Immatures of Rophitine Bees, with Notes on their Nesting Biology (Hymenoptera: Apoidea: Halictidae)

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ABSTRACT

This study is a taxonomic overview of the known mature larvae and pupae of the Rophitinae (Halictidae). We either describe and illustrate the mature or nearly mature larvae of the following taxa or provide references to their earlier descriptions: *Dufourea holocyanea* (Cockerell), *D. australis australis* Michener, *D. mulleri* (Cockerell), *D. novaeangliae* (Robertson), *Sphecodosoma* (*Sphecodosoma*) *dicksoni* (Timberlake), *Protodufourea eickworti* Bohart and Griswold, *Xeralictus timberlakei* Cockerell, *Systropha planidens* Giraud, *Rophites* (*Rhophitoides*) *canus* Eversmann, *R.* (*Rophites*) *algirus trispinosus* Pérez, *Conanthalictus* (*C.*) *conanthi* (Cockerell), and *C.* (*Phaceliapis*) *bakeri* Crawford. We present a key to known mature rophitine larvae. We also describe pupae of the following taxa for the first time and compare them with the pupa of *S. dicksoni*: *D. holocyanea*, *D. australis australis*, and *R. canus*. The phylogenetic relations of the treated taxa are discussed in light of larval characters, and we discuss the pupal characteristics of the entire family.

We offer notes on the nesting biology of various taxa whose immatures were treated and synthesize this information with previous accounts from the literature.

ABSTRAKT

Bu çalışma, Rophitinae (Halictidae)'nin bilinen olgun larva ve pupalarının taksonomik yönden gözden geçirilmesine yöneliktir. Bu alt familyada yer alan *Dufourea holocyanea* (Cockerell), *D. australis australis* Michener, *D. mulleri* (Cockerell), *D. novaeangliae* (Robertson), *Sphecodosoma* (*Sphecodosoma*) *dicksoni* (Timberlake), *Protodufourea eickworti* Bohart and Griswold, *Xeralictus timberlakei* Cockerell, *Systropha planidens* Giraud, *Rophites* (*Rhophitoides*) *canus* Eversmann, *R.*

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(*Rophites*) *algirus trispinosus* Perez, *Conanthalicus* (*C.*) *conanthi* (Cockerell), ve *C.* (*Phaceliapis*) *bakeri* Crawford türlerinin olgun veya olgun olmak üzere olan dönemlerdeki larvaları, ya tanımlanmış ve çizimleri yapılmış veya daha önce yapılan tanımlara atıflar yapılmıştır. Bilinen tüm rophitine olgun larvaları için tanı anahtarı hazırlanmış, *D. holocyanea*, *D. australis australis*, ve *R. canus* türlerinin pupaları ilk defa tanımlanmış ve bunlar, daha önce tanımı yapılmış olan *S. dicksoni* türünün pupası ile karşılaştırılmıştır.

Ele alınan türlerin larva özelliklerinin ışığı altında, filogenetik ilişkiler tartışılmış ve tüm familyanın pupa özellikleri değerlendirilmiştir.

Genç dönemleri çalışılan değişik türlerde yuva ile ilgili biyolojik notlar verilmiş, bu bilgiler daha önce bilinenlerle literarüre dayalı olarak karşılaştırılmış ve ayrı bir bölüm halinde makalenin sonunda verilmiştir.

INTRODUCTION

The immature stages of the Rophitinae were studied as a group well over a decade ago (Rozen, 1993), and the description of the larva of *Xeralictus* was published several years later (Snelling and Stage, 1995). Since then mature larvae (i.e., both predefecating and postdefecating larvae) of a number of additional taxa have become available. These are described here to provide a more complete understanding of the range of anatomical variation among mature larvae in the subfamily. Because the pupa of only *Sphecodosoma* (*Sphecodosoma*) *dicksoni* (Timberlake) has been described to date (Rozen, 1993), we include comparative descriptions of pupae of additional taxa to begin exploring anatomical variation in that life stage. In the process of excavating nests, we recorded information about the nesting biology of some of the species; this information is presented in the Remarks sections of the larval descriptions of each of these species. It is synthesized with previous accounts from the literature in "Discussion of Rophitine Nesting Biology".

Terminology and Methods

Species determinations of immatures are based on associated adults.

The term *mature larva* refers to the last larval instar after it completes defecation (postdefecating larva) or just after it consumes all or nearly all larval provisions but has not yet started to defecate (predefecating larva). In studies of bee larvae, the postdefecating form is usually described because this form is most commonly encountered (univoltine bees spend about 10 months per year in this stage) and because it is the form that can be most easily recognized and most reliably used to compare one taxon with another due to its thick, rigid integument as compared to that of predefecating forms. In the current study we used various earlier stages of the last instar when postdefecating representatives were not available. Because head characteristics (except for degree of pigmentation) do not change within an instar, even a young last instar offers many features of comparative value.

Although we describe the paired dorsal body tubercles of rophitine mature larvae as "conical", each is often wider than its longitudinal length. However, they contrast with paired dorsal body tubercles of halictines, which are so transverse that those on the same body segment nearly meet dorsally at the midline and extend laterally onto the sides of the segment.

In studying the specimen, we first examined and illustrated untreated specimens, either while they were alive or after they were preserved in Kahle's solution. Illustrations were prepared with a camera lucida attached to a stereomicroscope. Specimens were then decapitated, and the head and body were cleared in an aqueous solution of sodium hydroxide, washed in water, transferred to ethanol, and then stained with Chlorazol Black E. After preparation, the cleared specimens were examined in glycerin on well slides, and such information as internal head ridges, spiculation, and sensilla were added to the illustrations. Mandibles and spiracles were illustrated from cleared specimens. When possible, we studied both predefecating and postdefecating (prepupal) larvae. Because of their thick cuticle, the bodies of the latter tend to retain their original shape after preparation, whereas the postcephalic integument of the predefecating larva loses its shape and often tears.

Larvae were examined with a Hitachi S-5700 scanning electron microscope (SEM) in

the Microscopy and Imaging Facility of the AMNH after they had been critical-point dried and coated with gold/palladium. Postdefecating larvae that had not been cleared in an aqueous solution of sodium hydroxide were inadequate for such examination because many features were obscured by the flaking remnants of the dried coating that covers postdefecating larvae (see description under ''Remarks'' in treatment of *Dufourea a. australis*, below).

As demonstrated in a recent study of other bee larvae (Rozen and Kamel, 2007), the interesting variation in the internal structure of the salivary opening of cocoon-spinning rophitine bees apparently is revealed only after the specimen has been subjected to critical-point drying.

Pupae required no special treatment; they were drawn while in alcohol. In their descriptions, T = tergum and S = sternum, followed by Arabic numerals signifying the metasomal segment, e.g., S6 = sixth metasomal sternum.

AMNH = American Museum of Natural History.

DISCUSSION OF RELATIONSHIPS

To what extent do larval features reveal information about the monophyly of the subfamily Rophitinae? Although immatures of the South American genera as well as of *Morawitzella* and *Morawitzia* have yet to be discovered, larvae of the other genera suggest that the subfamily is monophyletic: On most species, paired dorsal prothoracic tubercles are smaller than the paired tubercles on the other thoracic segments (a feature that is best evaluated on postdefecating larvae) as well as on most abdominal segments. The only exception is *Conanthalictus*, in which the prothoracic tubercles are absent. However, that condition is likely a character-state transformation from the reduced prothoracic tubercles of other rophitines, since no other bee larva in any family is known to have paired dorsal tubercles only on the meso- and metathorax. *Xeralictus*, once placed in the Halictinae (Michener, 1944), was recently recognized as a rophitine on both larval and adult morphological features (Snelling and Stage, 1995). The current study shows that

additional larval features support this placement. The paired truncate dorsal body tubercles, a unique synapomorphy among bees, are evident in *Xeralictus*, *Protodufourea*, *Rophites*, and many *Dufourea*, although the degree of expression is variable. The close relationship between *Xeralictus* and *Protodufourea* is further supported by the long, curved declivity on the dorsal and ventral mandibular surfaces.

Do larval features inform us about the interrelationships within the Rophitinae? Several recent investigations using adult morphological and molecular data (Danforth et al., 2004, 2006) provide a number of cladograms showing somewhat variable topologies, due in part to different generic representation. In common to both studies were *Conanthalictus*, *Penapis*, *Xeralictus*, *Dufourea*, *and Systropha*, but one study included *Rophites* and the other examined *Goeletapis*, *Protodufourea*, and *Sphecodosoma*. Larval data do not include either *Penapis* or *Goeletapis*. Thus, substantive analyses based on all lines of evidence must await further studies incorporating adult and molecular data and the discovery of the immatures of additional taxa, particularly of the South American Rophitinae.

With pupae of only four rophitine taxa now studied, too few are known to shed light on the interrelationships of these taxa. Their pupae are similar, and, as discussed in the section ''Pupal Characters of the Halictidae'', below, pupal characters within the family are sufficiently variable to suggest that they may eventually be useful in determining relationships within the family.

MATURE LARVAE OF THE ROPHITINAE

Rozen (1993) presented a diagnostic description of the subfamily Rophitinae based upon larval characters. That characterization suffices now; it is unaltered by information from the current study, except for one feature that was not appreciated at that time: the anterior tentorial pits of rophitine larvae lie close to the anterior mandibular articulation. As a consequence they are immediately above the articulations or above and slightly laterad of them. In other Halictidae the pits are above and much farther mesad of the articulations

(Rozen, 2008). The following key treats all taxa whose mature larvae are known; it is expanded and modified from a previous one (Rozen, 1993). To be seen, many characters must be observed on cleared specimens.

