilla shorter, length about 2 times basal diameter 9
- 9(8). Spiracular atrium without spicules *Chelostoma (Gyrodromella) rapunculi* (Lepelletier)
- Spiracular atrium with spicules. *Chelostoma (Prochelostoma) philadelphia* (Robertson)
- 10(5). Abdominal segment 8 with lateral lobe bearing about 25 inconspicuous setae/spicules; body form of postdefecating larva robust (fig. 28) *Osmia (Hoplosmia) anceyi* (Pérez)
- Abdominal segment 8 with lateral lobe bearing 15 setae/spicules or fewer; body form variable 11
- 11(10). Body vestiture consisting of two lengths, i.e., longer, tapering setae and shorter setae/spicules of uncertain structure; head retracted into pronotum, so that only front visible in lateral view (fig. 20) *Atoposmia (Eremosmia) hypostomalis* (Michener)

- Body vestiture consisting of only setae; head normally exserted (figs. 4, 17) 11
- 11(10). Head of normal size (figs. 24, 25) compared to body; caudal annulets without bilobed median tubercle lacking setae (fig. 24); body setae pigmented, unusually bristlelike and stiff, stout basally, tapering evenly to fine, sharp apices; these setae arising from conspicuous alveoli *Heriades (Heriades) truncorum* (Linnaeus)
- Head size small (fig. 4) relative to body size; caudal annulets of abdominal segments 1–4 with posterior edge produced as low bilobed tubercle lacking setae (fig. 4); body setae normally slender, fine, inconspicuous, like those of other *Hoplitis*
- *Hoplitis (Proteriades) xerophila* (Cockerell)

DESCRIPTIONS OF OSMIINE LARVAE ARRANGED
ALPHABETICALLY BY GENERIC NAME

POSTDEFECATING LARVA OF *ASHMEADIELLA (ASHMEADIELLA) MELILOTI*
MELILOTI (COCKERELL)

Figure 12

DIAGNOSIS: As indicated by the key, above, treated larvae of *Ashmeadiella*, *Chelostoma*, and *Ochreriades* are so similar that they can scarcely be distinguished. Only those of *Chelostoma* because of their extremely small head are keyed separately. There exists some variation in the number of atrial spicules, width of the salivary lips, degree of expression of elevation of caudal annulets, and perhaps in body size. However, such features are difficult to quantify and therefore of little diagnostic value. Features shared by these three taxa include slender body form with thickest part of body being the midsection and with the body gradually, evenly narrowing at both ends. Furthermore, they display no middorsal intersegmental tubercles lacking vestiture. There is also a tendency for the caudal annulets to maintain their prominence with respect to the cephalic ones toward the posterior end of the body, contrary to many of the other osmiine taxa.

The following description of *A. m. meliloti* was originally based on the specimens from Bear Lake, Utah, collected and identified by Parker as *A. meliloti*?. Subsequently after examination of the Krombein material from Portal, Arizona, no features could be found to distinguish the specimens from the two localities.

DESCRIPTION: **Head:** Head moderately small in relation to body size (fig. 12); oriented in normal, hypognathous position relative to thorax. Labrum faintly pigmented except on some specimens transverse labral sclerite somewhat darker but unevenly so; maxillary sclerites faintly pigmented; salivary lips weakly to deeply pigmented; antennal papilla and maxillary and labial palpi all uniformly moderately pigmented to almost unpigmented. In lateral view, clypeus not projecting beyond frons, antenna not arising from prominence, and labrum not extending much beyond clypeus. Antennal papilla distinctly but not strongly pigmented, moderately large and elongate, longer than twice basal diameter, bearing approximately three sensilla apically. Labral sclerite unevenly pigmented.

Mandibular apex approximately parallel sided in outer views; both teeth on postdefecating larva narrowly acutely pointed with apices well separated; dorsal apical edge of dorsal tooth faintly, irregularly uneven; apical concavity defined; cuspal area not projecting; outer mandibular surface with single conspicuous long curved seta near base. Labial apex very narrow in frontal view; premental sclerite absent. Salivary lips very narrow, with inner surface questionably bearing parallel longitudinal grooves; width of lips slightly less than distance between bases of labial palpi.

Body (fig. 12): Body vestiture without spicules, consisting only of slender, pale, moderately elongate setae, tapering to fine points, arising from small but distinct alveoli; these setae inconspicuous; 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, 9, and 10; those below anus short and inconspicuous; dorsal surface elsewhere with scattered short inconspicuous setae; lateral lobe of abdominal segment 8 (i.e., area below level of spiracle) with approximately 8 setae. Body form of postdefecating larva moderate in lateral outline between robust and slender (fig. 12); body segments in lateral view gradually increasing in diameter with abdominal segments 3 to 5 having greatest diameters; caudal annulets of most body segments projecting farther than cephalic annulets and surprisingly uniform in appearance; mid-dorsal intersegmental tubercles totally absent. Body form of predefecating larva unknown. Spiracles with pigmented peritreme, subequal in diameter; atrium globular with width somewhat greater than depth, projecting above body wall, with rim; diameter of atrial opening about 3 times radial width of peritreme; atrial inner surface smooth or nearly so; primary tracheal opening with collar; subatrium long, with about 14–18 chambers; chambers increasing slightly in size from body surface inward.

MATERIAL EXAMINED: Four postdefecating larvae: Utah: Rich Co.: Bear Lake, 1973 (F.D. Parker) #7805. 6 postdefecating larvae:⁷ AZ: Cochise Co.: Portal VII-20-1959, V-19-1961, VI-10, 15, 19-1961 (K.V. Krombein).

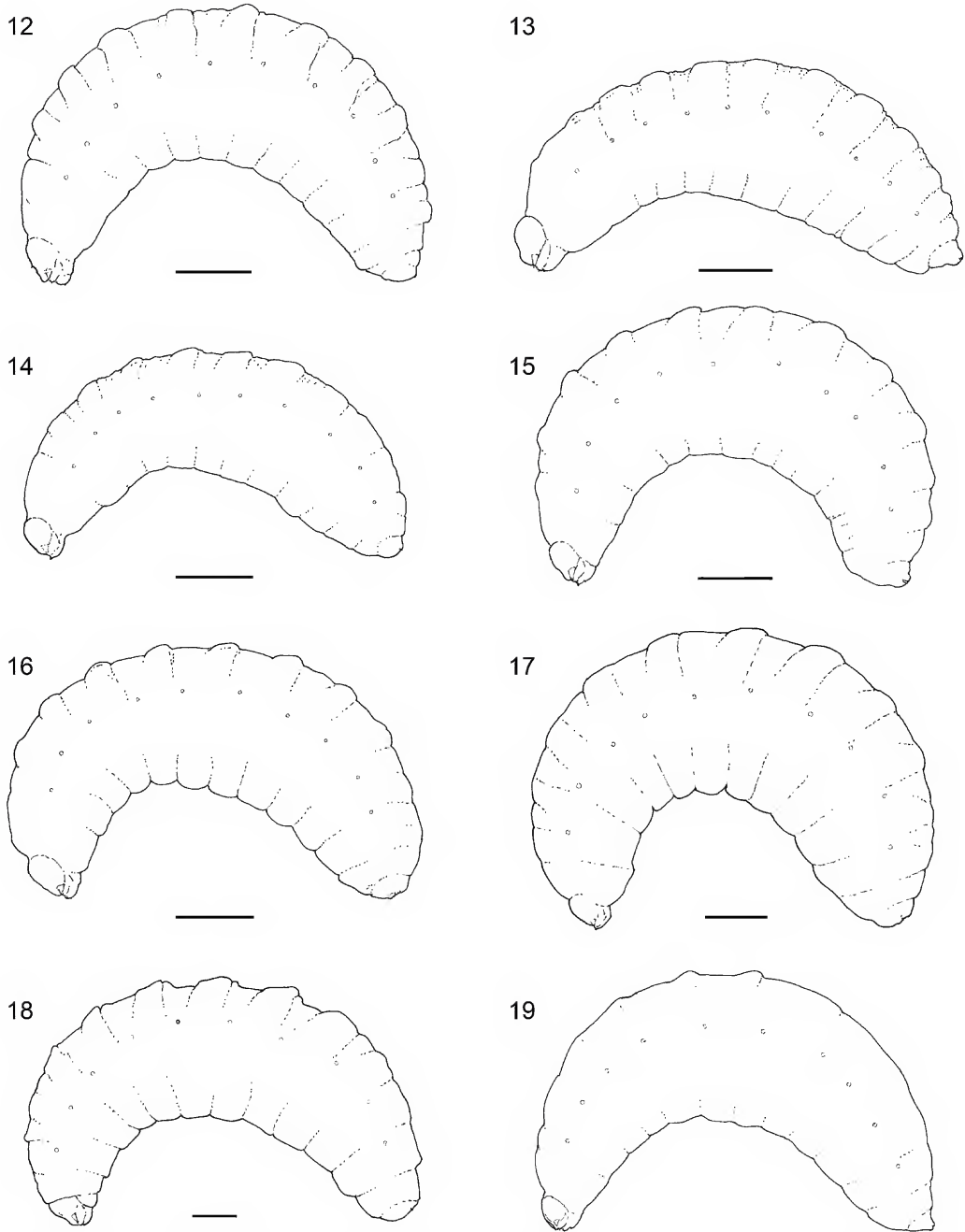
POSTDEFECATING LARVA OF *ASHMEADIELLA* (*ASHMEADIELLA*) *ARIDULA*
COCKERELL

Figure 13

The larva of this species is similar to that of *A. m. meliloti*, although the pigmentation is reduced and the body size is smaller. The peritreme is not or is only scarcely pigmented, and the atrial surface is more clearly ringed and with scattered small spicules that are less obvious than those of *A. breviceps*.

MATERIAL EXAMINED: Six postdefecating larvae: CA: Fresno Co.: 6 mi S Kerman, VIII-15-1962 (P. Torchio) #399. Nesting in 3/16" soda straw in competition with *Megachile rotundata*.

⁷ Krombein (1967) made no distinction between postdefecating larva, resting larva, and prepupa.



FIGURES 12–19. Entire larvae of *Ashmeadiella*, lateral view. 12. *A. m. meliloti*. 13. *A. (A.) aridula*. 14. *A. (A.) bigeloviae*. 15. *A. (A.) buconis denticulata*. 16. *A. (A.) c. cactorum*. 17. *A. (A.) opuntiae*. 18. *A. (A.) occipitalis* (postdefecating form). 19. *A. (A.) occipitalis* (defecating form).

POSTDEFECATING LARVA OF *ASHMEADIELLA* (*ASHMEADIELLA*) *BIGELOVIAE*
(COCKERELL)

Figure 14

The larva of this species can not be distinguished from that of *A. m. meliloti*. The two specimens examined were close to pupation, which apparently made spiracles impossible to identify; their position is approximated (fig. 14).

MATERIAL EXAMINED: One postdefecating larva (with pupal integument starting to form): AZ: Maricopa Co.: Scottsdale, V1-10-1961 (K. V. Krombein) resting, H 22, cell 1. 1 postdefecating larva (with pupal legs visible) AZ: Cochise Co.: Portal, V-19-1961 (K.V. Krombein) resting, G 25, cell 1.

PREDEFECATING LARVA OF *ASHMEADIELLA* (*ASHMEADIELLA*) *BUCCONIS*
DENTICULATA (CRESSON)

Figure 15

The single available specimen of this species had fecal material in its hind gut and also some apparently in the midintestine, indicating that it was preserved before it had reached the postdefecating stage. Unfortunately, the specimen tore apart while being cleared, so that placement of spiracles are approximate in figure 15, but other important features could be observed, none of which seemed to differ from those of postdefecating *A. m. meliloti*.

MATERIAL EXAMINED: One defecating larva: AZ: Cochise Co.; Portal, V1-10-1961 (K.V. Krombein) mature, C 15, cell 2.

POSTDEFECATING LARVA OF *A. M. MELILOTI*

Figure 16

Although somewhat smaller, the larva of this species appears similar to the of *A. m. meliloti*.

MATERIAL EXAMINED: One postdefecating larva: AZ: Maricopa Co.: Granite Reef Dam, I -9-1962 (K.V. Krombein) prepupa (stopper label: 1961 H 160, 3). 1 postdefecating larva: AZ: Cochise Co.: Portal, VII-20-1959 (K.V. Krombein) prepupa stopper label 1959 X 14 3).

POST- AND PREDEFECATING LARVAE OF *ASHMEADIELLA* (*ASHMEADIELLA*)
OCCIPITALIS MICHENER

Figures 18, 19

Although apparently with a larger body size, the larva of this species agrees closely with that of *A. m. meliloti* and shares with it the narrow salivary opening. However, the spiracles appear to have somewhat indistinct spicules. The difference between the two forms are illustrated (figs. 18, 19),

MATERIAL EXAMINED: One postdefecating larvae: AZ: Cochise Co.: Portal, VI-10-1961 (K.V. Krombein) G 48, cell 11. 1 defecating larva: same except VII-20-1959, X 58, cell 2-prepupa (Sic.!).

REMARKS: In 1959 Krombein collected a series of seven larvae of this species that he individually preserved in separate vials from Portal, AZ, each dated July 20 and identified as "prepupa." However, the specimen identified above as X 58 still had fecal material in its hind gut, an indication that it was still defecating when preserved, also as evidenced by its thinner integument. Other specimens of this series were clearly postdefecating, since pupal features were visible through larval integument of some specimens.