KEY TO MATURE LARVAE

1. Prothoracic paired dorsal tubercles present but smaller than those of following segments (figs. 1, 2, 23, 31, 50); labiomaxillary region not recessed (figs. 4, 33, 53); labium divided into prementum and postmentum; projecting transverse salivary lips present (figs. 4, 13, 19, 23, 42, 57); maxillary and labial palpi as long as or longer than basal diameters 3

–   Prothoracic paired dorsal tubercles absent, although paired dorsal tubercles of meso-, metathoracic, and many abdominal segments present (figs. 64, 65); labiomaxillary region greatly recessed (fig. 67; Rozen, 1993: fig. 35); labium undivided (Rozen, 1993: fig. 35) or weakly divided into prementum and postmentum (figs. 67); salivary opening without projecting lips (fig. 67); maxillary palpi (figs. 66, 67) scarcely evident; labial palpi undeveloped except for sensilla. *Conanthalictus*. 2

2(1). Paired dorsal body tubercles projecting less, apically rounded (figs. 64, 65) . . . . *C.* (*Phaceliapis*) *bakeri* Crawford (or *deserticola* Timberlake)

–   Paired dorsal body tubercles projecting more, apically more pointed (Rozen, 1993: fig. 37) . . . . *C.* (*Conanthalictus*) *conanthi* (Cockerell)

3(1). Articulating arm of stipes (as seen on cleared head capsule) not evident or rarely appearing as slight anterior projection on distal end of stipes; labium tending to project well beyond maxillary apices in lateral view (fig. 4) (*Dufourea* and *Sphecodosoma*) . . 4

–   Articulating arm of stipes (as seen on cleared head capsule) present; labium tending to project little beyond maxillary apices in lateral view (figs. 33, 53). 7

4(3). Antennal disc and papilla large; papilla apically rounded, with at least one sensillum removed from others by several diameters as seen on a cleared specimen with a compound microscope[3]; subatrium abnormally long, of considerably more than 15 chambers . . . . . . *Sphecodosoma* (*Sphecodosoma*) *dicksoni* (Timberlake)

–   Antennal disc variable in diameter but papilla smaller, apically more pointed, with sensilla tightly clustered as seen on cleared specimen with compound microscope[3], so that no sensillum farther removed from others by more than one diameter (*Dufourea*); subatrium shorter, usually composed of 15 or fewer chambers. . . . 5

5(4). Salivary lips very narrow, so that apical width of lips about same as distance from lips to labial palpus in frontal view (figs. 10, 18) . . . . *Dufourea australis australis* Michener

–   Salivary lips normally broad, so that apical width of lips much greater than distance from lips to labial palpus in frontal view (figs. 3, 12, 28; McGinley, 1987: fig. 27, 187a) 6

6(5). Antennal disc small, its diameter almost one-half distance from its lower margin to center of anterior tentorial pit (fig. 28); antennal papilla projecting more strongly, length more than one-half basal diameter as seen in maximum lateral profile (fig. 30) . . . *Dufourea mulleri* (Cockerell)[4]

–   Antennal disc moderately large, its diameter only slightly less than distance from its lower margin to center of anterior tentorial pit (fig. 3); antennal papilla projecting weakly, length at most one-half basal diameter as seen in maximum lateral profile (fig. 6). . . . . *Dufourea holocyanea* (Cockerell)

7(3). Labral tubercles forward directed, projecting beyond clypeus in lateral view (fig. 53; Rozen, 1993: fig. 42) (*Rophites*) 8

–   Labral tubercles at best low mounds, not projecting beyond clypeus in lateral view (as in fig. 33) 9

8(7). Salivary lips extremely narrow, their apical width much narrower than distance between their lateral edge and base of maxillary palpus in frontal view (Rozen, 1993: fig. 41); antennal papilla in maximum profile acutely rounded, as long as basal

[3] Antennal sensilla appear much larger when viewed with a compound microscope than with an SEM. With a compound microscope, the sensillum is identified by its much larger alveolus (fig. 3) whereas the sensillum itself is most apparent with an SEM where its alveolus is scarcely discernable (figs. 16, 43, 59).

[4] From the illustration provided by Eickwort et al. (1986: fig. 12), *Dufourea novaeangliae* (Robertson) would also key out here because of the strongly projecting antennal papilla.
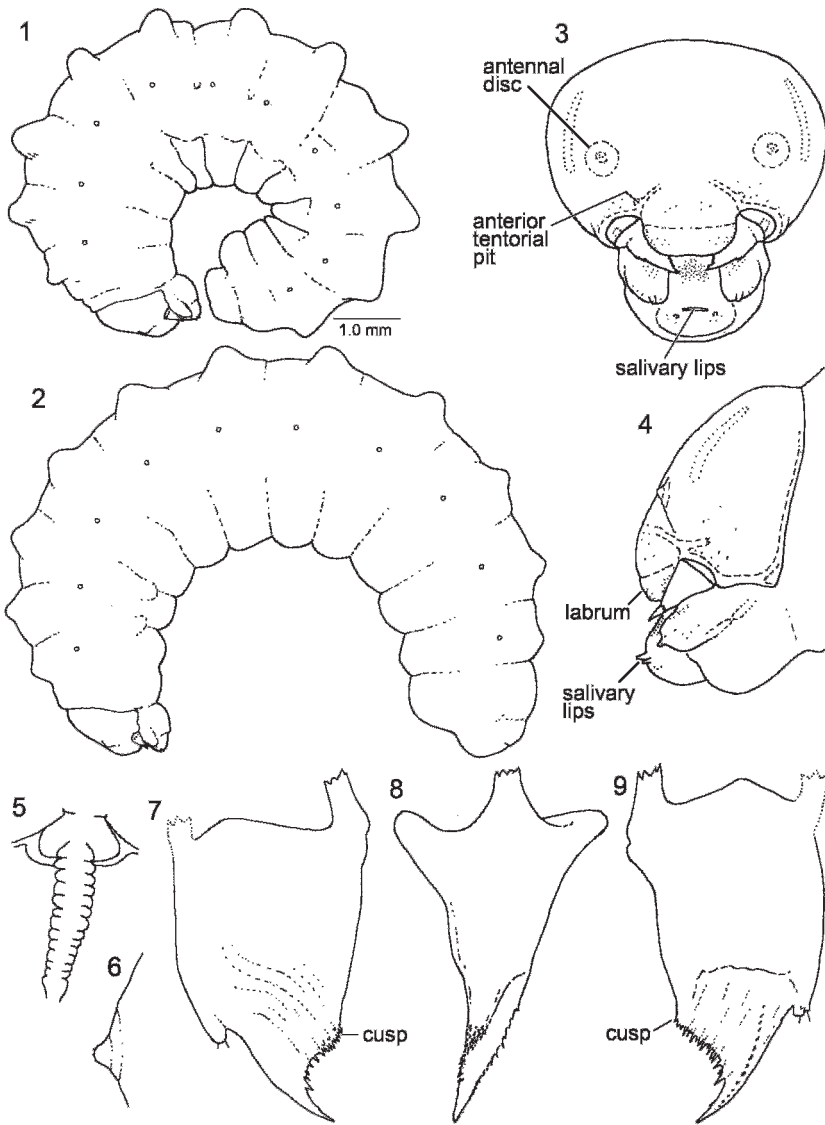
Figs. 1–9. *Dufourea holocyanea*. **1**. Entire postdefecating larva, lateral view. **2**. Predefecating larva, lateral view. **3**. Head, frontal view. **4**. Head, lateral view. **5**. Spiracle, side view. **6**. Antenna, maximum lateral profile. **7–9**. Right mandible, dorsal, inner, and ventral views, respectively. Scale refers to figs. 1, 2.

diameter . . . . *Rophites* (*Rophites*) *algirus trispinosus* Pérez

– Salivary lips wider, their apical width equal to distance between their lateral edge and base of maxillary palpus in frontal view (fig. 52); antennal papilla in maximum profile broadly rounded, much shorter than basal diameter . . *Rophites* (*Rhophitoides*) *canus* Eversmann

9(7). Mandible without declivity on ventral surface traversing from outer tubercle cluster to, or nearly to, base of cusp (fig. 41) (declivity easily confused with wrinkles in similar position on dorsal surface of cleared specimen). Old World . . . . *Systropha planidens* Giraud

– Mandible with declivity on ventral surface traversing as a line from outer tubercle

cluster to, or nearly to, base of cusp (fig. 35). North America. 10

10(9). Internal epistomal ridge mesad of anterior tentorial pit pigmented, fading out halfway between pit and head midline; pigmented internal secondary ridge extending partway toward antenna from anterior tentorial pit. . . . . *Xeralictus timberlakei* Cockerell

– Internal epistomal ridge mesad of anterior tentorial pit unpigmented, virtually absent; pigmented internal secondary ridge extending from anterior tentorial pit toward antenna not evident . . . . . *Protodufourea eickworti* Bohart and Griswold

Mature Larvae of *Dufourea*

DIAGNOSIS: Mature larvae of *Dufourea* can immediately be distinguished from those of *Conanthalictus* because the latter have a recessed labiomaxillary region, the salivary opening lacks projecting lips, and the prothoracic dorsal tubercles are absent. The labiomaxillary region of *Dufourea* is forward projecting with pronounced salivary lips, and the prothorax bears a distinct pair of dorsal tubercles. Unlike all other known rophitines except for *Sphecodosoma*, mature larvae of *Dufourea* lack a well-defined articulating arm of the stipes. The large, rounded antennal papilla of *Sphecodosoma* separates that genus from *Dufourea*, all known mature larvae of which have smaller antennal papillae, with the sensilla tightly clustered at the apex of the papilla. The characters presented in the key should distinguish the species of *Dufourea* whose larvae were available for this study. These larvae, however, are very similar one to another.

Mature Larvae of *Dufourea holocyanea* (Cockerell) Figures 1–9, 12–17

DIAGNOSIS: The combination of normally broad salivary lips (fig. 3) and moderately large antennal disc (fig. 3) distinguish the mature larva of *Dufourea holocyanea* from those of *D. mulleri*, which has a small antennal disc (fig. 28), and *D. australis australis*, which has narrow salivary lips (fig. 10).

HEAD (figs. 3, 4): Integument of head capsule with scattered small sensilla that are
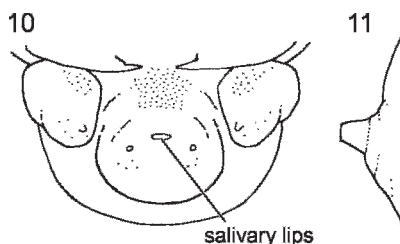
Figs. 10, 11. *Dufourea a. australis*, postdefecating larva. **10**. Frontal view of labiomaxillary region showing narrow salivary opening. **11**. Antenna, maximum lateral profile.

not obviously setiform; those of mouthparts with small setae; spiculation as described below. Integument unpigmented except for mandibular apices and anterior and posterior mandibular articulations.