POSTDEFECATING LARVA OF *ASHMEADIELLA* (*ASHMEADIELLA*) *OPUNTIAE* (COCKRELL)

Figure 17

Postdefecating larvae of this species (fig. 17) have an unusually enlarged midbody compared with most other known larvae of this genus. As a result, the head size of the species appears very small compared to body size, forcing the species to key out separately from the other *Ashmeadiella*, above.

MATERIAL EXAMINED: One postdefecating larva: AZ: Cochise Co.: Portal, III-21-60 (K.V. Krombein) prepupa X 67, cell 5. 1 postdefecating larva: AZ: Cochise Co.: Portal, VII-20-59 (K.V. Krombein) prepupa X 67, cell 4.

POSTDEFECATING LARVA OF *ASHMEADIELLA* (*AROGCHILA*) *BREVICEPS* MICHENER

The smallest of the *Ashmeadiella* species examined here, the larva of *A. breviceps* has the mandibular teeth apically rounded, similar to those of *Ashmeadiella* sp. studied by Michener (1953: figs. 138, 139), not acute as in *A. m. meliloti* and other species in the subgenus *Ashmeadiella*. Further, the salivary lips and labial apex, though not broad, do not seem as narrowed as those of the subgenus *Ashmeadiella*. Atria often have several spicules. The posterior part of the lateral lobe of abdominal segment 8 has approximately four setae positioned in a roughly linear sequence.

MATERIAL EXAMINED: Two postdefecating larvae: CA: San Bernardino Co., Rice, 1973 (F.D. Parker) #7635.

POSTDEFECATING LARVA OF *ATOPOSMIA* (*EREMOSMIA*) *HYPOSTOMALIS* (MICHENER)

Figure 20

DIAGNOSIS: Because of the enlarged posterior part of the abdomen and loss of definition of cephalic and caudal annulations in general and particularly toward the posterior of the body, the larva of *Atoposmia hypostomalis* keys out with larvae of *Heriades truncorum*, *Osmia* (*Hoplosmia*) *anceyi*, and perhaps *Hoplitis xerophila*. No doubt *Atoposmia copelandica* would also be included in this group if it had not been excluded from the key because of its poorly preserved condition. The mature larvae of all of these species exhibit low, transverse, presumably eversible swellings middorsally between many of the more anterior abdominal segments, presumably homologous with the dorsal midline tubercles of other species.

DESCRIPTION: **Head:** Head size moderate in relation to body size (fig. 20), oriented in normal, hypognathous position relative to thorax: unlike most other osmiines except for *Osmia chalybea* and *Osmia* (*Hoplosmia*) *anceyi*, head deeply imbedded into prothorax, so that only front

of face exposed (fig. 20) (perhaps heads of *A. hypostomalis* and *H. anceyi*, fig. 28, more deeply retracted than that of *O. chalybea*, fig. 1). Labrum faintly pigmented; transverse labral sclerite reduced to small darkish sclerite at median apex of labrum; salivary lips slightly narrower than distance between labial palpi but broad because palpi widely separated; lips somewhat pigmented; antennal papilla, maxillary and labial palpi uniformly unpigmented. In lateral view, clypeus not projecting much beyond frons, antenna arising from faint prominence, and labrum not extending much beyond clypeus. Antennal papilla distinctly but not strongly pigmented, moderate in size, moderately pointed, as long as basal diameter, bearing perhaps three sensilla apically.

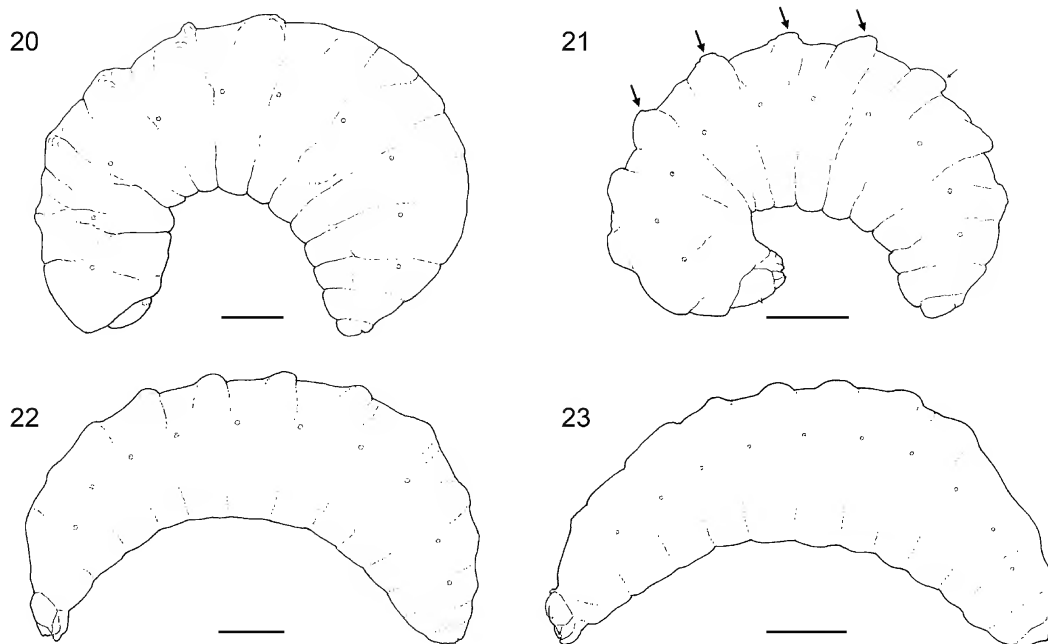
Mandibular apex somewhat spoon shaped in inner and outer views; both teeth broadly rounded apically; apical edge of both faintly, irregularly uneven; apical concavity defined; extent of development of cuspal area unknown; outer mandibular surface with single conspicuous long, curved seta arising from small tubercle near base. Maxillary and labial palpi faintly pigmented. Labial apex moderately narrow in frontal view; premental sclerite absent. Salivary lips with inner surface bearing parallel longitudinal grooves; width of lips distinctly slightly less than distance between bases of labial palpi.

Body: Body vestiture consisting of fine small setae tapering to slender points and shorter small, sharp-pointed spicules; this vestiture sparse and widely dispersed on dorsal surfaces, virtually absent on all ventral body surfaces; setae especially abundant on abdominal segment 10 clustered immediately below anus; lateral lobe of abdominal segment 8 (i.e., area below level of spiracle) with approximately eight setae intermixed with approximately five spicules, all small and obscure. Body form of postdefecating larva moderately robust (fig. 20); unlike in any other known osmiine taxon except for *Osmia chalybea* and *H. anceyi* prothorax of postdefecating form greatly swollen because of recessed head capsule (fig. 20); because predefecating form unavailable, its prothoracic shape unknown; body segments gradually increasing in height with abdominal segments 4 to 6 having greatest diameters; caudal annulets of most body segments projecting farther than cephalic annulets; middorsal intersegmental tubercles weakly represented as follows: mid-dorsal integument of posterior part of cephalic annulet slightly nodular; same area of abdominal segment slightly more distinctly so; exaggeration of this area on following segments decreasing. Spiracles unpigmented, subequal in diameter; atrium globular with width not much greater than depth, projecting slightly above body wall, with rim; diameter of atrial opening about 3× radial width of peritreme; atrial inner surface with distinct ridges wrinkles concentric with primary tracheal opening; some ridges bearing denticles; primary tracheal about same as other subatrial chambers; subatrium of normal length, about 10-15 chambers of approximately equal size.

MATERIAL STUDIED: One postdefecating larva: AZ: Mohave Co.: 3 mi S. Oatman, 1973 (F.D. Parker) #7842.

POSTDEFECATING LARVA OF *ATOPOSMIA* (*HEXOSMIA*) *COPELANDICA* (COCKERELL)

As indicated in the Diagnosis of *Atoposmia hypostomalis*, the larva of this species is not included in the key to osmiine larvae because the only available specimen was poorly preserved and did not reveal whether the postdefecating larva had a head retracted into the pronotum as seems characteristic of *A. hypostomalis* and several other taxa. In most respects that larva is like that of *A. hypostomalis*, but the two species can immediately be distinguished by the much larger setae of *A.*



FIGURES 20–23. Entire larvae, lateral view. **20.** *Atoposmia* (*Eremosmia*) *hypostomalis*. **21.** *Haetosmia* *vechti*. **22.** *Chelostoma* (*Gyrodromella*) *rapunculi*. **23.** *Chelostoma* (*Prochelostoma*) *philadelphia*.

copelandica. If its head does retract into the prothorax, it will key out to *A. hypostomalis* in the above key but could be easily recognized by the large setae arising from conspicuously large alveoli.

MATERIAL STUDIED: One postdefecating larva; Utah: Weber Co.: Willard Peak (F.D. Parker) #8325. No date.

POSTDEFECATING LARVA OF *CHELOSTOMA* (*GYRODROMELLA*) *RAPUNCULI*
(LEPELETIER)

Figure 22

DIAGNOSIS: Although the postdefecating larva of this species is fully described here, it is similar to the larvae of *Ashmeadiella m. meliloti*, *A. aridula*, *A. breviceps*, and the larva of *Ochreriades fasciatus* (fig. 27). The one distinctive feature is its unusually small head compared with body size (fig. 22). The spiracular atrial surface completely lacks spicules, a feature unlike that found in the related *C. philadelphia*.

DESCRIPTION: **Head:** Head distinctly small in relation to body size (fig. 22); oriented somewhat prognathously, possibly because of elongate postmentum resulting in projecting labium. Salivary lips deeply pigmented; maxillary and labial palpi moderately pigmented. In lateral view, clypeus scarcely projecting beyond frons, antenna arising from only slight prominence, and labrum not extending much beyond clypeus. Antennal papilla not pigmented, moderately large and perhaps slightly longer than twice basal diameter. Labral sclerite transverse, well defined by pigmentation.

Mandibular apex approximately parallel sided in inner and outer views; both teeth moderately short, curving gradually to broadly acute apices; dorsal apical edge of dorsal tooth faintly,

irregularly uneven; ventral apical edge of ventral tooth also faintly uneven; apical concavity defined; cuspal area not projecting; outer surface with single long curved seta near base. Maxillary and labial palpi pigmented, somewhat longer but slightly thinner than antennal papilla, which is not pigmented. Labial apex moderately narrow in frontal view; premental sclerite absent; postmentum extremely elongate, nonsclerotized. Salivary lips with inner surface bearing parallel longitudinal grooves; width of lips about same as distance between bases of labial palpi.

Body (fig. 22): Body vestiture without spicules, consisting only of slender, pale setae, tapering to fine points, arising from small but distinct alveoli; these setae inconspicuous, moderate in length; 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 segments 8, 9, and 10 and on ventral surface of abdominal segments 8–10; dorsal surface elsewhere with scattered short, inconspicuous setae; lateral lobe of abdominal segment 8 (i.e., area below level of spiracle) with approximately 6–7 setae. Body form of postdefecating larva moderate in lateral outline between robust and slender (fig. 22); body segments gradually increasing in height with abdominal segments 4 and 5 having greatest diameters; caudal annulets of most body segments projecting only faintly farther than cephalic annulets and surprisingly uniform in appearance; integument of caudal annulets faintly thicker (thus staining slightly more) than that of cephalic annulets, and with faint longitudinal ridging; middorsal intersegmental tubercles totally absent. Body form of predefecating larva unknown. Spiracles unpigmented, subequal in diameter; atrium globular with width not much greater than depth, projecting above body wall, with rim; atrium appear rather small compared with robust diameter of subatrium; atrial inner surface essentially smooth with only faint wrinkles concentric with primary tracheal opening, without spicules; subatrium long, gradually widening from body surface inward, with about 20 chambers.

MATERIAL STUDIED: Fourteen postdefecating larvae: Switzerland: Neuchâtel Botanical Garden, X-2-2014 (C. Praz).

PREDEFECATING LARVA OF *CHELOSTOMA* (*PROCHELOSTOMA*) *PHILADELPHI* (ROBERTSON)

Figure 23

The description of this larva was recently published by Rozen and Go (2015). Because a bee larva that was preserved while defecating is obviously mature, it can be considered comparable to a predefecating form (see Methods). The larva of *C. philadelphia* is similar to the postdefecating larva of *C. rapunculi*, but the presence of spicules on the atrial wall of *C. philadelphia* contrasts with their complete absence on the atrial wall of *C. rapunculi*.

POSTDEFECATING LARVA OF *HAETOSMIA* *VECHTI* PETERS

Figure 21 (from Gotlieb et al., 2014)

The postdefecating larva of this species was recently described and illustrated by J.G.R. in Gotlieb et al. (2014).⁸ In body form, *Haetosmia*, as represented by *H. vechti*, seems to stand

⁸ Reexamination of the single postdefecating larva of *Haetosmia vechti* revealed that bimodal middorsal tubercles occurred on the posterior edge of the caudal annulet of abdominal segments 1–5 (fig. 21, arrows). Tubercle of segment 5 may be somewhat smaller than the others.

apart from other osmiines. Its very robust body contrasts with the somewhat more slender forms of *Ashmeadiella*, *Chelostoma*, and *Ochreriades* treated here, although all taper posteriorly toward the rear. Additionally, its body form is very different from that of most *Hoplitis* since the intersegmental constrictions are far shallower than those of *Hoplitis* and its body is not elongate. The well-differentiated caudal annulets (fig. 21, arrows) toward the posterior end of its body are unique among the taxa treated in this paper.

POST- AND PREDEFECATING LARVAE OF *HERIADES* (*HERIADES*) *TRUNCORUM*
(LINNAEUS)

Figures 24, 25

DIAGNOSIS: Please see diagnosis of *Atoposmia hypostomalis*, above. The main larval features of *Heriades truncorum* seem to be shared by the larva of *Heriades* (*Heriades*) *crenulatus* Nylander, according to Grandi (1961).

Description of pigmentation, below, refers only to the postdefecating larva. Pigmentation is much reduced in the predefecating form, in that only mandibular apices are conspicuously pigmented. The single predefecating specimen still contained pollen in its mid- and hind intestine.

DESCRIPTION: Head: Head moderately small in relation to body size (figs. 24, 25); oriented in normal, hypognathous position relative to thorax. Labrum deeply emarginated apically, with narrow, transverse labral sclerite moderately pigmented and defined; maxillary sclerites faintly pigmented; salivary lips somewhat pigmented; antennal papilla scarcely pigmented; maxillary and labial palpi all lightly pigmented. In lateral view, clypeus projecting only slightly beyond frons, antenna arising from faint prominence, and labrum not extending much beyond clypeus. Antennal papilla scarcely pigmented, moderately tapering apically, large, and elongate; length about twice basal diameter, 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.

Mandibular apex approximately parallel sided in inner and outer views, apically bidentate, with ventral tooth longer; both teeth on postdefecating larva pointed apically; dorsal tooth shorter, in postdefecating larva more rounded, ventral tooth distinctly more elongate and narrowly acute, margins of teeth quite linear; apical concavity well defined, scoop shaped; cuspal area not projecting; outer mandibular surface right mandible with single conspicuous, long, curved seta near base; left mandible of only postdefecating form with two such setae. Maxillary and labial palpi lightly pigmented. Labial apex moderately narrow in frontal view; premental sclerite absent. Salivary lips with inner surface bearing parallel longitudinal grooves; width of lips about equal to distance between bases of labial palpi.

Body (figs. 24, 25): Body vestiture without spicules, consisting only of well-developed, basally stiff, evenly tapering setae, arising from conspicuous alveoli; these setae conspicuous when viewed on cleared specimens with compound microscope; setae tending to be arranged in more or less transverse fascialike arrangement that extends around posterior part of most segments and, though reduced in numbers on ventral areas, setae present on all surfaces of abdominal segments 8, 9, and 10; lateral lobe of abdominal segment 8 (i.e., area below level of spiracle) with approximately 14 setae, but these arising along posterior boundary of lobe and as part of fascia that

extends around entire segment. Body form of postdefecating larva moderately robust in lateral outline (fig. 24; body segments gradually increasing in diameter in lateral view with abdominal segments 4 to 6 having greatest diameters; caudal annulets of most body segments projecting slightly farther than cephalic annulets, but intrasegmental lines weakly expressed; middorsal tubercles absent. Body form of predefecating larva (fig. 25) more elongate with head exerted and caudal annulets even less conspicuous. Spiracles unpigmented, externally small, subequal in diameter; atrium globular with diameter considerably greater than depth, projecting above body wall, with rim; diameter of atrial opening about three times radial width of peritreme; atrial inner surface with ridges concentric with primary tracheal opening; ridges bearing conspicuously large concentrically directed spicules; primary tracheal opening with collar; subatrium long, with about 20–25 or more chambers with most inward chambers tending to be slightly larger than others.

MATERIAL STUDIED: Nine postdefecating, 1 predefecating larvae: Switzerland: Neuchâtel, X-1-2014 (C. Praz, J.G. Rozen) from nests #1, 2, 4, and 6.

PREDEFECATING LARVA OF *HERIADES (NEOTRYPETES) CARINATA* CRESSON

Figure 26

The larva and biology of *Heriades carinata* were treated in depth by Matthews (1965).

MATERIAL STUDIED: One defecating larva: NY: Erie Co.: Derby, VIII-21-1961 (K.V. Krombein) mature, L 41, cell 5.

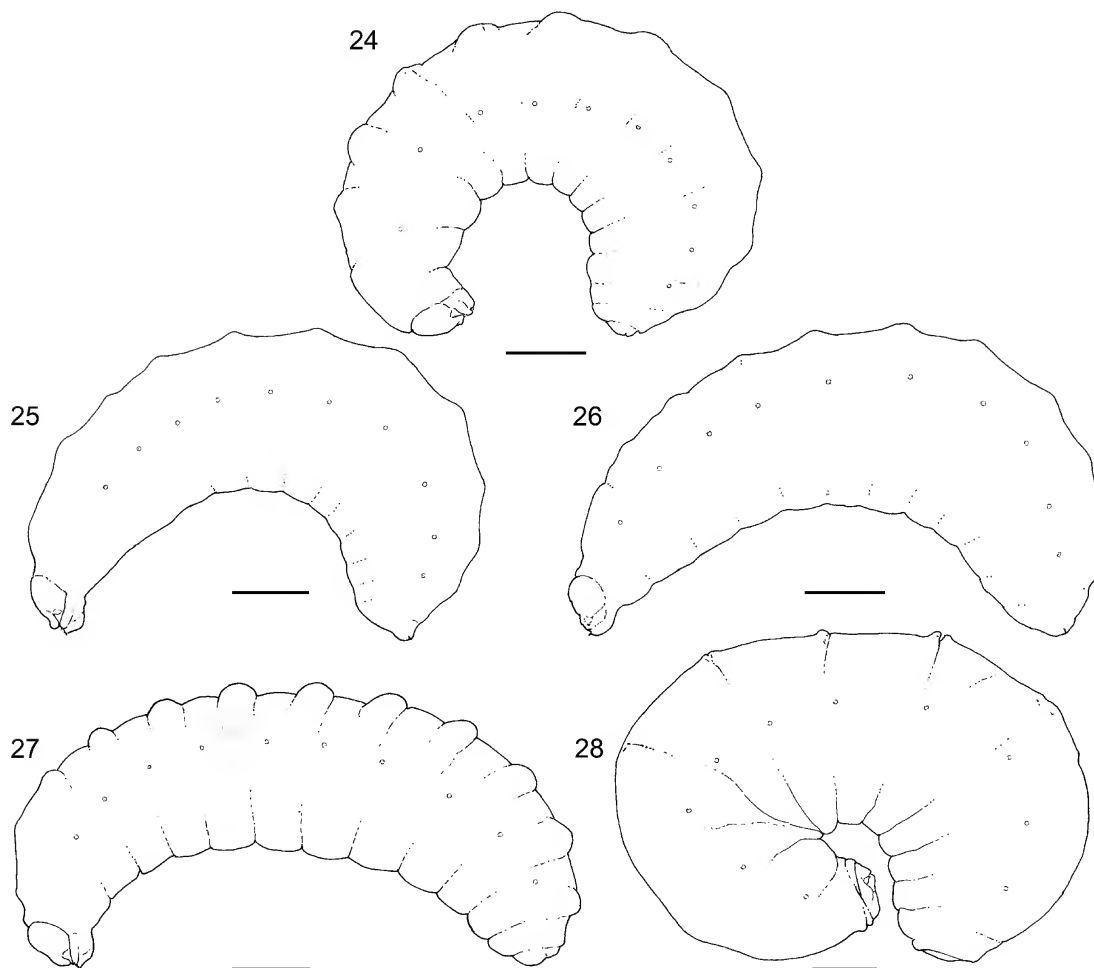
POSTDEFECATING LARVA OF *HOPLITIS (ALCIDAMEA) HYPOCRITA*
(COCKERELL)

Figures 3, 5, 9, 30, 33

Because the quality of preservation and the relatively large body size, specimens of *Hoplitis hypocrita* were selected to provide the baseline account of the larval anatomy of the genus, against which other species are compared.

DIAGNOSIS: The first couplet of the key, above, separates all *Hoplitis* taxa except one (*H. (Proteriades) xerophila*) from other osmiines described here, as follows: The larvae of these *Hoplitis* have intersegmental lines deeply incised, so that the caudal annulets of the anterior abdominal segments tend to override the anterior part of the following cephalic annulets (fig. 3). Also, the body integument of the postdefecating larva is relatively stiff, so that body shape is retained even after clearing. Further, the body form is elongate, especially in lateral view (fig. 3). With the exception of *H. (Proteriades) xerophila*, separate diagnoses of other *Hoplitis* species presented below are omitted since their descriptions are reduced to serve the same function.

Hoplitis is a large genus consisting of 27 subgenera (Michener, 2007). For the current study larval representatives of only two subgenera were available for study, and the larva of only one other (*Hoplitina*) has been described, by Thorp (1968).



FIGURES 24–28. Entire larvae, lateral view. **24.** *Heriades (Heriades) trunchorum* (postdefecating form) . **25.** *Heriades (Heriades) trunchorum* (predefecating form). **26.** *Heriades (Neotrypetes) carinata*. **27.** *Ochreriades fasciatus*. **28.** *Osmia (Hoplosmia) anceyi*.

DESCRIPTION: Head: Head moderately small in relation to body size (fig. 3), oriented in normal, hypognathous position relative to thorax. In addition to usually pigmented areas on mouthparts and head capsule, following also pigmented: both hypopharyngeal mounds, salivary lips, palpi, apex of labium; following areas moderately pigmented: transverse labral sclerite, front and dorsal surface of labium (including dorsal bridge of prementum) to hypostomal mounds, articulate arms of stipes, cardo, and stipital rod. Coronal ridge faintly present, but integument of capsule moderately well sclerotized. In lateral view, clypeus projecting strongly beyond frons, antenna not arising from prominence, and labrum not extending much beyond clypeus. Vertex without low mound as seen in lateral profile. Antennal papilla strongly pigmented, moderately small, with length slightly greater than basal diameter. Labral sclerite well defined because of pigmentation.

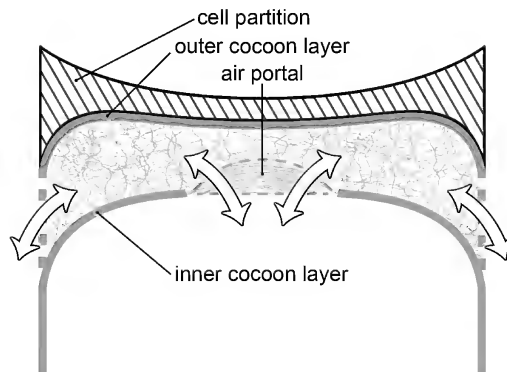
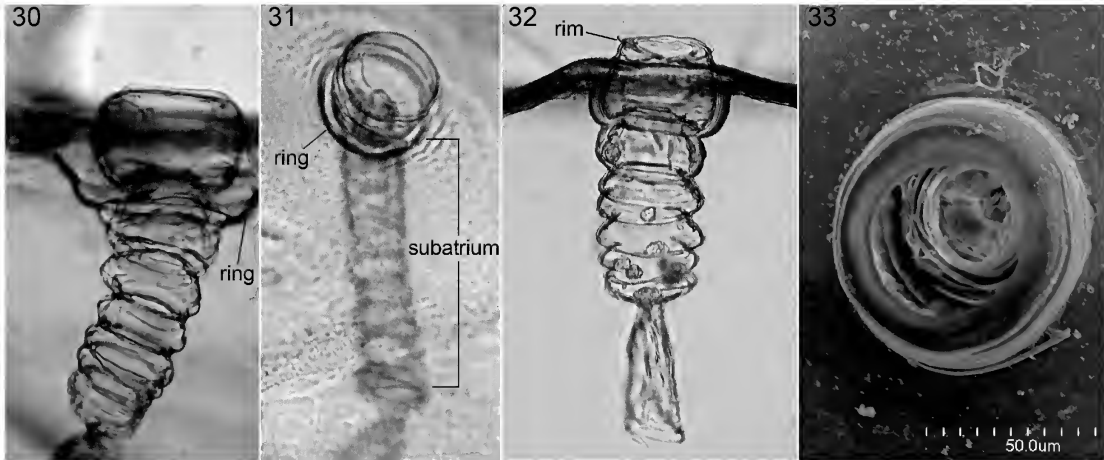


FIGURE 29. Generalized diagram of front end of osmine cocoon showing paths (arrows) of air diffusion. In this diagram position of feces not demonstrated, but: if *Hoplitis hypostomalis*, fecal pellets mostly exterior to outer surface of cocoon front (fig. 58); if *Pseudoheriades grandiceps*, fecal pellets mostly between anterior and inner cocoon layers at front (fig. 68); if *Chelostoma*, feces incorporated in cocoon fabric (figs. 45, 52); if *Ochreariades fasciatus*, feces between front end of cocoon and front cell partition and in cocoon fabric at rear of cocoon (Rozen et al., 2015: figs. 14, 15); if *Haetosmia vechti*, feces appressed to entire cell wall except for cell closure before cocoon spinning (Gotlieb et al., 2014: fig. 16); if *Heriades truncorum*, perhaps mostly outside of cocoon fabric (fig. 55). In the cocoon of *Haetosmia vechti* the front end consists only of a single silk layer with fenestrations more or less centrally located where silk contacts the rough inner surface of the cell closure (new information!), although most of the cocoon's front end is removed from this surface (Gotlieb et al., 2014).