Head (figs. 1, 2) moderately small compared with body size; head capsule wider than length measured from top of vertex to lower clypeal margin in frontal view. Tentorium complete, including dorsal arms. Anterior tentorial pit close to anterior mandibular articulation (fig. 3); posterior tentorial pits in normal position; postoccipital ridge moderately developed, becoming weaker toward vertex; median longitudinal thickening of head capsule nearly absent; hypostomal ridge moderately developed, its posterior section dividing into dorsally curving ramus that fuses with postoccipital ridge while ventral ramus bending mesad to join postoccipital ridge at posterior tentorial pit (best seen in postero-ventral view of cleared head capsule); pleurostomal ridge well developed; epistomal ridge laterad of anterior tentorial pit short because of closeness of pit to anterior mandibular articulation; ridge between pits fading out before reaching midline. Parietal bands evident as integumental scars. Antennal prominence rather weak; antennal disc moderately large, its diameter only slightly less than distance from its lower margin to center of anterior tentorial pit (latter distance measured in maximum profile); papilla projecting moderately, its height no more than one-half basal diameter, each bearing 3 sensilla (figs. 6, 16). Vertex evenly rounded, moderately broad, as seen from side, without projections. Labrum not projecting anteriorly as far as clypeus in lateral view (fig. 4), moderately short in
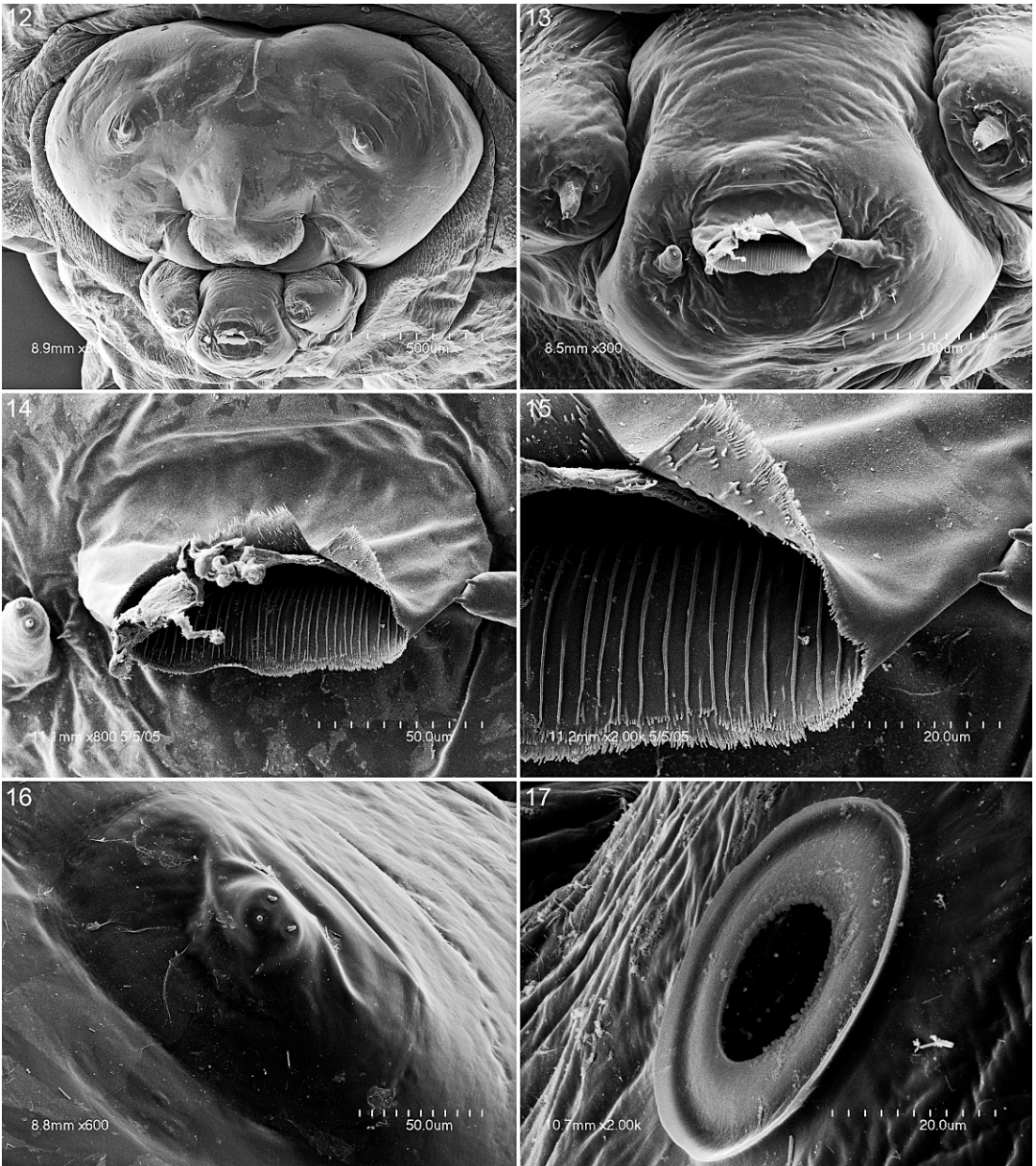
Figs. 12–17. SEM micrographs of predefecating larva of *Dufourea holocyanea*. **12**. Head, frontal view. **13**. Labiomaxillary region. **14**. Apex of labium. **15**. Close-up of salivary opening. **16**. Antenna, showing three sensilla. **17**. Spiracle.

frontal view (figs. 3, 12), apically shallowly bilobed when viewed anterodorsally; labrum spiculate laterally.

Mandible in adoral view tapering to narrowly pointed apex; dorsal apical edge with

sharp teeth; ventral apical edge with evenly spaced, sharp teeth; cusp moderately produced in dorsal and ventral views (figs. 7, 9), with numerous teeth; apical concavity shallow, facing hypopharyngeal surface; outer
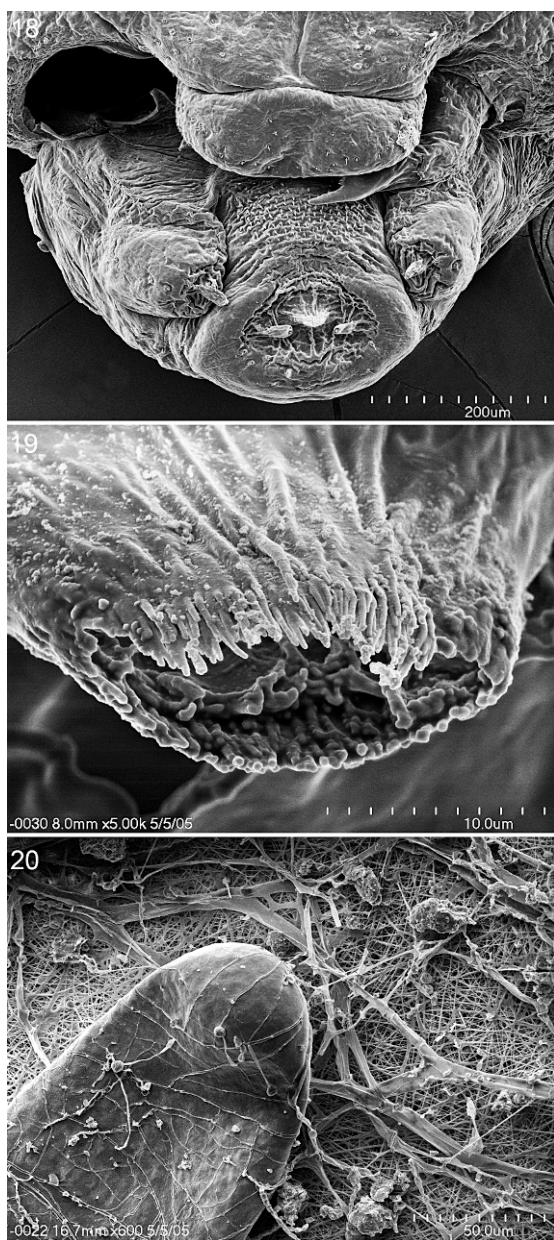
Figs. 18–20. *Dufourea a. australis*. **18**. SEM micrograph of postdefecating larva that had been cleared before being critical point dried and coated, showing mouthparts, with right mandible removed, approximate frontal view. **19**. Same, close-up of salivary opening. **20**. SEM micrograph of inner surface of cocoon showing one end of blackish object of unknown origin and silk strands of variable diameters; for photograph, see fig. 23; for discussion, see text.

mandibular surface with cluster of three or four conspicuously projecting tubercles, each bearing single short sensillum; apical dorsal surface with series of parallel ridges (some apparently with fine denticles) running in same direction as cuspal teeth; ventral surface with transverse declivity extending from outer tubercles toward cups, but this declivity not as pronounced or long as that of *Xeralictus timberlakei* and apparently *Protodufourea eickworti*. Labiomaxillary region strongly projecting in lateral view (fig. 4) with labium projecting well beyond apex of maxilla. Maxilla with dorsal surface spiculate; cardo, stipes evident but not pronounced; articulating arm of stipital sclerite not evident; maxillary palpus moderately large, longer than basal diameter, arising from maxillary apex. Labium strongly divided into prementum and postmentum, moderately long; premental sclerite not evident; labial palpus subequal in size to maxillary palpus. Salivary lips projecting, transverse, moderately narrow in frontal view (figs. 3, 13); as seen with SEM, upper and lower lips with apical fringe of papillae (figs. 14, 15); lower lip with internal surface consisting of parallel longitudinal ridges; upper lip with internal surface without such ridges but with scattered papillae. Hypopharynx protuberant, spiculate toward mouth, not longitudinally grooved; hypopharyngeal groove absent, so that hypopharynx curving onto labial apex.