Mandibular apex nearly parallel sided in inner and outer views but slightly flared beyond start of apex; both teeth with apices slightly acute; outer edges of both teeth microscopically uneven in outer or inner view; apical concavity defined; cuspal area not projecting, outer surface with two conspicuous long curved seta near base. Stipital apex pigmented light brownish like labial apex; maxillary and labial palpi pigmented like antennal papilla but distinctly larger and longer than papilla. Labial apex moderately narrow in frontal view; defined premental sclerite not present, but integument stiff allowing articulation with postmental cuticle posteriorly (see Special Anatomical Features, above) (also, definition of sclerite uncertain because brownish pigmentation of labium not defined by limits of sclerites.⁹ Salivary lips with inner surface bearing parallel longitudinal grooves; width of lips slightly less than distance between bases of labial palpi.

Body (figs. 3, 5, 30, 33): Body integument unusually thick, so that integument of postdefecating larva maintains its shape even after clearing. Body vestiture consisting of numerous slender, pale, tapering moderately long to long setae and of numerous moderately short, often sharply pointed, pigmented spicules; setae moderately abundant on elevated dorsal surfaces of thorax and widely scattered on anterior ventral surface of thorax; vestiture widely distributed on many parts of body but patterned (i.e., some areas with long setae but few spicules, other areas without setae but with spicules); lateral lobe of abdominal segment 8 (i.e., swollen area below level of spiracle) with 50 or more moder-

⁹ This brownish coloration observed in the postdefecating larva of this species and several other species of *Hoplitis* is not fully understood. It may result from a thickening of the cuticle of postdefecating forms, and therefore it may be a phenomenon that can be resolved through examining predefecating last larval instars. This matter deserves further investigation.



FIGURES 30–32. Microphotographs of spiracles of postdefecating larvae that have been cleared. **30.** *Hoplitis hypocrita*, side view. **31.** *H. sambuci*, oblique view, showing ring and long subatrium. **32.** *H. biscutellae*, side view, showing lipped rim and short subatrium. **FIGURE 33.** SEM micrograph of spiracle of *Hoplitis hypocrita*, showing projecting atrium lacking lipped rim.

ate to long, tapering setae and with many short, pigmented spicules. Body form of postdefecating larva elongate, tending to be parallel sided, but not particularly slender; caudal annulets of most body segments projecting considerably farther than cephalic annulets; hence, most intersegmental lines strongly expressed; cephalic annulets of abdominal segments lacking transverse groove near anterior margin; middorsal tubercles present on many body segments; these tubercles ending in single lobe with smooth, nonsetose apex; tubercles restricted to posterior margin of caudal annulets of following; metathorax (tubercle on some specimens more pronounced than on others), abdominal segment 1 (tubercle erect, strongly expressed), abdominal segments 2–6 (tubercles directed more posteriorly, decreasing in size, and pointing more posteriorly farther to rear until absent from abdominal segments 7–10). Abdominal segment 10 with projecting unpigmented ridge ringing anus except for ventral one-quarter.¹⁰ Spiracles (figs 30, 33) pigmented, subequal in diameter; internal shape of atrium globular with internal width about 1.5 times internal depth; atrial wall with concentric ridges with intermediate swellings but lacking spicules; atrium projecting well beyond body wall; exterior opening of atrium not surrounded by flat peritreme with a rim defining its circumference; exterior part of atrial wall curving inward before reaching external spiracular opening (fig. 30); inward of body wall, atrial wall formed by circular, ringlike ingrowth of thick cuticle of body wall; subatrium short, with about eight chambers decreasing in diameter before attaching to trachea.

DISCUSSION: The dark pigmentation and relatively large size of the larva of *H. hypocrita* has permitted it to be studied and pictured in some detail. The spiracle of this species as described here seems unusual compared with those of most bees. First, it appears to lack a peritreme (fig. 30), because the outer wall of the atrium that extends beyond the body wall curves as it gradually extends toward the external atrial opening. However, it merely lacks a rim around its outer circumference. Second, the integument, at least of the postdefecating larva

¹⁰ The partial ring that surrounds the anus on abdominal segment 10 readily stains when subjected to treatment with Chlorazol Black E.

of this species, is extremely thick. This integument underlies and forms the inner wall of the atrium. On a cleared specimen this extra thickness provides a large ring around the atrium as seen from the outside (fig. 30). Lastly, the subatrium is relatively short.

These features vary considerably among the other species of *Hoplitis* described here, although this has not been fully documented for some of the other species due to lack of sufficient material. The integument of *H. hypocrita* is perhaps the thickest and the internal ring around the base of the atrium is perhaps the most exaggerated (fig. 30) although it is also quite apparent in *H. sambuci* (fig. 31). While the peritreme appears totally lacking in *H. hypocrita*, it is clearly present in *H. biscutellae* (fig. 32), in which it has a distinct circular rim and overhanging lip. The shortness of the subatrium of *H. biscutellae* surpasses that of *H. hypocrita*, and the longest subatrium appears in *H. sambuci* (fig. 31).

MATERIAL STUDIED: Ten postdefecating larvae: Utah: Cache Co.: U.S.D.A. greenhouse. Nesting in elderberry and wild carrot (P.F. Torchio) #729. 3 larvae: Utah: Rich Co.: Bear Lake, 1973 (F.D. Parker) #7788.

POSTDEFECATING LARVA OF *HOPLITIS (ALCIDAMEA) BISCUTELLAE*
(COCKERELL)

Figures 8, 11, 32

DESCRIPTION: **Head:** As described for *Hoplitis hypocrita* except for following: In addition to usual pigmented areas on mouthparts and head capsule, following also lightly pigmented: both hypopharyngeal mounds, salivary lips, palpi, apex of labium; following areas moderately pigmented: transverse labral sclerite, front and dorsal surface of labium (including dorsal bridge of prementum) to hypostomal mounds, articulate arms of stipes, cardo, and stipital rod. In lateral view, clypeus projecting beyond frons, antennal prominence strongly projecting, and labrum projecting beyond clypeus. Unlike in *H. hypocrita*, vertex with low but distinct mound near midline as seen in profile (fig. 11). Antennal papilla well pigmented, large, conical in shape. Labral sclerite faintly pigmented like labral apex.

Mandible as described for *H. hypocrita* except apical teeth more sharply acute and with dorsal tooth distinctly smaller than ventral tooth. Stipital apex pigmented light brownish like labial apex; maxillary and labial palpi pigmented like antennal papilla but smaller and more parallel sided than large conical papilla. Other mouthparts as described for *H. hypocrita* except salivary lips as broad as distance between centers of bases of labial palpi.

Body (fig. 8): Body integument and vestiture as described for *H. hypocrita*, except spicules ending sharply; lateral lobe of abdominal segment 8 (i.e., swollen area below level of spiracle) with 60 or more setae and spicules combined. Unlike that of *H. hypocrita*, body form of postdefecating larva more robust, with thickest part of body centered at abdominal segment 5 in lateral view; caudal annulets of most body segments projecting somewhat farther than cephalic annulets; as demonstrated in figure 8, posterior edge of caudal annulet terminating shortly before reaching midline, and at midline intersegmental membrane, forming large, posteriorly directed tubercle because of transverse groove of following cephalic annulet; these conspicuous tubercles extending along midline posterior margins of abdominal segments 1-6. As in *H.*

hypocrita, abdominal segment with projecting unpigmented ridge ringing anus except for ventral one-quarter. Spiracles faintly pigmented, subequal in diameter; internal shape of atrium globular with width not much greater than depth; atrial wall without rings or spicules; peritreme with rim (fig. 32); primary tracheal opening with collar; subatrium short, with about five chambers tending to decrease in diameter before attaching to trachea.

MATERIAL STUDIED: Fourteen larvae: CA: San Bernardino Co.: Rice, 1973 (F.D. Parker) #7620, #7621.

POSTDEFECATING LARVA OF *HOPLITIS* (*ALCIDAMEA*) *FULGIDA* (CRESSON)

DESCRIPTION: As described for *Hoplitis hypocrita* except for following: **Head:** Unlike in *H. hypocrita* both hypopharyngeal mounds scarcely pigmented. Coronal ridge not evident. In lateral view, clypeus projecting weakly beyond frons, antennal prominence low, and labrum extending slightly beyond clypeus. Antennal papilla moderately pigmented, moderate in size, with length distinctly greater than basal diameter.

Mouthparts as described for *H. hypocrita*, except both postmentum and prementum somewhat more extensively sclerotized.

Body: Body integument sufficiently thick so that integument of postdefecating larva maintains shape after clearing. Body vestiture about as described for *H. hypocrita* but finer and sparser and lacking pigmented spicules. Body form as described for *H. hypocrita* (including absence of transverse groove near anterior margin) except for following; middorsal tubercles bilobed with smooth, nonsetose apex; metathorax without tubercle; abdominal segment 1–4 with bilobed tubercle low, faintly sclerotized when viewed on stained specimen; tubercles absent from abdominal segments 5–10. Abdominal segments as described for *H. hypocrita*. Spiracles faintly pigmented, subequal in diameter; atrium quite small when compared with width of subatrium, internal shape of atrium globular with width not much greater than depth; atrial wall with faint concentric rings, which give rise to rows of concentrically directed spicules; primary tracheal opening with collar; subatrium with perhaps 16–20 chambers, most of equal diameter except for innermost 3–4, which decrease in size.

MATERIAL STUDIED: Utah: Weber Co.: 20+ postdefecating larvae: Utah: Weber Co.: Willard Peak, 1973 (F.D. Parker) #8311, #8314, #8304, #8303, #8300, and #8354.

POSTDEFECATING LARVA OF *HOPLITIS* (*ALCIDAMEA*) *PRODUCTA* (CRESSON)

Figure 10

As indicated by the key, differences between the known larvae of the subgenus *Alcidamea* are slight, and they cannot be easily differentiated.

DESCRIPTION: **Head:** As described for *Hoplitis hypocrita* except for following: In addition to usually pigmented areas on mouthparts and head capsule, following only lightly pigmented: both hypopharyngeal mounds, salivary lips, palpi, apex of labium; following areas moderately pigmented: labrum, maxillary apex, front and dorsal surface of labium (including dorsal bridge of prementum) to hypostomal mounds, articulate arms of stipes, cardo, and stipital rod. Coronal

ridge evident for less than half distance to level of antennae. In lateral view, clypeus projecting little beyond frons, antenna extending about as far as clypeus, and labrum extending little beyond clypeus. Antennal papilla weakly pigmented. Labral sclerite not well defined by pigmentation.

Mandible as described for *H. hypocrita* except mandibles with single basal seta on single specimen cleared. Other mouthparts as described for *H. hypocrita*.

Body: Body as described for *H. hypocrita* except lateral lobe of abdominal segment 8 (i.e., swollen area below level of spiracle) with less than 50 setae and spicules combined. Transverse groove of abdominal segment 3 shallower than that of *H. uvulalis* (fig. 7) and *H. sambuci* (fig. 6); low middorsal bilobed tubercles present on abdominal segments 1–5; these tubercles with smooth, nonsetose apices restricted to posterior margin of caudal annulets. Spiracles similar to those described for *H. hypocrita* but differing as follows: atrial wall tending to exhibit faint concentric rings with several small spicules; interior to body wall, atrial wall thicken less than that of *H. hypocrita*; primary tracheal opening with collar; subatrium moderately long, with about 15 chambers with about 10 outermost chambers of uniform diameter and seemingly covered and fused together by cuticular sleeve; innermost chambers with slightly increased diameter and freely articulating with one another.

MATERIAL STUDIED: Two postdefecating larvae: Utah: Rich Co.: Bear Lake, 1973 (F.D. Parker) #7782.

POSTDEFECATING LARVA OF *HOPLITIS (ALCIDAMEA) BISCUTELLAE*
(COCKERELL)

Figures 8, 32

DESCRIPTION: Head: As described for *Hoplitis hypocrita* except for following: In lateral view, clypeus projecting somewhat beyond frons, antennal prominence moderately projecting, and labrum not extending much beyond clypeus. Unlike in *H. hypocrita* vertex with low but distinct mound near midline as seen in profile (as in fig. 11). Antennal papilla somewhat pigmented, small, with length slightly greater than basal diameter.

Mandible and other mouthparts as described for *H. hypocrita*.

Body (fig. 8): Body as described for *H. hypocrita* except for following: Cephalic annulets of abdominal segments 1–6 with pronounced transverse groove near anterior margin; on abdominal segment 3, this groove more pronounced than that of *H. uvulalis* (fig. 8); middorsal bilobed tubercles present on abdominal segments 1–5; these tubercles with smooth, nonsetose apex restricted to posterior margin of caudal annulets, visible from above as faintly dye-stained, paired sclerotizations; these sclerotizations absent posterior to abdominal segment 5. Spiracle pigmented, similar to that of *H. hypocrita* in that atrial wall extending well beyond body wall and with concentric patterning but lacking distinct spicules; inward from body wall, atrial wall and collar of primary tracheal opening somewhat thickened; subatrium very long, in some cases with more than 20 chambers, increasing in diameter before attaching to trachea.

MATERIAL STUDIED: Seven postdefecating larvae: Utah: Rich Co.; Bear Lake, 1973 (F.D. Parker) #7792.