BODY: Integument with fine scattered nonsetiform sensilla and with spiculate areas laterally behind head and toward rear of abdomen; some dorsal body tubercles faintly wrinkled apically, those of abdominal segment 3 and 4 somewhat flattened apically on postdefecating (but not predefecating) larva (see "Discussion of Relationships"). Body form (figs. 1, 2) moderately robust; intersegmental lines moderately weakly incised on predefecating form; on postdefecating form ventral intersegmental lines, particularly of abdomen, deeply incised; paired prothoracic dorsal tubercles present, smaller than those of mesothorax, metathorax, and most abdominal segments (figs. 1, 2); all tubercles conical (not transverse); abdominal segment 9 strongly produced ventrally; abdominal segment 10 positioned dorsally on 9 as seen in lateral

view (figs. 1, 2); on predefecating larva (fig. 2), ventral integument of segments 9 extended, causing segment 10 to be partly tilted and making anus appear dorsal on 10; on post-defecating larva (fig. 1), ventral integument of segment 9 strongly retracted. Spiracles small, those of thorax slightly larger than those of abdomen, those of predefecating larva without sclerites, not on tubercles, those of postdefe-cating larva on low tubercles composed of presumably thick chitin surrounding atrium (these tubercles so low as to be easily overlooked on specimens that are not stained); peritreme (figs. 5, 17) present, narrow; atrium projecting slightly beyond wall, with rim, globose; atrial wall smooth; primary tracheal opening with collar; subatrium normal in length, consisting of about 12 chambers. Male with median, transverse, integumental scar ventrally near apex of protrusion of segment 9 of predefecating larva but closer to posterior margin of segment of postdefecat-ing larva; female sexual characters visible only on some predefecating larva as pair of small, pale, subcutaneous imaginal discs arranged ventrally on each of abdominal segments 7, 8, and 9, with those of 7 farthest apart and those of 9 closest.

MATERIAL STUDIED: 3 postdefecating, 6 predefecating larvae, USA: Washington: Kittitas Co.: 21 km N of Yakima, between Yakima River and Highway 821 at 10.5 mi mark, June 2000 (E. Miliczky); 4 last larval instars, same except 15 km S of Ellensburg, along Umtanum Creek, 2 km W Yakima River, July 1996.

REMARKS: Eugene Miliczky is preparing a manuscript on the nesting biology of this species, specimens of which he kindly donated for this study.

Mature Larvae of *Dufourea australis australis*
Michener
Figures 10, 11, 18, 19

The mature larva of this species is known only from the postdefecating form.

DIAGNOSIS: Although there are several subtle differences distinguishing the postdefe-cating larva of this species from that of *Dufourea holocyanea* (as indicated in the following description) and *D. mulleri*, the extremely narrow salivary lips (fig. 10), of *D. a. australis* are the most reliable and easily used diagnostic feature.

HEAD (fig. 10): Integument as described for *Dufourea holocyanea*.

Head (figs. 10, 11, 18, 19) size and width, and tentorium as described for *Dufourea holocyanea*. Postoccipital ridge well developed, not becoming weaker toward vertex, in contrast to *D. holocyanea* and *D. mulleri*; other internal head ridges as described for *D. holocyanea*. Parietal bands evident as integu-mental scars. Antennal features as described for *D. holocyanea* except papilla (fig. 11) more elongate, its length nearly equal to basal diameter. Vertex and labrum as described for *D. holocyanea*.

Mandible similar to that of *Dufourea holocyanea* except tubercles on outer mandib-ular surface smaller, less conspicuous. Labiomaxillary region as described for *D. holocyanea* including absence of articulating arm of stipital sclerite and premental sclerite. Salivary lips projecting, transverse, extremely narrow in frontal view (figs. 10, 18), so that their apical width no greater that distance from their base to base of labial palpus. Hypopharynx as described for *D. holocyanea*.

BODY: Integument with fine, scattered, nonsetiform sensilla and with finely spiculate areas laterally behind head, toward rear of abdomen, and on many dorsal body tubercles; some dorsal body tubercles faintly wrinkled apically and somewhat flattened apically, suggesting apices of tubercles subject to defor-mation when larva resting on them (but see "Remarks" in treatment of *Protodufourea eickworti*). Body form, intersegmental lines, and dorsal body tubercles as described for postdefecating larva of *D. holocyanea*. Spiracles small, subequal in size, otherwise similar to those *D. holocyanea* except subatrial chambers may be numerous. Male with median, trans-verse integumental scar ventrally close to posterior margin of segment 9 of postdefecat-ing larva; female sexual characters unknown.

MATERIAL STUDIED: 2 postdefecating lar-vae, USA: Arizona Pima County: Desert Station, E. side of Tucson Mts., April 28, 1993 (J.G. Rozen); 12 postdefecating larvae, same except May 1, 1993; 7 postdefecating larvae, same except May 10, 1993.

REMARKS: JGR discovered nests of *Dufourea a. australis* on the steeply sloping (but not vertical) bank of a ravine at Desert Station in 1993. He visited the site on April 28, May 1, and May 10, when the following brief observations were recorded. These observations are augmented with others made during the preparation of the current paper on cells preserved in 1993 and retained in the collection of the AMNH.

One main tunnel and presumably others were open and 4 mm in diameter. Numerous cells were scattered about 15 to 20 cm deep into the bank. When first studied on April 28, they consisted of vacated cells, representing an earlier generation, and cells occupied by feeding and diapausing larvae of both *D. a. australis* and its cleptoparasite, *Neopasites cressoni* Crawford (Apidae: Nomadinae: Biastini). When examined on May 10, all larvae were postdefecating, an indication that both *D. a. australis* and *N. cressoni* are univoltine. Cell walls (figs. 21, 22) were thick, often 0.5 mm or more on sides and rear, harder than the substrate, and could be extracted intact from the ground as small hard nuggets. Female *D. a. australis* presumably impregnated the wall with a hardening substance, possibly nectar. When submerged in water, a piece of cell wall started to disassemble immediately and completely fell apart in a minute, as would be expected if the hardening substance were nectar.[5] The inner surface of the wall (fig. 21) was dull, even, but with small projecting soil particles, and was unlined, contrary to the reflective cell linings of most bees. When the cell wall disassembled in water, the inner surface may have had slightly more cohesion, possibly resulting from compression of very fine particles by some action (tamping?) by the female. Cell shape, like that of other rophitines, was symmetrical around its long axis, with floor and ceiling equally curved in side view, and wide compared with its length, measure from rear to center of closure (maximum diameter 5.0–

5.5 mm, length 6.0–6.5 mm, N = 8). Cell closures (fig. 22) were even spirals of four coils to the radius, concave on the inside, with a diameter of 2.5–3.0 mm, and on the outside smoothly concave with an even surface. The closures were about 0.5–0.8 mm thick in the middle where the outer and inner surfaces approach one another but much thicker on the periphery.

Completed cocoons of *Dufourea a. australis* (its cleptoparasite does not spin cocoons) were very thin and adhered tightly to the cell wall, so that the cocoon fabric could not be pulled away from the wall. The cocoon completely filled the cell lumen; its shape corresponded to the internal shape of the cell. The inner surface was slightly shiny, thereby contrasting with the dull cell wall before cocoon construction. In some cells, the cocoon was semitransparent, so that feces and tan substrate indistinctly showed through. In these cases, the cocoon gradually became opaque and paler toward the front end, and at the closure, its inner surface turning white (fig. 23). In other cells the cocoons were more uniformly pale and opaque. The cocoon fabric was a single layer; individual silk strands were usually not clearly identifiable under stereomicroscopic examination. Under SEM examination, white fabric at the closure end seemed to consist of extremely fine, crisscrossing silken strands as well as some coarser strands (fig. 20). In many cells uniformly shaped, elongate, blackish objects (figs. 20, 23), about 0.4 mm long, were scattered on the inner surface of whitish silk. Their flattened shapes suggested that they had desiccated. Although their uniformity of shape suggested that they might have been eggs, they showed no discernable microstructure under high SEM examination (fig. 20). Their identity and source are unknown.

In cells examined before cocoon construction, feces were deposited longitudinally as elongate flattened yellowish stripes[6] from the rear of the cell partway toward the closure end, so that the rear 2/3s to 3/4s of the cell wall

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[5] Nectar has been suspected to harden the cell wall of another but distantly related ground nesting bee, *Ashmeadiella holtii* Cockerell (Megachilidae) (Rozen, 1987), and has been definitely identified as forming part (i.e., mixed with masticated leaves) of the cell lining of another member of that genus that nests in preformed cavities (Rozen and Eickwort (1997).

[6] The fecal deposition of *Dufourea a. australis* should not be confused with that of its cleptoparasite, *Neopasites cressoni*. With the latter species, the fecal pellets are much shorter, so that they appear to be dabbed on the rear cell surface (fig. 26), giving the appearance of polka dots distributed over the surface, and, as with all Nomadinae, they are not covered by a cocoon.
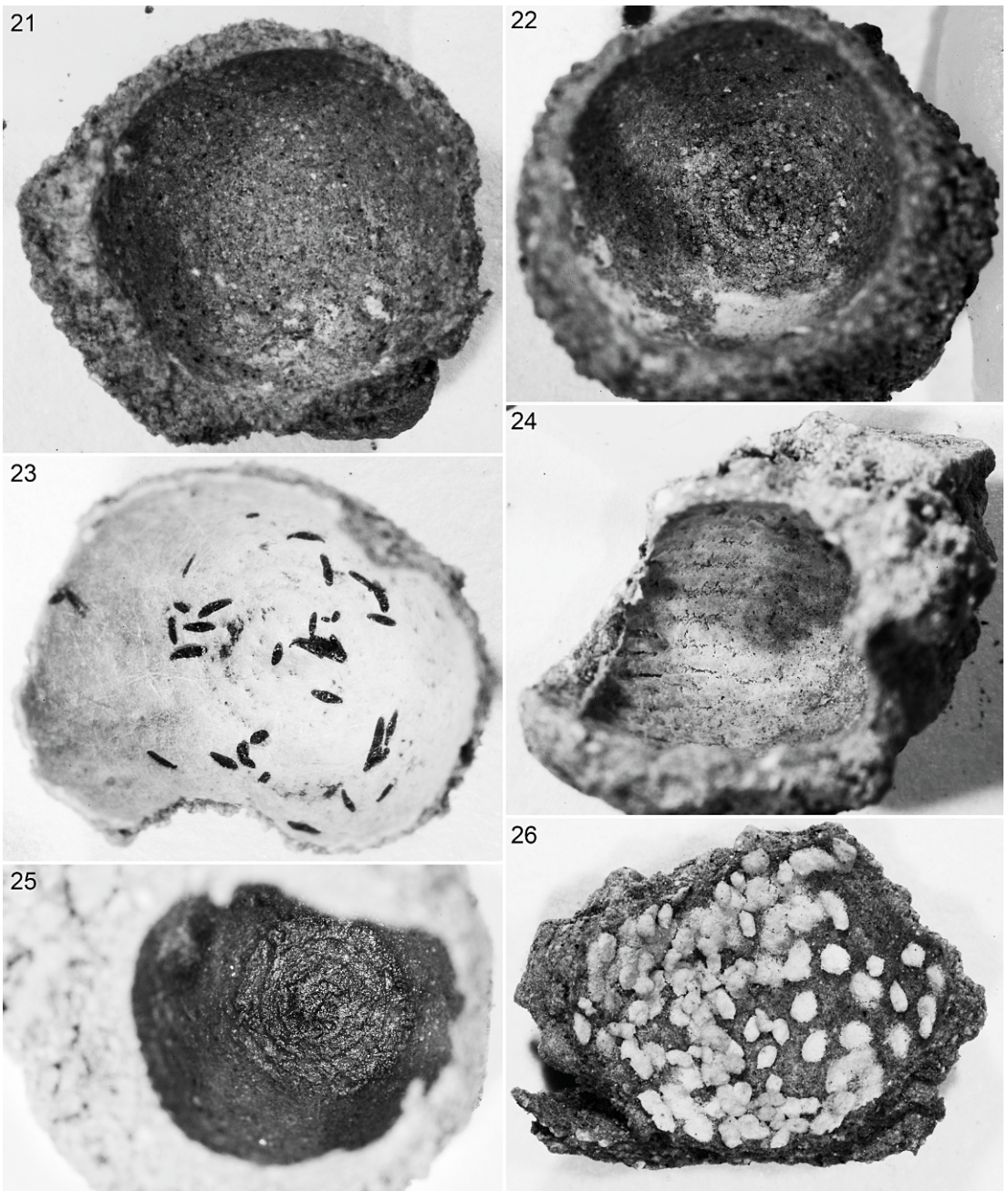
Figs. 21–26. Photographs of cells of *Dufourea a. australis*. **21**. Rear part showing matt finish of lining. **22**. Front end showing spiral closure; closure diameter 3.0 mm. **23**. Inner surface of cocoon showing white silken cocoon surface with elongate dark bodies. **24**. Rear sidewall of cell, front end toward left, showing parallel streaks of pale feces, deposited before cocoon spinning. **25**. Front end of cell, showing glistening, brownish material covering cell closure and front wall deposited before cocoon spinning. **26**. Cell wall showing feces of cleptoparasite *Neopasites cressoni*.

was evenly coated (fig. 24) but the remainder was uncoated. However, apparently before the feces are so deposited, the larva deposits a thin, brownish, glistening, semitransparent, coating over the anterior end of the cell, with the thickest part covering the cell closure (fig. 25). The source of the material, whether anal or salivary, is unknown, but it is visible as a nearly black mass at the center of the cell closure when the closure particles are removed from the outside, either mechanically or by submersion in water. After the cocoon is spun, this dark material and even the feces toward the rear of the cell are hidden by the cocoon fabric.

Diapausing larvae were invariably found curled in their cocoons with the abdominal apex touching the venter of the head and prothorax, as depicted for *Rophites canus* (fig. 50).

Vacated cells indicate that fresh adults emerge by chewing through the front end of the cocoon and cell closure.

On each visit, the ratio of recovered host larvae to cleptoparasite larvae was: April 28, 6:8; May 1, 19:9; May 10, 24:6; grand total 49:23. These ratios seem to suggest that *Neopasites cressoni* may be much more successful finding and parasitizing host cells earlier rather than later in the nesting season.

Predefecating Larva of *Dufourea mulleri* (Cockerell)
Figures 27–30

McGinley (1981) listed some of the important features of the mature larva of *Dufourea mulleri* and later (McGinley, 1987) presented illustrations of the larva. The following description is based only on predefecating larvae.

DIAGNOSIS: The normally broad salivary lips and small antennal disc, as presented in the key, will best separate the larvae of this species from those of other known *Dufourea*.

HEAD (fig. 28): Integument as described for *Dufourea holocyanea*.

Head size and width as described for *Dufourea holocyanea*. Tentorium and internal head ridges as described for *D. holocyanea* (including weakening postoccipital ridge toward vertex). Parietal bands and antennal

features as described for *D. holocyanea* except antennal disc small, its diameter almost one-half times distance from it lower margin to center of anterior tentorial pit (latter distance measured in maximum profile); antennal papilla (fig. 30) projecting moderately strongly, its height more than one-half basal diameter. Vertex and labrum as described for *D. holocyanea*.

Mandible as described for *D. holocyanea*, except outer mandibular surface with tubercles less pronounced (fig. 29) but clearly present, as in all known Rophitinae, contrary to McGinley (1987: 693, fig. 12.187c). Labiomaxillary region, salivary lips, and hypopharynx as described for *D. holocyanea*.

BODY: Integument as described for *Dufourea holocyanea* except dorsal body tubercles of postdefecating larva unknown. Body form of predefecating larva (fig. 27) as described for *D. holocyanea*. Spiracles of predefecating larvae as described for those of *D. holocyanea* except subatrium slightly longer, consisting of approximately 15 chambers. Male and female sex characters unknown.

MATERIAL STUDIED: 12 predefecating larvae, USA: Arizona: Cochise County: 3 mi S of Rodeo, New Mexico, V-4-1966 (J.G. Rozen, M.S. Favreau).

REMARKS: Torchio et al. (1967) described the nesting biology of this species (note especially their fig. 5 showing typical rophitine diapausing posture) and that of the following species whose mature larvae were not collected: *D. malacothricis* Timberlake, *D. pulchricornis* (Cockerell), and *D. trochantera* Bohart.

Mature Larva of *Dufourea novaeangliae* (Robertson)
Eickwort et al., 1986: figs. 10–15

DESCRIPTION: Eickwort et al. (1986) presented an account of the biology and mature larva of this species and compared the larva with others that had been described previously. Although we have been unable to locate the specimens they studied, most of the larval features described and depicted correspond closely with cocoon-spinning rophitine larvae treated here. They stated that the hypopharyngeal groove was present, but their illustration (their fig. 11) does not reveal a groove
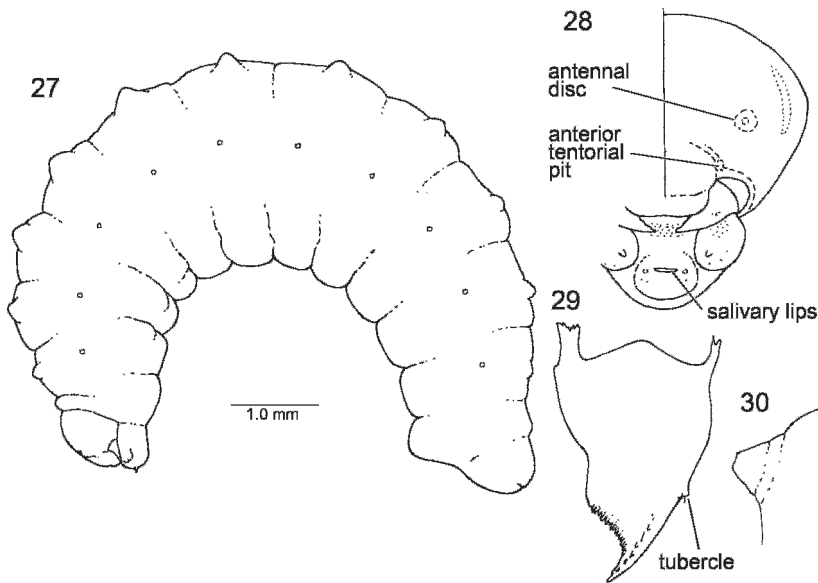
Figs. 27–30. *Dufourea mulleri*. **27**. Predefecating larva, lateral view. **28**. Head, frontal view (atp = anterior tentorial pit). **29**. Right mandible, ventral view. **30**. Antenna, maximum lateral profile. Scale refers to figure 27.

immediately above the salivary lips where the groove should be. Rather it shows a transverse line much farther toward the mouth, so that we suspect that they misidentified the true groove, which normally is a simple folding of the integument associated with the articulating arms of the maxillae. In their comparisons of larvae, they state that larvae of *Dufourea novaeangliae*, *D. mulleri*, *Rophites canus*, and *Systropha punjabensis* Batra and Michener are "only slightly lower than the other thoracic tubercles", contrasting with a statement that the tubercles of these genera were "markedly smaller than the following" tubercles (Rozen and McGinley, 1976). Although we have not been able to examine larvae of *D. novaeangliae*, larvae of the other cocoon-spinning rophitines examined for the current study have prothoracic tubercles that are noticeably smaller than the other thoracic tubercles, as indicated in figs. 1, 2, 27, 31, and 50. It is inappropriate to compare the description and illustrations of the larva of *S. punjabensis* (Batra and Michener, 1966: figs. 13–15) with that of the others since that was not a last larval instar.

REMARKS: An interesting discovery made by Eickwort et al. (1986) was the presence of a thin, clear, waterproof coating on the provisions of *Dufourea novaeangliae*, subsequently also noted on the provisions of *Sphecodosoma dicksoni* (Rozen, 1993). Such covering of provisions had heretofore been observed only among certain Panurginae (Andrenidae) (Rozen, 1958, 1967).

Mature Larvae of *Sphecodosoma*
(*Sphecodosoma*) *dicksoni* (Timberlake)
Rozen, 1993: figs. 25–32

DIAGNOSIS: The large, rounded antennal papilla (Rozen, 1993: fig. 28) in combination with the actually or near absent articulating arm of the stipes distinguishes this species from all known cocoon-spinning larvae of the Rophitinae.

DESCRIPTION: See Rozen (1993) in which the mature larvae are described and illustrated.