POSTDEFECATING LARVA OF *HOPLITIS (ALCIDAMEA) UVULALIS* (COCKERELL)

Figure 7

DESCRIPTION: Head: As described for *Hoplitis hypocrita* except for following: Pigmentation of mouthparts less than in *H. hypocrita*, but mandibular apices, hypopharyngeal mounds, labral sclerite and lower margin, maxillary sclerites including articulating arms of stipes, and dorsal bridge of prementum distinctly pigmented. Coronal ridge evident only close to postoccipital ridge. In lateral view, clypeus projecting somewhat beyond frons, antennal prominence low but evident, and labrum not extending much beyond clypeus. Unlike in *H. hypocrita* vertex with low but distinct mound near midline as seen in profile (as in fig. 10), but mound not as distinct as that of *H. biscutellae* (fig. 11) or *H. sambuci*. Antennal papilla faintly pigmented, small, with length slightly greater than basal diameter.

Mandibular apex as described for *H. hypocrita* except outer surface with single seta at base. Other mouthparts as described for *H. hypocrita*.

Body (fig. 8): As described for *H. hypocrita* except for following; Body vestiture similar to but not as dense as that of *H. hypocrita*; lateral lobe of abdominal segment 8 (i.e., swollen area below level of spiracle) with about 28 tapering setae and shorter, sharp-pointed pigmented spicules combined. Body form of postdefecating larva elongate, tending to be parallel sided, but not particularly slender; caudal annulets of most body segments projecting considerably farther than cephalic annulets; hence, most intersegmental lines strongly expressed; cephalic annulets of most abdominal segments with transverse groove near anterior margin; middorsal bilobed tubercles present on abdominal segments 1–5; these tubercles with smooth, nonsetose apex restricted to posterior margin of caudal annulets; metathorax indistinctly, faintly bilobed. Spiracles weakly pigmented; atrial wall without patterning except for few small irregularities; atrium strongly projecting beyond body wall; atrial rim distinct because of flared rim; atrial wall beyond body wall normally thin; inward of body wall, atrial wall and collar of primary tracheal opening only slightly thicker; subatrium moderately long with about 12 chambers steadily increasing in diameter until attaching to trachea.

MATERIAL STUDIED: Thirteen postdefecating larvae: Utah: Weber Co.: Willard Peak, 1973 (F.D. Parker) #8296, #8297, and #8328. 9 postdefecating larvae: Utah: Weber Co.: Willard Peak, 1973 (F.D. Parker) #8298, #8312.

POSTDEFECATING LARVA OF *HOPLITIS (PROTERIADES) XEROPHILA*
(COCKERELL)

Figure 4

DIAGNOSIS: As indicated in the above key, the mature larva of this subgenus, as represented by *Hoplitis (Proteriades) xerophila*, is quite different from species in other subgenera within *Hoplitis*. Its body form in some ways seems to more closely resemble that of *Atoposmia*, *Heriades*, and *Osmia (Hoplosmia)* in that it is more robust and the deeply incised intersegmental lines of other *Hoplitis* are lacking. On the other hand, the swelling of the rear part of the body, characteristic of these three other genera, is not pronounced. Thus, the grouping of this species

with these three other genera is uncertain. However, it is markedly different from the larvae of the subgenus *Alcidamea* treated here and strongly suggests the need for examining larvae of additional taxa.

The mature larva of this species was first described by Michener (1953). Specimens he examined were from the collection of U.C. Berkeley. The following account is based in part on the same material.

DESCRIPTION: Head: Head as described for *Hoplitis hypocrita* except for following: Pigmentation less extensive, though mandibular apices and salivary lips dark. In lateral view, clypeus projecting little beyond frons, antennal prominence moderately developed, and labrum not extending much beyond clypeus. Antennal papilla well pigmented, moderately large, distinctly conical, and unlike in other *Hoplitis* treated here, arising from swollen basal ring of antenna, making antenna conspicuous. Labral sclerite narrow but well defined because of pigmentation.

Mandible as described for *H. hypocrita*, except for outer surface with single conspicuous long curved seta near base. Other mouthparts as described for *H. hypocrita* except for reduced pigmentation.

Body (fig. 4): Unlike in *H. hypocrita*, body integument of normal thinness and not unusually stiff. Body vestiture seeming to consist only of inconspicuous fine setae¹¹ mostly on dorsal and lateral surfaces; lateral lobe of abdominal segment 8 (i.e., swollen area below level of spiracle) with fewer than 15 setae. Unlike that of other larval *Hoplitis* treated here, body form robust, with widest part of body in lateral view posterior to midbody (i.e., abdominal segments 4–5); intersegmental lines weakly incised; annulets of posterior part of abdomen weakly defined; cephalic annulets of abdominal segments tending to have only shallow depression (fig. 4, arrow) near anterior margin; small middorsal tubercles present on some anterior abdominal segments; these tubercles questionable (because of small size and poor preservation) bilobed with smooth, nonsetose apex; tubercles restricted to posterior margin of caudal annulets of abdominal segment 1–4 with faint indication on segment 5. Spiracles as described for *H. hypocrita* except atrial wall with concentrically directed spicules; atrial wall beyond body wall normally thin; inward of body wall, atrial wall and collar of primary tracheal somewhat thicker; diameter of atrial opening about two times radial width of peritreme; subatrium moderately short, with about 10 chambers of approximately equal diameter.

MATERIAL STUDIED: Five postdefecating larvae: CA: San Bernardino Co.: 18 mi W. Blythe, 1973 (F.D. Parker) #9356. Eight postdefecating larvae: CA: Inyo Co.: Little Lake, II-29-1940 (Linsley, Bohart, MacSwain).

MATURE LARVAE OF *OCHRERIADES FASCIATUS* (FRIESE)

Figure 27

The pre- and postdefecating larva of this species was recently described in a paper that also treated its nesting biology (Rozen et al., 2015). As pointed out under *Ashmeadiella m. meliloti*, above, the larva is nearly identical to those of *Ashmeadiella* and *Chelostoma rapunculi* treated herein.

¹¹ A few projections each of which lacks a long, slender terminal filament are provisionally interpreted to be setae in which the filaments were accidentally removed in handling.

POSTDEFECATING LARVA OF *OSMIA* (*HOPLOSMIA*) *ANCEYI* (PÉREZ)⁴

Figure 28

The larva of this species was originally described by Torres et al. (1997), who kindly donated the specimens to the American Museum of Natural History.

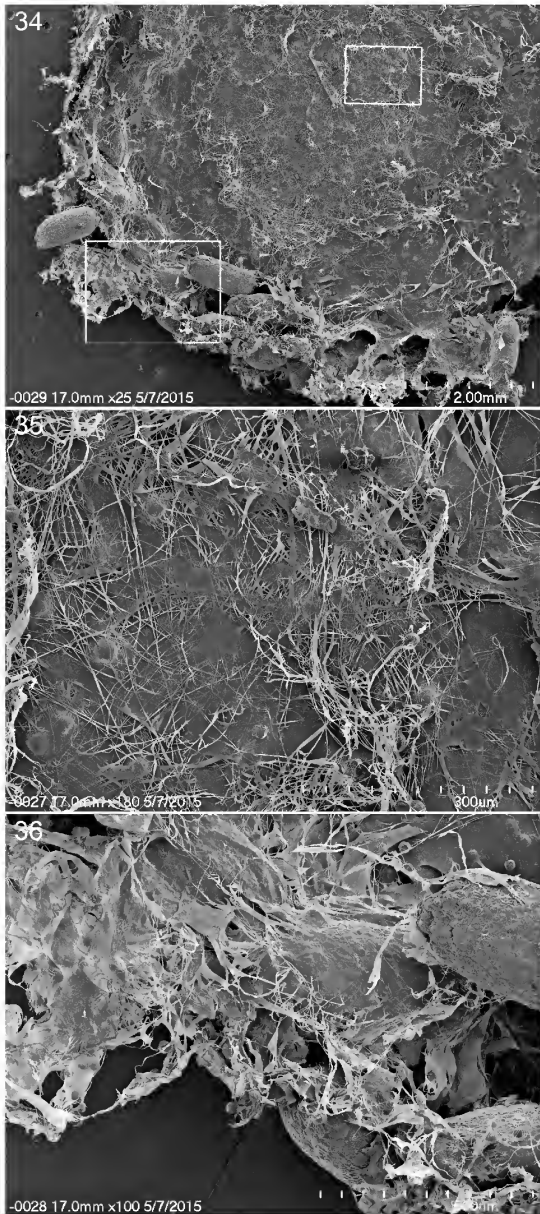
DIAGNOSIS: Please see larval diagnosis of *Atoposmia hypostomalis*.

DESCRIPTION: **Head:** Head moderate in size in relation to body size (fig. 28); oriented in normal, hypognathous position relative to thorax, and as in *Atoposmia hypostomalis* and *Osmia chalybea*, head of postdefecating larva partly retracted into pronotum (fig. 28). Setae moderately long but scarce to nonexistent on upper part of head capsule, although those of maxillary and labial apices large, curved, moderately abundant, and conspicuous. Labrum faintly pigmented except transverse labral sclerite slightly more so; bridge of prementum and premental sclerite including salivary lips pigmented; antennal papilla, maxillary and labial palpi not pigmented. In lateral view, clypeus not projecting much if at all beyond frons, antenna arising from faint prominence, and labrum not extending much beyond clypeus. Antennal papilla indistinctly pigmented, very small, shorter than twice basal diameter.

Mandibular apex approximately parallel sided in inner and outer views both teeth on postdefecating larva broadly rounded apically; apical concavity defined; outer surface with single conspicuous, long, curved seta near base; other features of mandible not observed because of insufficient material. Maxillary and labial palpi moderately small, but each about twice as long as basal diameter, each larger than antennal papilla. Labial apex moderately wide; premental sclerite present laterally. Salivary lips moderately wide, about equal to distance between centers of bases of labial palpi.

Body (fig. 28): Body vestiture apparently consisting of small inconspicuous setae although some may be setiform spicules all tapering to fine points; vestiture most conspicuous on dorsal surfaces of thorax but found on all dorsal and lateral abdominal surfaces; setae and setiform spicules tending to be inconspicuous because of overall shortness and lack of pigmentation; vestiture absent (or reduced) on middorsal tubercles; lateral lobe of abdominal segment 8 (i.e., area below level of spiracle) with approximately 35 fine setae; dense patch of short setae on abdominal segment 10 immediately below anus. Body form of postdefecating larva moderately robust in lateral outline (fig. 28); body segments gradually increasing in height with abdominal segments 5, 6, and 7 having greatest diameters; middorsal intersegmental tubercles inconspicuous but present between abdominal segments 1 and 2, 2 and 3, 3 and 4, 4 and 5, and 5 and 6 with more strongly projecting part of each tubercle on rear margin of caudal annulet of anterior segment; tubercles tending to be faintly transversely bimodal; dorsal projection of caudal annulets tending to be somewhat greater because of elevation of middorsal tubercles. Spiracles unpigmented, subequal in diameter; atrium globular with width somewhat greater than depth, projecting well above body wall, with rim; atrial wall ringed with rows of sharp spicules; primary spiracular opening with collar; subatrium moderately short with approximately 10 chambers of approximately equal diameter.

MATERIAL STUDIED: Three postdefecating larvae: Spain: Salamanca: Salvatierra de Tormes, 1994 (F. Torres et al.) (Reference numbers: 94290902004, 94290902005, and 94290902006).



FIGURES 34–36. SEM micrographs of cocoon of *Chelostoma florissomne*. 34. Outer layer of front end of cocoon, inner view. 35. Close-up of inner surface identified in figure 34, upper rectangle, showing lack of fenestrations and showing fibers that extend to inner cocoon layer. 36. Close-up of figure 34, lower rectangle, showing openings in periphery allowing air exchange with exterior.

DISCUSSION OF LARVAL ANATOMICAL FEATURES

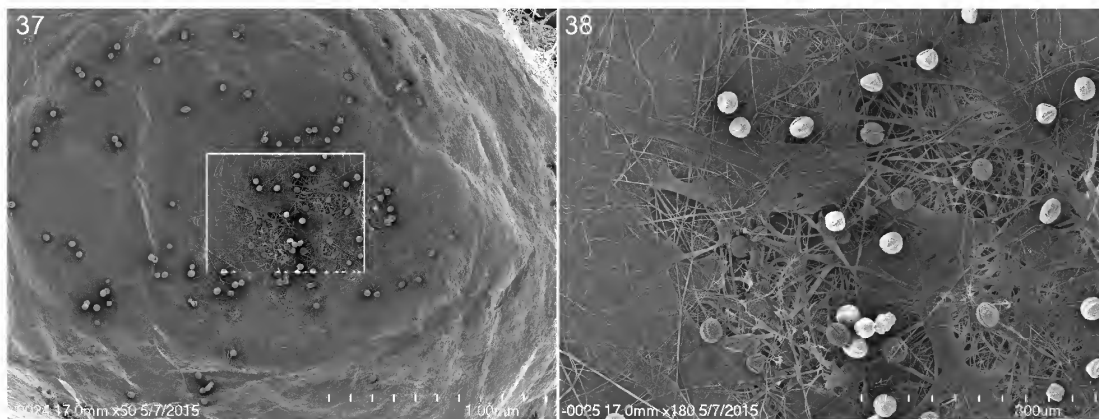
The above tribal description of the Osmiini based on postdefecating larvae is unlikely to help to distinguish last-instar Osmiini from those of other megachilid tribes, despite that having been one of the purposes for undertaking the study. From our present knowledge we have been unable to identify one or even a combination of larval features that uniquely characterizes this tribe. This finding was not unexpected as Michener (1953) stressed the larval similarity of many megachilid taxa.