REMARKS: The nesting of this species was briefly described by Rozen and McGinley (1976), and Rozen (1993) subsequently gave a more complete account of its nesting biology.
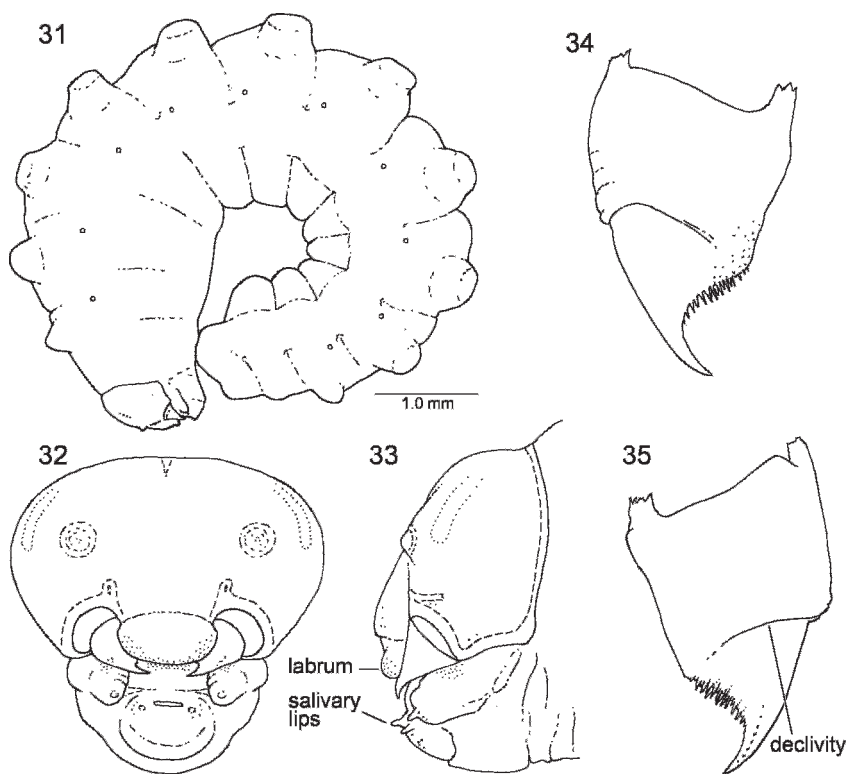
Figs. 31–35. *Protodufourea eickworti*. **31**. Live postdefecating larva, lateral view. **32, 33**. Head, frontal and lateral views, respectively. **34, 35**. Right mandible dorsal and ventral views, respectively. Scale refers to fig. 31.

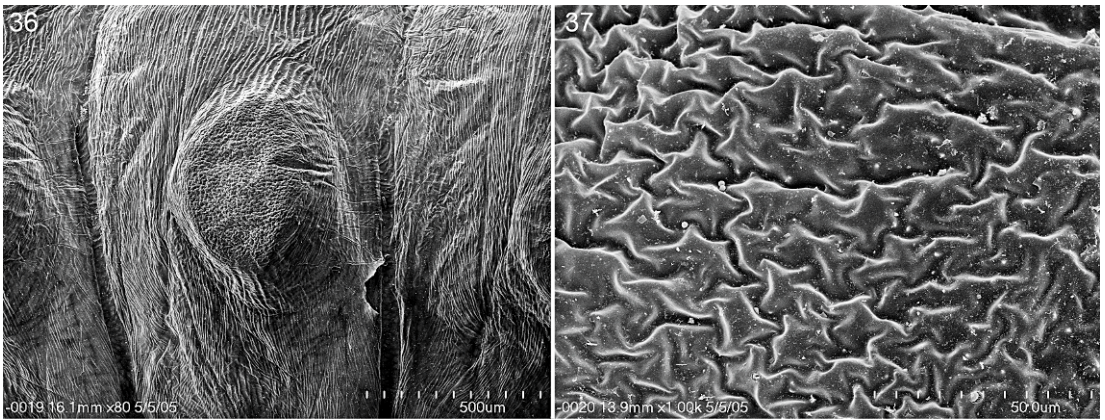### Postdefecating Larva of *Protodufourea eickworti* Bohart and Griswold
Figures 31–35, 36, 37

DIAGNOSIS: The postdefecating larva of this species and that of *Xeralictus timberlakei* can be distinguished from those of other known genera in the Rophitinae by pronounced truncate dorsal tubercles on the midbody segments and the ventral transverse declivities on their mandibles. They are quite similar to one another even though *Protodufourea eickworti* is considerably smaller, has a far broader head when seen in frontal view, and its antennal disc is larger than that of *X. timberlakei*. Many larval features of these two genera are similar to those of the Old World *Systropha planidens*.

HEAD (figs. 32, 33): Integument of head as described for *Dufourea holocyanea*.

Head features as described for *Dufourea holocyanea* except for following: Postoccipital ridge well developed its entire length; median longitudinal thickening well developed but short; epistomal ridge between anterior tentorial pits weak, scarcely visible, fading out before reaching midline. Diameter of antennal disc about 0.8 times distance from its lower margin to center of anterior tentorial pit; antennal papilla with 3–4 sensilla. Labrum apically broadly rounded when viewed anterodorsally; labral tubercles scarcely evident.

Mandible (figs. 34, 35) in general similar to, and as described for, that of *Dufourea holocyanea*, except for following: dorsal apical edge distal to dentate cusp apparently without teeth; ventral apical edge with extremely fine teeth; tubercles on outer mandibular surface not strongly projecting, without setiform sensilla, but on dorsal and ventral surfaces giving rise to long, curved declivity that fades before reaching inner mandibular edge, this declivity similar to, and presumably homologous with, that found in *Xeralictus timberlakei*

Figs. 36, 37. SEM micrographs of left dorsal tubercle on abdominal segment 3 of postdefecating larva of *Protodufourea eickworti* and close-up of same, dorsal view, respectively.

(Snelling and Stage, 1995: figs. 16, 17). Labiomaxillary region moderately projecting in lateral view. Maxilla with dorsal surface spiculate; cardo, stipes evident; articulating arm of stipital sclerite pronounced even if not strongly pigmented; maxillary palpus moderately large, longer than basal diameter, arising from maxillary apex. Labium strongly divided into prementum and postmentum, moderately long; premental sclerite not evident; labial palpus distinctly smaller than maxillary palpus. Salivary lips projecting, transverse, moderately narrow in frontal view (fig. 32). Hypopharynx protuberant, spiculate toward mouth, without longitudinal groove; hypopharyngeal groove created by articulating arms of stipes.

BODY: Integument with fine, scattered, nonsetiform sensilla. Body form moderately robust; on postdefecating form ventral intersegmental lines particularly of abdomen deeply incised; paired prothoracic dorsal tubercles present, smaller than those of mesothorax, metathorax, and most abdominal segments (figs. 31, 36, 37); all tubercles conical (not transverse); paired dorsal body tubercles of meso- and metathorax and of abdominal segments 1–8 tending to be subtruncate to truncate, their flattened surface finely wrinkled, faintly convex to concave (see "Remarks", below, and "Discussion of Relationships"; abdominal segment 9 strongly produced ventrally; abdominal segment 10 positioned dorsally on 9 as seen in lateral

view (fig. 31). Spiracles small, subequal in size; peritreme present, narrow; atrium projecting slightly beyond wall, with rim, globose; atrial wall smooth; primary tracheal opening with collar; subatrium normal in length, consisting of about 12 chambers. Male with median, transverse, integumental scar near posterior margin of segment; female sexual characters unknown.

MATERIAL STUDIED: 1 postdefecating larva, USA: Arizona: Pima County: Desert Station, E side of Tucson Mts., March 30, 1995 (J.G. and B.L. Rozen); 1 postdefecating larva, same except collected March 30, 1995, preserved July 8, 2003; 1 postdefecating larva, same except collected March 29, 1995, preserved April 12, 1995.

REMARKS: Rozen et al. (1997) described the nesting biology of this species in connection with a study of its cleptoparasite, *Rhopalolemma rotundiceps* Roig-Alsina (Apidae: Nomadinae: Biastini).

The midbody segments of this species as well as of *Xeralictus timberlakei*, and very probably *Systropha planidens* have paired dorsal tubercles that are more or less conspicuously truncate apically. The midbody dorsal tubercles of *Rophites canus* and even of *Dufourea a. australis* also tend to be truncate, but the flattened surfaces are smaller and less noticeable. Further, at least in the cases of *X. timberlakei*, *Protodufourea eickworti*, and *S. planidens*, the apical integument of these tubercles is finely wrinkled with the wrinkles

forming a nondirectional pattern (e.g., not a transverse or longitudinal pattern) compared with the surrounding integument; thus the surface appears almost pebbled at first viewing (figs. 36, 37). There is some indication that the integument on the sides of these tubercles is soft so that the tubercles can be compressed, accentuating their truncate shape (see figs. 36, 60, 61). It may be that nondirectional wrinkling of the apices provides the tubercles with integumental strength compared with the sides of the tubercles. In the case of predefecating larva of *S. planidens* the apices, when stained, have a well-defined, thicker integument than the surrounding integument. However, in *R. canus* and species of *Dufourea*, the apices of the tubercles seem soft because they become rounded and even truncate by the weight of the larva when lying on its dorsum. The anatomy and functioning of body tubercles, whether truncate or not, in the Rophitinae need further study; dorsal tubercles somehow may enable the larva to move while feeding, defecating, and/or cocoon spinning.

Postdefecating Larva of *Xeralictus timberlakei* Cockerell
Snelling and Stage, 1995: figs. 12–18

DIAGNOSIS: See "Diagnosis" in the treatment of *Protodufourea eickworti*, above.

DESCRIPTION: The larva of this species is still known from a single specimen, the original description and illustrations of which appeared in a paper by Snelling and Stage (1995). The diameter of its antennal disc measures about 0.5 times the distance between the lower edge of the disc and the center of the anterior tentorial pit.

REMARKS: A seemingly remarkable feature of this unique specimen was the truncate dorsal body tubercles, which at the time of the original description were thought to be an artifact, the result of the larva being confined to a small cell. This conclusion now must be revised in light of similar truncate dorsal body tubercles discovered on the larva of *Protodufourea eickworti* (fig. 31, 36) and to a lesser extent on larvae of some other species. Please see "Remarks" in the treatment of *P. eickworti* for a reinterpretation of

this anatomical feature shared by these genera.

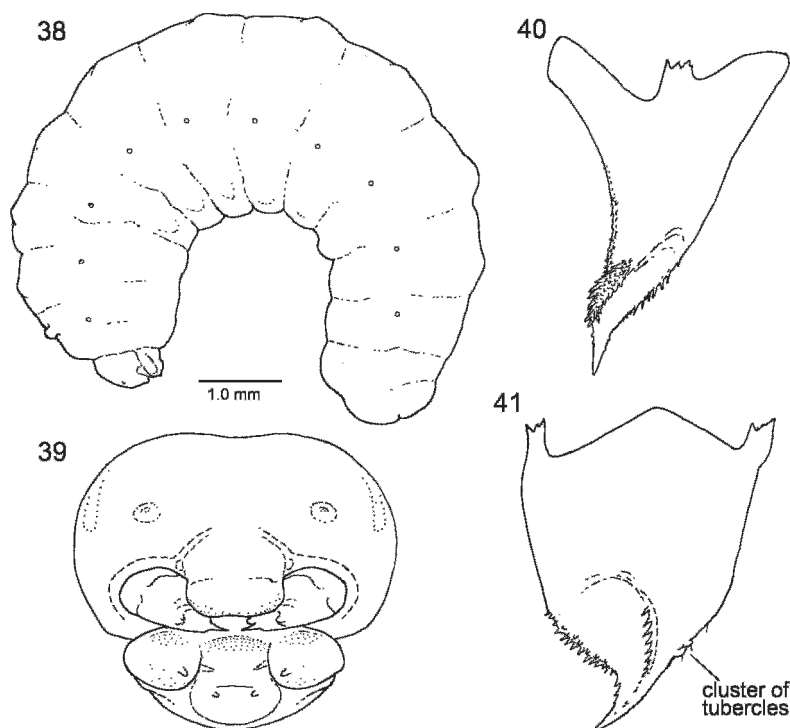Predefecating Larva of *Systropha* (*Systropha*) *planidens* Giraud
Figures 38–46

DIAGNOSIS: Because of its projecting labio-maxillary regions, this species can easily be distinguished from *Conanthalictus*. The clear presence of the articulating arm of the stipes separates it from all known *Dufourea* and *Sphecodosoma*, and characters presented in the key will enable it to be separated from the other taxa treated here.

HEAD (figs. 39, 42): Integument of head capsule as described for *Dufourea holocyanea*. Integument unpigmented except for mandibular apices.

Other head features as described for *Dufourea holocyanea* except for following: median longitudinal thickening of head capsule absent; antennal disc moderate in size, its diameter about 0.8 times distance between its lower margin and center of anterior tentorial pit; antennal papilla projecting less than one-half basal diameter; labrum with low labral tubercles (rather than merely bilobed as in *D. holocyanea*) though not surpassing clypeus in lateral view.

Mandible (figs. 40, 41) as described for *Dufourea holocyanea* except more sinuate in aboral and adoral views (figs. 40, 44) and tubercle cluster less projecting on outer surface (fig. 41). Labiomaxillary region projecting in lateral view but not as strongly as in *Dufourea* and *Sphecodosoma*. Inner surface of lower lip with parallel ridges (figs. 45, 46) similar to those of *D. holocyanea*; microstructure of inner surface of upper lip uncertain. Other feature of maxilla and labium as described for *D. holocyanea*, except for following: articulating arm of stipital sclerite evident. Hypopharynx as described for *Dufourea holocyanea*.

BODY: Integument as described for predefecating *Dufourea holocyanea*. Body shape-[?or change "form" 3X in this same clause to "larva"?] of postdefecating form unknown; intersegmental lines moderately weakly incised on predefecating form, unknown on postdefecating form; paired prothoracic dorsal tu-
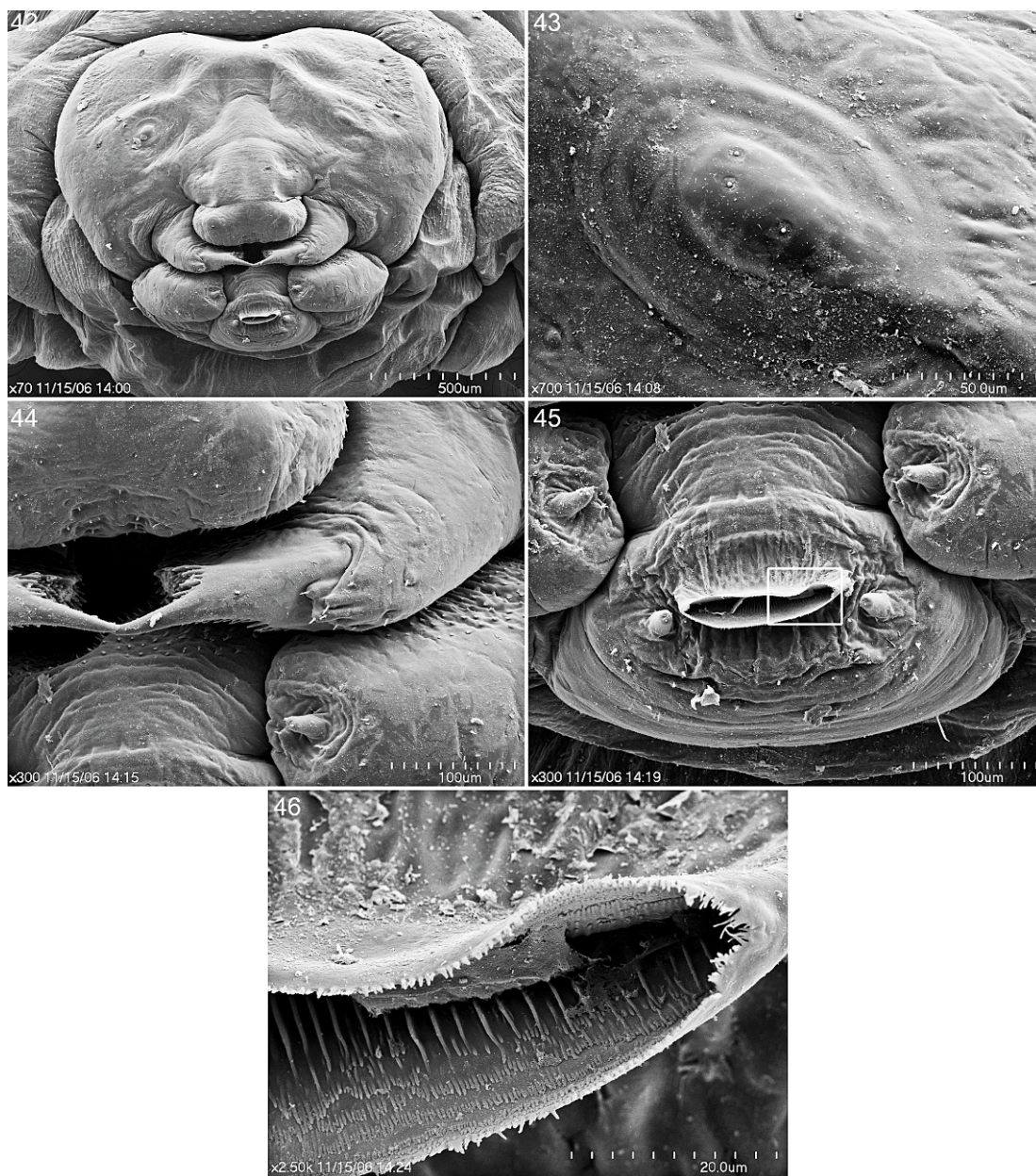
Figs. 38–41. *Systropha planidens*. **38**. Predefecating larva, lateral view. **39**. Head, frontal view. **40, 41**. Right mandible, inner and ventral views, respectively. Scale refers to fig. 38.

bercles present, more sharply defined but apparently smaller than those of mesothorax, metathorax, and most abdominal segments (fig. 38); all tubercles conical (not transverse); midbody tubercles appearing apically rounded but with apical surfaces thicker and finely wrinkled, so that those of postdefecating larva possibly truncate; abdominal segment 9 strongly produced ventrally; abdominal segment 10 positioned dorsally on 9 as seen in lateral view (fig. 38); on predefecating larva, ventral integument of segments 9 extended, causing segment 10 to be partly tilted and making anus appear somewhat dorsally on 10; ventral integument of segment 9 on postdefecating larva unknown. Spiracles small; those of thorax slightly larger than those of abdomen, those of predefecating larva without sclerites; those of postdefecating larva unknown; other spiracular features as describe for *D. holocyanea* except subatrium consisting of about 10 chambers. Male with median, transverse, integumental scar ventrally near apex of protrusion of segment 9 of predefecat-

ing larva, unknown on postdefecating larva; female sexual characters visible on predefecating larva as small, paired, ventral, pale, subcutaneous imaginal discs arranged sublaterally on abdominal segments 7, 8, and 9, with those of 7 farthest apart and those of 9 closest.

MATERIAL STUDIED: 4 predefecating larva, Turkey: Erzurum: Atatürk University campus, N 39°54′09″ E 41°14′06″, July 4, 2001 (J.G. Rozen); 2 predefecating larvae, same except July 1, 2001 (J.G. Rozen, H. Özbek).