However, a number of anatomical features were revealed that may show relationships among the osmiines. Most larvae fall into one of the following three groups on the basis of body form (included taxa in parentheses):

(1) Larvae in which middle body is thickest and posterior part gradually tapering while cephalic and caudal annulations of abdomen tending to remain distinct; intersegmental middorsal tubercles absent (figs. 12–19, 22, 23, 27). (*Ashmeadiella*, *Chelostoma*, *Ochreriades*);

(2) Larvae with enlarged abdomens compared with anterior half of body; cephalic and caudal annulations disappearing toward rear of body; middorsal intersegmental tubercles evident on anterior abdominal segments (figs. 20, 24–26, 28). (*Atoposmia*, *Osmia* (*Hoplosmia*), *Heriades*, and questionably *Hoplitis* (*Proteriades*) *xerophila*, fig. 4);

(3) Elongate larvae with most body segments overlapping so that separation of segments are well defined and with anterior abdominal segments with middorsal tubercle on posterior edge of caudal annulet accompanied by modification of the dorsal anterior edge of following cephalic annulet (figs. 3, 5–8).



FIGURES 37, 38. Same cocoon as figs. 34–36, inner layer at front end showing silk strands of air-exchange portal surrounded by airtight inner cocoon surface, and close-up of portal identified by rectangle in figure 37, respectively.

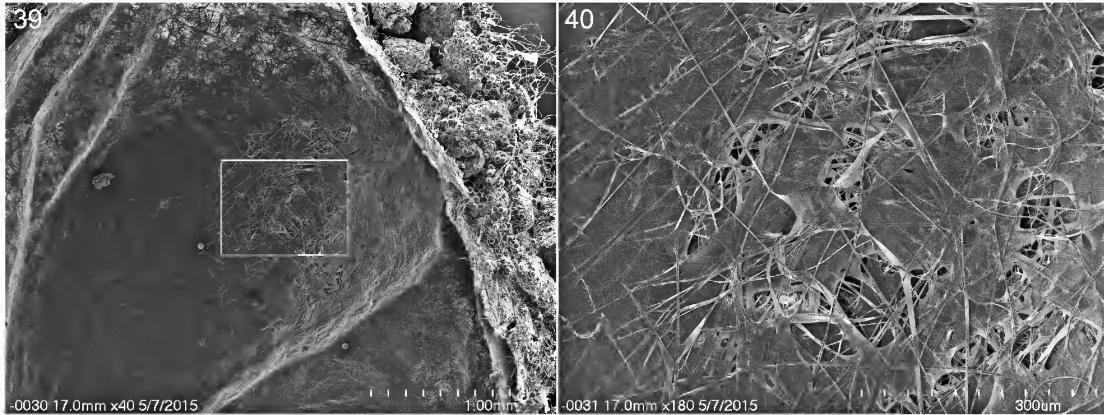
(*Hoplitis*, except for *H. (Proteriades) xerophila*, fig. 4). Judged on the basis of accompanying illustrations in literature accounts, this also includes *H. (Alcidamea) tridentata* (Dufour and Perris) (Enslin, 1925) and *H. (Hoplitis) loti* (Morawitz) (Micheli, 1931).

The only osmiine genus available to us other than *Osmia* not included in the above groupings is *Haetosmia* as is discussed above in the treatment of *H. vechti* (fig. 21). The larval anatomy may shed some light on the relationships among the osmiine lineages. It appears that larvae of the genus *Hoplitis*, with the exception of *H. (Proteriades) xerophila*, are of a distinct type within osmiine and in this respect larval anatomy supports the recognition of this genus, in line with Michener's classification and the results of Praz et al. (2008). However, the other two morphological groups based on larval anatomy do not seem to support a natural grouping: our results may suggest a close affinity between *Ocheriades* and *Chelostoma*, in line with the morphology-based phylogeny of Gonzalez et al. 2012. But there has been no suggestion that *Ashmeadiella*, with superficially nearly identical larvae, is close to either *Chelostoma* or *Ochre-riades*, but rather it was established as belonging to a well-supported clade containing beside *Ashmeadiella* the genera *Atoposmia* and *Osmia*. Similarly, no phylogenetic hypothesis has suggested a close relationship between *Heriades*, *Atoposmia* and *Osmia*, although their larvae appear to fall in the same group.

Differences in body form, abdominal annulations, and presence or absence of middorsal intersegmental tubercles would seem to relate to the movements of the last stage larva in the cell as it completes feeding, defecates, and spins its cocoon. Studies should be carried out to explore the function and adaptive significances of the different larval morphologies.

NESTING BIOLOGY

Information presented below comes from the authors' own field observations (see specimens described above for collection data) or from observations of material collected by



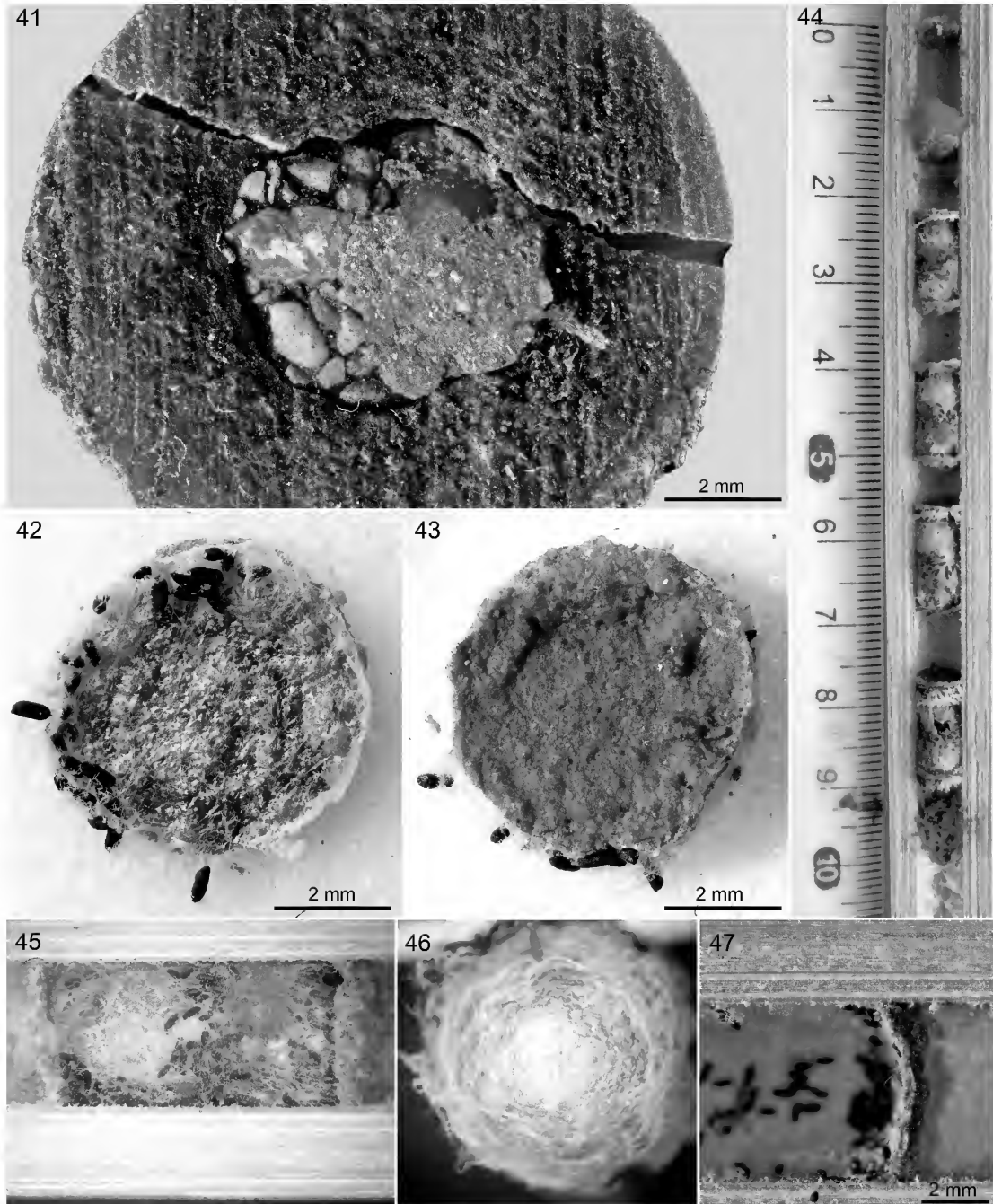
FIGURES 39, 40. Inner layer of front end of cocoon of *Chelostoma rapunculi*, showing silk strands of air-exchange portal surrounded by airtight cocoon fabric, and close-up of portal identified by rectangle in figure 39, respectively.

others either recently or over a long period of time. This section is not a complete survey of nesting biology of the Osmiini but it is hoped it will contribute to such a study. Michener (2007) presented a general overview of the subject, and the nesting biology of North American *Osmia* was reviewed and presented in Cane et al. (2007). Available information (both a thorough review of the published literature and personal observations) on all Palearctic osmiine is given in the “Palearctic Osmiine bees” website (Müller, 2016). Here we offer what new information is available and try to integrate it with accounts by others, such as Krombein (1967), Westrich (1989), and Müller et al. (1997).¹²

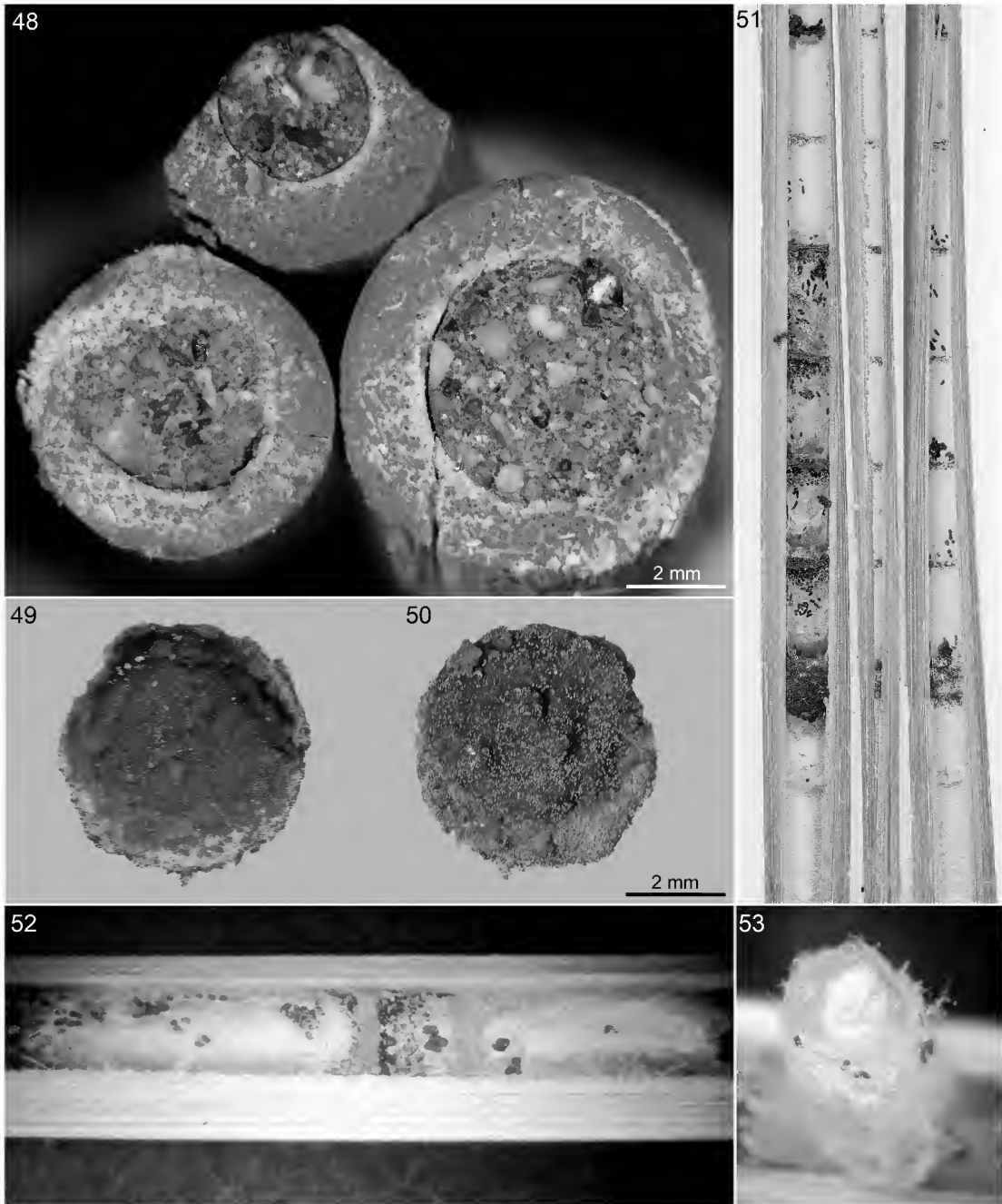
CHELOSTOMA

Nests of *Chelostoma* (*Gyrodromella*) *rapunculi* (Lepeletier) and *C. (Chelostoma) florisomne* (Linnaeus) are treated together because of many shared similarities, and both, from The Botanical Gardens of the City of Neuchâtel, were studied together by J.G.R and C.J.P. Nests of these species have been extensively described before (Westrich, 1989, and references therein); we briefly redescribe them here to precise some aspects related to cocoon spinning, structure, and function. Nests of *C. rapunculi* were in slender bamboo sections (outside diameter 5–10 mm) from which C.J.P. collected larvae. They contained numerous cells in uninterrupted linear series, end to end (figs. 44, 51). Those of *C. florisomne* were found in bamboo sections that had slightly larger diameters. Although some cells of this species were in uninterrupted linear series, others were in series in which cells were separated by open spaces somewhat shorter than cell length (fig. 44) (i.e., these are called “intercalary cells” by Krombein, 1967). Cell partitions of both species (figs. 43, 50) were dark soil that appeared to be identical in color to the

¹² Reexamination of the cocoon of *Haetosmia vechti* originally described in Gotlieb et al. (2014) shows that the front end consists only of a single silk layer with fenestrations more or less centrally located *where silk touches the rough inner surface of the cell closure* (new information), although most of the cocoon’s front end does not contact this surface.



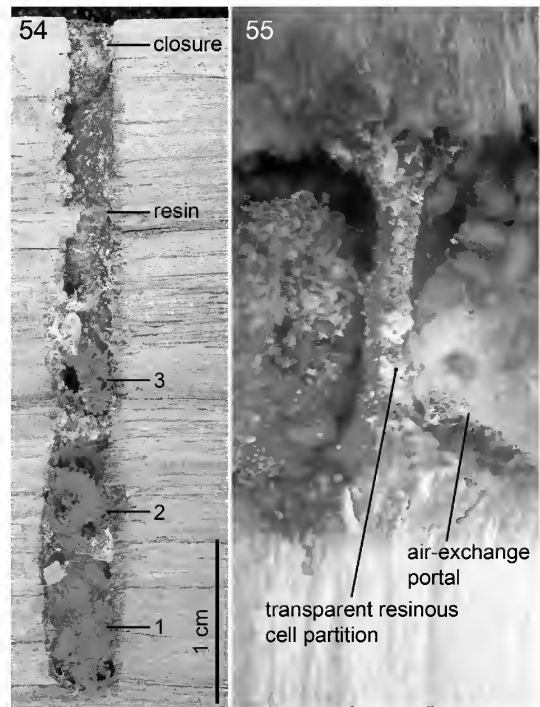
FIGURES 41–47. *Chelostoma florissomne*. 41. Nest closure showing imbedded small stones. 42. Outer layer of transparent cocoon covering cell closure. 43. Uncoated cell partition. 44. Nest in split bamboo section consisting of 6 cells; cells 1 and 2 abutting but other cells separated by empty spaces; cell 6 containing pollen mass and dead larva; all other cells with cocoon. 45. Cell (front end left) containing cocoon. 46. Cocoon showing white air-exchange portal on outer surface of front of inner cocoon layer. 47. Cell partition showing thinness, front end left.



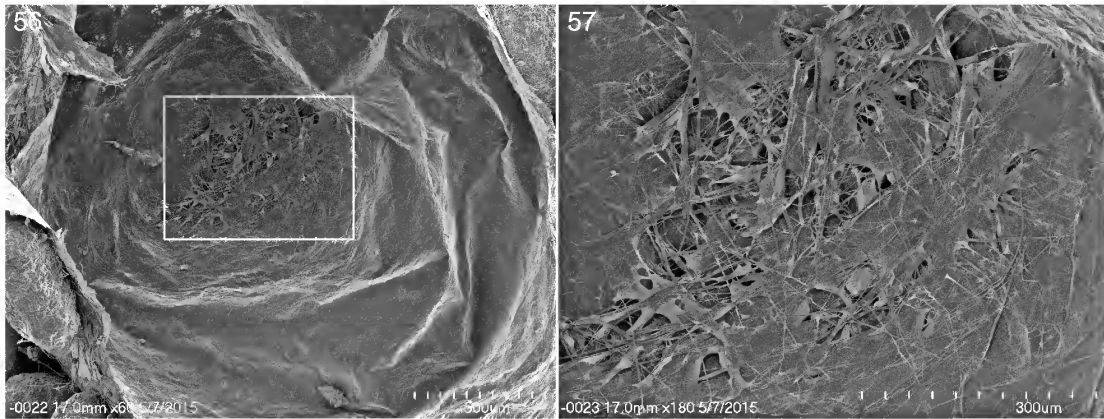
FIGURES 48–53. *Chelostoma rapunculi*. 48. Nest closures showing small stones imbedded in outer surface. 49, 50. Cell partitions, front and rear surfaces, respectively. 51. Nest in split bamboo section, showing cells in linear series. 52. Two cocoons in linear series, front ends at left. 53. Anterior end of front end of inner layer showing white air-exchange portal.

thicker nest closure material but lacked the small, whitish pebbles that the nest maker added to the closure on sealing the completed nest (figs. 41, 48). Almost certainly, cell partitions and nest closure when first constructed are made of mud, perhaps moistened with nectar. The tunnel between the last cell constructed and nest closure (i.e., the “vestibular cell” by Krombein, 1967) was open. Accounts of nests of species of *Chelostoma* offered by Krombein (1967), Westrich (1989), Müller et al. (1997), and Rozen and Go (2015) provide similar descriptions.

Cocoons of *C. florissomme* (figs. 34–38, 45, 46) and *C. rapunculi* (figs. 39, 40, 52, 53) are structured and function like the cocoon of *Ochreoides fasciatus* (Friese), as described by Rozen et al. (2015). After initiating defecation but while still defecating, the larva deposits a thin nearly clear layer of silk that covers over and adheres to the front end of the cell closure including any fecal pellets that happened to be deposited there (figs. 34, 36). (In the case of *Heriades carinata*, Matthews, 1965, referred to this layer as the “operimentum”). The inner surface of this layer, though appearing reflective in normal light, is covered with a fine webbing of silk strands (fig. 35). The larva starts spinning the body of the cocoon and attaches the inner layer of the front of the cocoons to this webbing. As a final step in cocoon construction, the larva applies a thin but completely airtight final layer of silk to the inner surface of the entire cocoon except for a cottony mass of silk fibers (figs. 46, 53) centered at the front of the cocoon. This mass, termed the “air-exchange portal” (Rozen et al., 2015), is thick, but the fibers are not fused and consequently there is an exchange of air between the inside of the cocoon and the space between the two cocoon layers forming the cocoon front (fig. 29). At the periphery of the front end, the inner and outer layers are only loosely attached (figs. 34, 36) with the result that air exchange takes place between the outside of the cocoon and the space between the two front layers of the cocoon. Thus, univoltine larvae are provided with air for their ca. 10 month diapause before emerging the following year, and simultaneously they are protected from parasites and the cell humidity is controlled by the airtight, waterproof cocoon wall. Feces of both species were black or nearly so (figs. 42, 47, 51).



FIGURES 54, 55. *Heriades truncorum*. 54. Nest containing three cells in trap nest; note orange color of feces contrasting with black feces of *Chelostoma* and partly resin-filled tunnel leading to cells. 55. Close-up of cell (front end left) showing clear cell partition of resin (arrow).



FIGURES 56, 57. SEM micrographs of inner surface of cocoon showing central air-exchange portal surrounded by smooth, presumably airtight, thin layer of silk and close-up of air-exchange portal identified by rectangle in figure 56, respectively.

The availability of unmodified surfaces of cell partitions of *C. florissomne* permitted observations obscured by cocoon silk in other species. Partitions of this species, presumably made of mud, dry quickly, each forming a hard wafer that is slightly concave on the surface directed toward the nest closure and slightly convex on the other side (fig. 47). Both surfaces are rather uneven with the rear surface more or less nodular (fig. 43), so that partition thickness varies from point to point. At minimum, the thinness is a remarkable: 0.3 mm. When J.G.R. visited Neuchâtel in early October 2014, most of the cells of this species were occupied by well-pigmented pupae contrasting with cells of *C. rapunculi* containing white larvae, suggesting a noteworthy lack of developmental synchronization of the two related species, probably related to the fact that in *C. florissomne*, the pupa overwinters (Westrich, 1989), while in *C. rapunculi*, the larva overwinters. *Chelostoma florissomne* is active already in April, while *C. rapunculi* flies late May and June.

HERIADES (H.) TRUNCORUM (LINNAEUS)

Most nests examined by J.G.R. and C.J.P. were in trap nests (fig. 54), and four of them were each 4.0 cm long and circular in cross section with a diameter of 4.0 mm. Cell partitions and nest closure were uniformly constructed with clear yellowish resin (fig. 55), which on hardening was quite brittle but easily chipped with forceps, suggesting that emerging bees could easily remove partitions and nest closures with their mandibles. Cells were arranged in linear series occasionally with empty spaces between, and always with a more or less elongate space between the last cell built and the nest entrance. This tunnel was sometimes empty and other times partly filled with resin (fig. 54). Several cells of a nest in a section of bamboo were also recovered. These cells were 7.5 cm from the nest entrance stoppered by a large amount of resin, but the tunnel itself was completely resin free although the rear of the nest was a 4 mm long cylinder of solid resin. Feces (figs. 54, 55) in all nests tended to be pellets of various shades of orange, from light to dark, which seemed to be mostly exterior to the cocoon fabric and only loosely fastened to the cocoon with threads of silk. Cocoon structure was not closely examined,



FIGURES 58–60. Adult and cocoon of *Hoplitis hypocrita*. 58. Adult pinned to cocoon capsule, which had deflated when adult emerged; cocoon capsule attached to unaltered front end of cocoon, which had been constructed after larval feces discharged into anterior part of cell. 59. Same but with outer layer of front end tilted back to reveal pale, air-exchange portal of inner layer of front end. 60. Close-up of figure 59. Photographs provided by Harold W. Ikerd II.

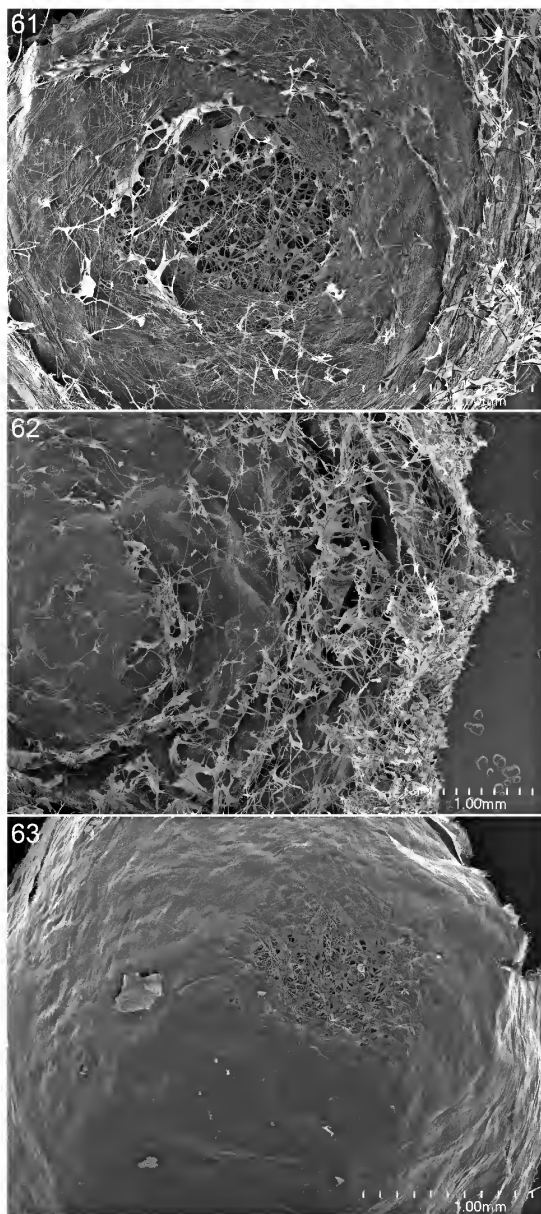
but did not seem unlike those of *Chelostoma* or *Hoplitis* in that at the front end it bore a dense, white air-exchange portal (fig. 55) and SEM scans of the inner surface at the front end revealed the screened openings surrounded by smooth silk (figs. 56, 57).

Nest closures observed by J.G.R. and C.J.P. were flush with the exposed surface and were not implanted with pebbles or other debris as reported by Westrich (1989) and as discussed recently by Rozen et al. (2015).

The rest of the information correlates well with the nest descriptions provided by Westrich (1989). Both he and Müller et al. (1997) pointed out that this species also nests in vacated beetle burrows in old wood and in stems of such plants as blackberries. They also noted that cells were arranged in linear series separated by septa of resin, sometimes with empty chambers between cells. Nest closures were also made of resin in which were implants of pebbles, wood fiber, or other debris.

HOPLITIS (ALCIDAMEA) HYPOCRITA (COCKERELL)

An empty cocoon of *Hoplitis hypocrita* was pinned with the adult that had emerged from it through a tear along the side (fig. 58). Hence, the front of the cocoon was intact. It possessed a well-formed anterior outer cocoon layer bearing on its anterior surface an orderly stack of yellowish fecal pellets, each about 1.0 mm long and 0.25 mm in maximum diameter. These pellets had been deposited on the cell closure at the front of the cocoon before the cocoon was spun. Either at the time of adult eclosion or when the entire cocoon was removed from the cell, the anterior outer layer of the front with attached feces had been partly pulled away from the body of the cocoon (fig. 59), thus partly exposing the front of the now seemingly shrunken inner cocoon layer behind it. This permitted one to see the opaque yellowish-white air-exchange portal, central on the front of the inner layer (arrow) and also the passageway for air exchange between the outer layer and the inner layer. The passageway was strewn with erect fibers connecting the two layers and serving as screening thereby excluding parasites. After the outer layer was completely detached from the body of the cocoon, the erect fibers connecting the two layers were densest around their peripheries (figs. 61, 62). Thus the openings of the pas-



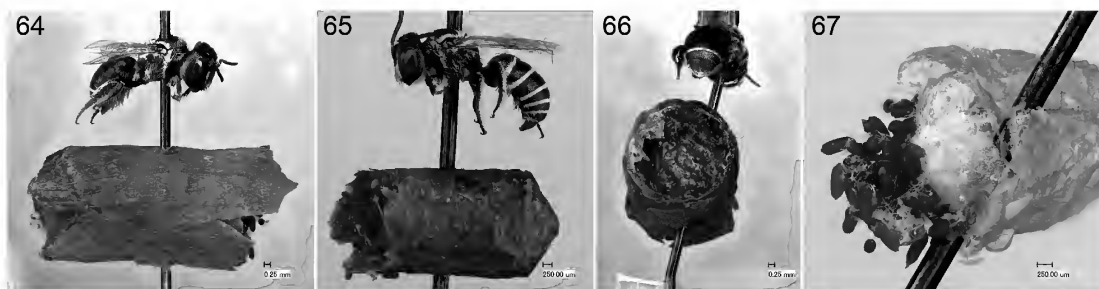
FIGURES 61–63. SEM micrographs of front end of cocoon of *Hoplitis hypocrita*. **61.** Front end of inner lining showing air-exchange portal, center. **62.** Part of inner surface of outer layer, center to the left, showing bands of webbing to the right through which air is exchanged around periphery of front end of cocoon. **63.** Inner surface of front end of cocoon showing webbing of air-exchange portal.

sageway completely ringed the anterior sides of the cocoon. The air-exchange portal centered on the outer surface front of the inner layer and consisted of a tight cluster of densely screened fenestrations when viewed externally (fig. 61) and facing the inner surface of the outer layer (fig. 62). The inner surface of the inner layer (fig. 63) reveals the screened opening of the air exchange-portal typical of all osmiines.

MATERIAL STUDIED: One cocoon: Utah: Cache Co.: Logan Cyn #4, 41 45 39.01N 111 42 26.83W (F.D. Parker). Rearing No. 22757C. From collection in USDA laboratory, Logan, Utah.

HOFFERIA SCHMIEDEKNECHTI
(SCHLETTERER)

The following brief notes are about a nest found in wood of a dead cypress tree in Israel. This same nest was described by Müller and Trunz (2014) in which photographs of the habitat and nest were presented. Two cells were arranged in linear series, and one cell measured 9.0 mm long and 4.5 mm in maximum width. The nest entrance tunnel was 10 mm long, open except for a mass of pollen in front of cell 2, perhaps an indication that the female intended to place a third cell there. The dark, semitransparent nest closure was composed of clear but dark resin on the inside and a mixture of soil, small pebbles, and resin toward the outside. Cell partitions are reported to be made with resin alone (Müller and Trunz, 2014), and a reexamination of the nest after reading this publication confirmed that cell walls were not lined with resin. The cocoon was semitransparent, faintly darker than that of *Heriades*, with black fecal pellets pressed to the inner cocoon surface, an indication of cocoon spinning during defecation.



FIGURES 64–67. Photographs of *Pseudoheriades grandiceps*. **64.** Female pinned to leaf covered nest cell from which it had emerged. **65.** Male pinned to petal-covered nest cell. **66.** Same specimen as figure 64, posterior view of cell partition. **67.** Cocoon, frontal view, showing air-exchange portal of inner cocoon layer and feces. Photographs provided by Harold W. Ikerd II.

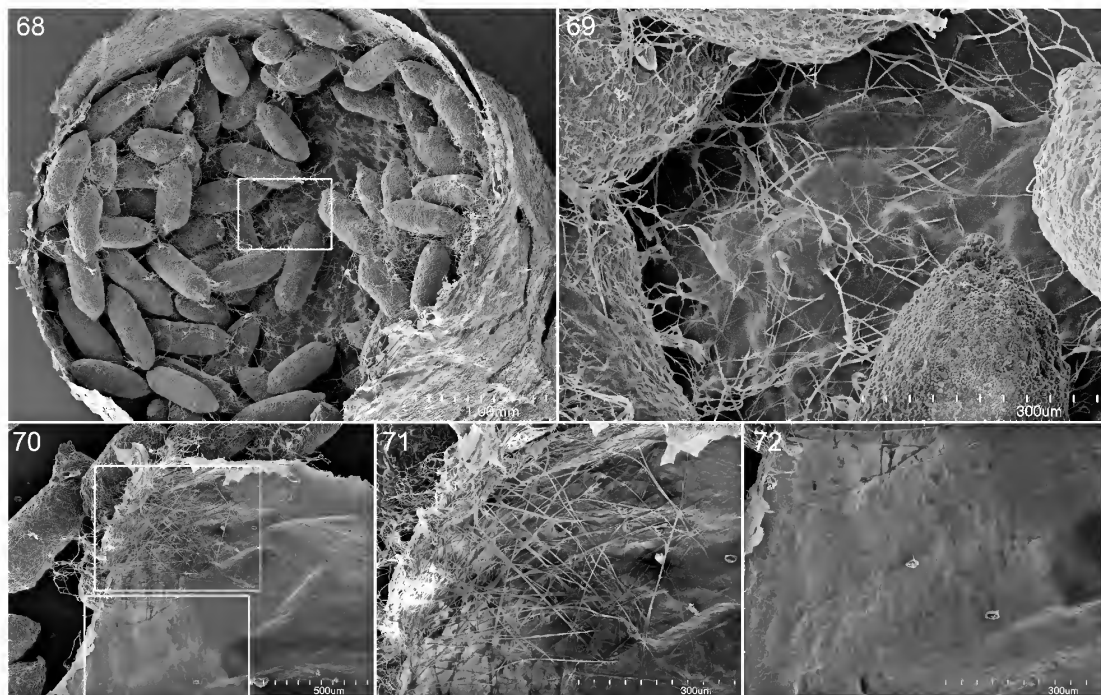
MATERIAL STUDIED: One nest: Israel: Lehavot, V-3-2013 (V. Trunz, D. Bénon) in oval tunnel presumably made by buprestid in wood of a dead *Cupressus*.

PSEUDOHERIADES GRANDICEPS PETERS

Notes on *Pseudoheriades grandiceps* are based on nest fragments and cocoons pinned with adults from the United Arab Emirates. E.A. Sugden collected this material from trap-nest blocks in which holes presumably 4 mm in diameter had been drilled. J.G.R.'s original interpretation was that females first lined the burrows with small leaves (or large leaf pieces) (fig. 64) or less commonly with petals (fig. 65) after which she provisioned the cell, oviposited in it, and then constructed a cell partition presumably made with resin since it was partly transparent, with a reflective (glassy) surface. However, see Remarks, below, for another possible explanation provided by C.J.P. The next cell was provisioned in front of the first, i.e., in linear series. Because cell partitions were constructed after the tunnel had been lined with leaves (or petals), they were attached to the leaf lining and not to the burrow wall.

An interesting feature that still needs confirmation was that the front end of the cocoon was apparently deposited before defecation started. This was revealed only with a close-up SEM micrograph of the glassy cell partition against which fecal pellets had been deposited (fig. 68). In normal light the transparent sheet of silk was invisible (fig. 66) but its texture with short silk threads was revealed on another specimen with the SEM (figs. 68, 69).

At the beginning of defecation, the first fecal pellets deposited were dark, approximately 0.625 mm long and 0.25 mm in maximum diameter, and rounded to tapering on the ends (fig. 68). Their shapes were discrete; when deposited, they did not fuse with one another (as they do in *Ochreriades fasciatus*, Rozen et al., 2015, fig. 15). A few pellets, possibly among the last to be deposited, were extremely pale (fig. 67), possibly a discharge from the Malpighian tubules, as has been noted with other megachilids (e.g., *Trachusa*, Rozen and Hall, 2012). At the posterior end of cocoons flattened fecal streaks composed of opaque yellowish material as well as a few dark fecal pellets were often detected.



FIGURES 68–72. SEM micrographs of cell of *Pseudoheriades grandiceps*. **68.** Front end of cocoon from which air-exchange portal of inner layer has been removed showing discrete fecal pellets. **69.** Close-up of rectangle identified in figure 68, showing fibrous nature believed to be inner surface of outer layer of cocoon. **70.** Front end of inner layer of cocoon showing air portal and smooth cocoon surface immediately behind it, side view. **71, 72.** Close-ups of same identified by rectangles in figure 70.

At the front end of the cocoon but behind the transparent silk outer layer, the seemingly loose fecal pellets were actually tethered one to another by silk strands, which presumably represents part or the outer cocoon layer (figs. 68, 69). Immediately behind the feces was the broadly curved front of the inner cocoon layer. The dense, opaque, white air portal (figs. 67, 70–72), centrally located on the front of the inner layer, could be identified because it contrasted with thin semitransparent fabric of the rest of the cocoon. Likely, air exchange between the interior of the cocoon and the outside occurs through the portal and from there, air diffuses in and round the feces and around the leaves to the exterior. No immature stages were preserved, and, consequently, none is available for description.

MATERIAL STUDIED: Two cocoons: United Arab Emirates: Nakhali, 40 km inland from Dubai. Reared blocks (E.A. Sugden) 54095F, 54127F; 1 cocoon: Dubai (Zabeel). Reared blocks (E.A. Sugden) 53888D. From collection in USDA laboratory, Logan, Utah.

REMARKS: When J.G.R first examined the three cocoons, two of which had been pinned with the adults and cells from their nests, he was impressed by the fact that nest partitions were attached to the leaf-/petal-lined burrow wall. He interpreted this to mean that the nest-making female had first lined the burrow wall with the plant material and subsequently started making and provisioning the series of cells, one after another. C.J.P. suggested another explanation:

might the female have appropriated the vacated nest of a *Megachile*, the cell of which had been lined with leaves and petal snippets since no other megachilid is known to use both petal-leaf-lining and resin in nest construction? Although none of the preserved nest materials gave a hint of the cocoons or feces of an original owner of the cells, the preserved nest material is limited. It is hoped the discovery of the next nest of *P. grandiceps* will provide a definitive interpretation. Terry Griswold kindly pointed to us an account on the nest of *Pseudoheriades moricei* by Krombein (1969). *P. moricei* also uses trap nests and uses resin for the construction of both partitions and plug, the latter also including pebbles. No hint of the use of petals or leaves is given by Krombein, suggesting that the leaves and petals observed in nests of *P. grandiceps* may have been previously placed by leafcutter bees.

DISCUSSION OF COCOON FEATURES

Matthews (1965) in his detailed account of the nesting biology and immature stages of *Heriades carinata* was strongly impressed by the larva's initial discharge of silk that covered the cell partition at the front of the cell. He considered this so-called operimentum in the larval cell served "as a vital cue to the larva in cocoon positioning and orientation." There is nothing discovered in the current study indicating that Matthews's conclusion is incorrect, for this first silk deposit may well orient the larva in the subsequent cocoon construction. However, it is postulated here that the first part of producing the cocoon (that is, the deposition of the operimentum) in these bees serves a broader adaptive function; it is an integral part of an elaborate humidity-control and air-exchange mechanism that simultaneously excludes parasite and predator from the cocoons of many of these bees.

ACKNOWLEDGMENTS

This study was made possible by the extensive collection of bee larvae, nests, and cocoons preserved by the U.S. Department of Agriculture at Utah State University, Logan, Utah, under the care of Terry L. Griswold. The collection resulted primarily from the research efforts of the eminent bee biologists the late George E. Bohart, the late Philip F. Torchio, and Frank D. Parker, although others also contributed. The U.S.D.A. should be commended for its foresight in preserving and maintaining these valuable specimens. There are few collections of bee immatures and their nests as complete anywhere else.

The larval specimens that the late Karl V. Krombein preserved during his years of studying the nesting biology of bees and wasps (see Krombein, 1967) was another rich resource of specimens. Thanks are extended to Seán Brady and Brian Harris of the Smithsonian Institution for the loan of these specimens. Other material examined for this study were on long-term loan from the Essig Museum, University of California, by agreement with the late Paul D. Hurd, Jr.

J.G.R. extends special thanks to coauthor C.J.P. for collecting and/or storing nests and immatures so that he and J.G.R. could study them when J.G.R. visited the University of Neuchâtel in Switzerland in early fall of 2014.

Harold W. Ikerd II in Logan, Utah, kindly prepared the macrophotographs of *Hoplitis* and *Pseudoheriade* used in describing their cocoons and nesting habits. F. Torres shared specimens from his 1997 study that contributed to current treatment of osmiine larvae.

Senior Scientific Assistant Stephen Thurston expertly arranged and labeled all diagrams, micrographs, and photographs for presentation and diagrammed figure 29. Curatorial Assistant Eli S. Wyman took all SEM micrographs after undertaking all necessary critical-point drying and coating with gold-palladium. J.G.R. extends thanks to Eileen Westwig for translating the works written in German.

The authors extend their appreciation to two anonymous reviewers for their helpful suggestion and comments.

J.G.R.'s trip to Neuchâtel, Switzerland, where he worked with C.J.P. was supported through the Goelet Bee Fieldtrip Fund thanks to the kindness of Robert G. Goelet, Chairman Emeritus, Board of Trustees, American Museum of Natural History.

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