REMARKS: We studied two nests of this species July 1, 2001, on the campus of Atatürk University (see fig. 63). Main burrows were open, with diameters of 5.0 and 5.5 mm, and descended more or less vertically. Cells were arranged singly and occurred between the depths of 8 and 14 cm. Because the nests were still early in construction, other cells would likely have been added at lower depths. Cells, symmetrical around their long axis, were nearly horizontal, their rears tilted slightly downward. They appeared ovoid (fig. 47), like the cells of other rophitines, in that their

Figs. 42–46.   SEM micrographs of predefecating larva of *Systropha planidens*. **42**. Head, frontal view. **43**. Left antenna. **44**. Close-up of left mandible, outer view, showing outer, apical tubercle cluster and sinuate shape of apex. **45**. Apex of labiomaxillary region. **46**. Close-up of salivary opening identified by rectangle in fig. 45.

length ranged from 9.5 to 12.0 mm (N = 3) and their maximum diameter was 8.0 mm (N = 2). Cell walls were dull, smooth, without any evidence of a shiny lining, but the fine-grained surface was presumably smoothed by some activity of the female. When a water droplet was applied to the wall, the droplet was absorbed almost immediately. A number

of cell walls had irregular gouges (fig. 47), very possibly created by the *Systropha* female removing cleptoparasite eggs with her mandibles. *Biastes brevicornis* (Panzer) (Apidae: Nomadinae: Biastini), a confirmed parasite of this and another species of *Systropha* (Warnke, 1982), was collected in the area. One cell closure (fig. 48) was shallowly concave on the inner surface and had 3–4 coils to the radius. Laterals, backfilled after cell closure, were 8–10 mm in length (N = 2). Provisions were spherical, and two were 5.0 mm in diameter. The above information is consistent with that presented by Malyshev (1925a) concerning the nesting biology of this species, the larva of which, as he points out, "spins a cocoon and ejects excrements" and "hibernates curled up and lying freely in the cocoon." Grozdanić and Vasić (1968) described nests of this species and reported that one nest was 48 cm deep, far deeper than ours. In most other respects the nest construction was similar to that of our nests including burrow diameter and cell size. However, they reported that inner surface of the cells were shiny ("glänzed"); we think this is unlikely since all other rophitines about which we have information characteristically have dull inner surfaces, including those of *S. planidens* preserved in the AMNH from the current study.

Batra and Michener (1966) described a nest and an immature larva of the closely related *Systropha* (*Systropha*) *punjabensis* Batra and Michener.

Mature Larvae of *Rophites* (*Rhophitoides*) *canus* Eversmann
Figures 50–62

DIAGNOSIS: The mature larva of this species can be distinguished from those of *Conanthalictus*, *Dufourea*, and *Sphecodosoma* by the combination of the presence of both projecting labiomaxillary region and the articulating arm of the stipes. Its labral tubercles are forward directed as is also the case with *Rophites algirus trispinosus*, but unlike in the latter, the salivary lips are moderately wide, their apical width at least equal to the distance between their lateral edges and the base of the maxillary palpi, as seen in frontal view (fig. 52).

HEAD (figs. 52, 53, 56): Integumental setation of head capsule as described for *Dufourea holocyanea*. Integument unpigmented except for mandibular apices, anterior and posterior mandibular articulations, and anterior and posterior tentorial pits.

Head morphology as described for *Dufourea holocyanea* except for following: Antennal disc much smaller than that of *Dufourea holocyanea*, its diameter about 0.6 times distance from its lower margin to center of anterior tentorial pit (latter distance measured in maximum profile). Vertex (fig. 53) narrowly rounded as seen from side because of backward slant of frons. Labrum projecting beyond clypeus in lateral view (fig. 53) because of moderately projecting labral tubercles.

Paired mouthparts as described of *Dufourea holocyanea* except for following: Mandible (fig. 54) with ventral apical edge lacking teeth. Labiomaxillary region moderately projecting in lateral view, with labium projecting only moderately beyond apex of maxilla (fig. 53). Articulating arm of stipital sclerite evident on cleared specimen, though not pigmented; maxillary palpus moderately slender, as long as twice basal diameter. Labial palpus slender, twice as long as basal diameter, subequal in size to maxillary palpus. Salivary lips projecting, transverse, moderately wide in frontal view (figs. 52, 57); as seen with SEM, upper and lower lips with apical fringe of papillae (figs. 57, 58); lower lip with internal surface covered with dense rows of papillae contrasting with the longitudinal ridges in *D. holocyanea*; upper lip with internal surface also covered by dense papillae; thus salivary lips of this species differing substantially from those of *D. holocyanea*. Hypopharynx as described for *Dufourea holocyanea*.

BODY: Integument with fine, scattered, nonsetiform sensilla and with finely spiculate areas ventrally. Body form approximately as described for *Dufourea holocyanea* including paired prothoracic dorsal tubercles present, smaller than those of mesothorax, metathorax, and most abdominal segments (figs. 50, 60); all tubercles conical (not transverse); midbody tubercles (figs. 60, 61) tending to be truncate with apices finely wrinkled as in *Protodufourea eickworti* and *Xeralictus timberlakei* (see dis-
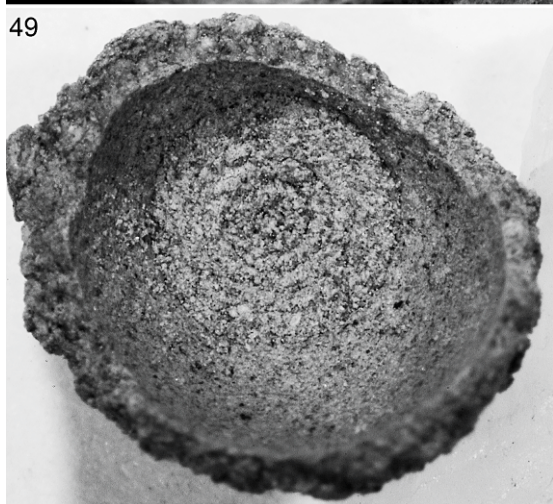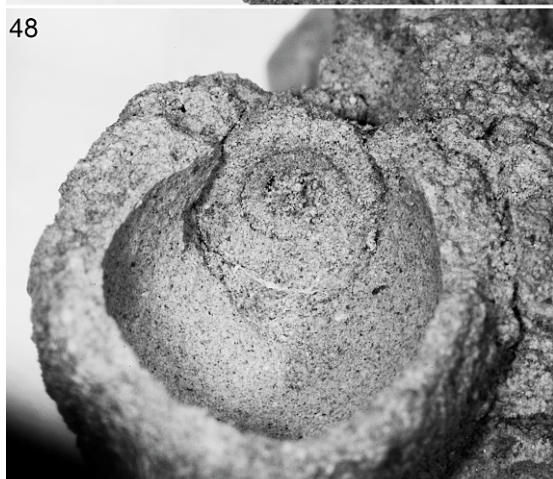
Fig. 47. *Systropha planidens*, cell, side view, front end toward left, showing dull wall with gauge marks (arrows) presumably caused by female

cussion under "Remarks" in treatment of *P. eickworti*); terminal abdominal segments as described for *Dufourea holocyanea*. Spiracles (fig. 62) as described for *Dufourea holocyanea*. Male and female sex characters as described for *Dufourea holocyanea*.

MATERIAL STUDIED: 4 postdefecating larvae, Turkey: Erzurum: Atatürk University campus, N 39°54′09″ E 41°14′06″, elevation. 1850 m, August 5–9, 2004 (H. Özbek); 10 last larval instars, same except August 21, 2001.

REMARKS: Enslin (1921) presented an extensive account of the life history of *Rophites canus* and described its mature larva and cocoon. Subsequently, Malyshev (1925b) also described aspects of its nests. More recently Wilkaniec et al. (1985) gave an account of its nesting and also evaluated its pollination potential with respect to seed production of alfalfa. The following refers to the nesting site (fig. 63) where we collected the larvae, described above, on the campus of Atatürk University, Erzurum, Turkey, in the last days of June 2004. We first discovered the site because of the many males searching low over the ground for females at a corner of a seldom-used soccer field. We excavated the site on July 6 and 10, 2004, by which time nesting activity was obvious because of nest-entrance tumuli among the low vegetation of herbs and grasses that partly covered the area. Because the nesting season was early, HÖ returned to the site August 5–9, 2004, to retrieve the postdefecating larvae. We also include here data, inserted parenthetically, from a single nest that we excavated not far from the 2004 site on July 4, 2001.

The site occupied an area of about 1 m^2 with a horizontal surface. We were able to identify nest entrances by the tumuli of loose, dry soil surrounding them. Main tunnels, approximately 3.0 mm in diameter (3.5 mm in diameter in the 2001 nest), descended vertically in a meandering fashion probably caused by pebbles and roots. Laterals leading

←

removing cleptoparasite eggs; cell length 11.0 mm. Fig. 48. Same, front end of cell showing spiral closure; closure diameter 4.3 mm. Fig. 49. *Rophites canus*, front end of cell showing spiral closure; closure diameter 3.0 mm.
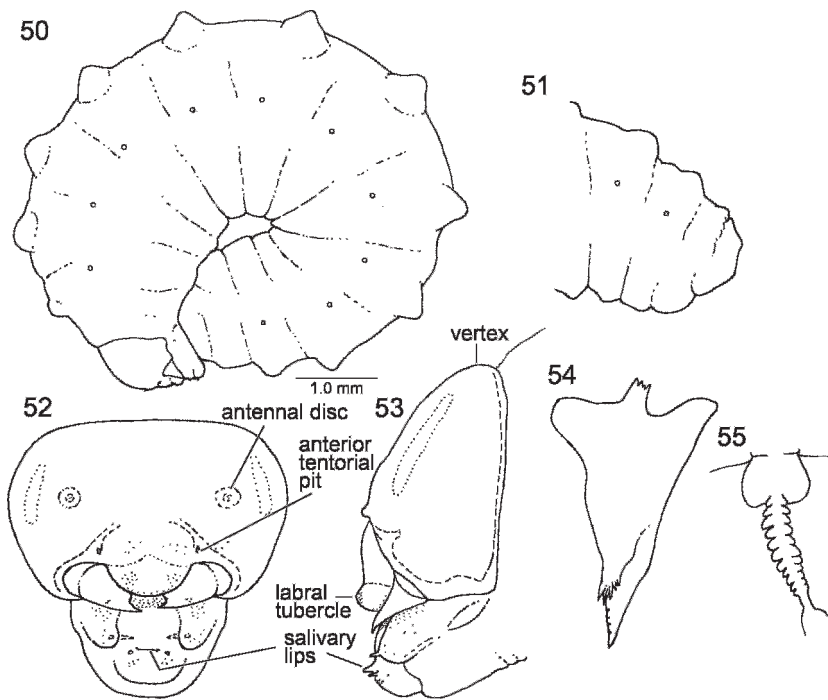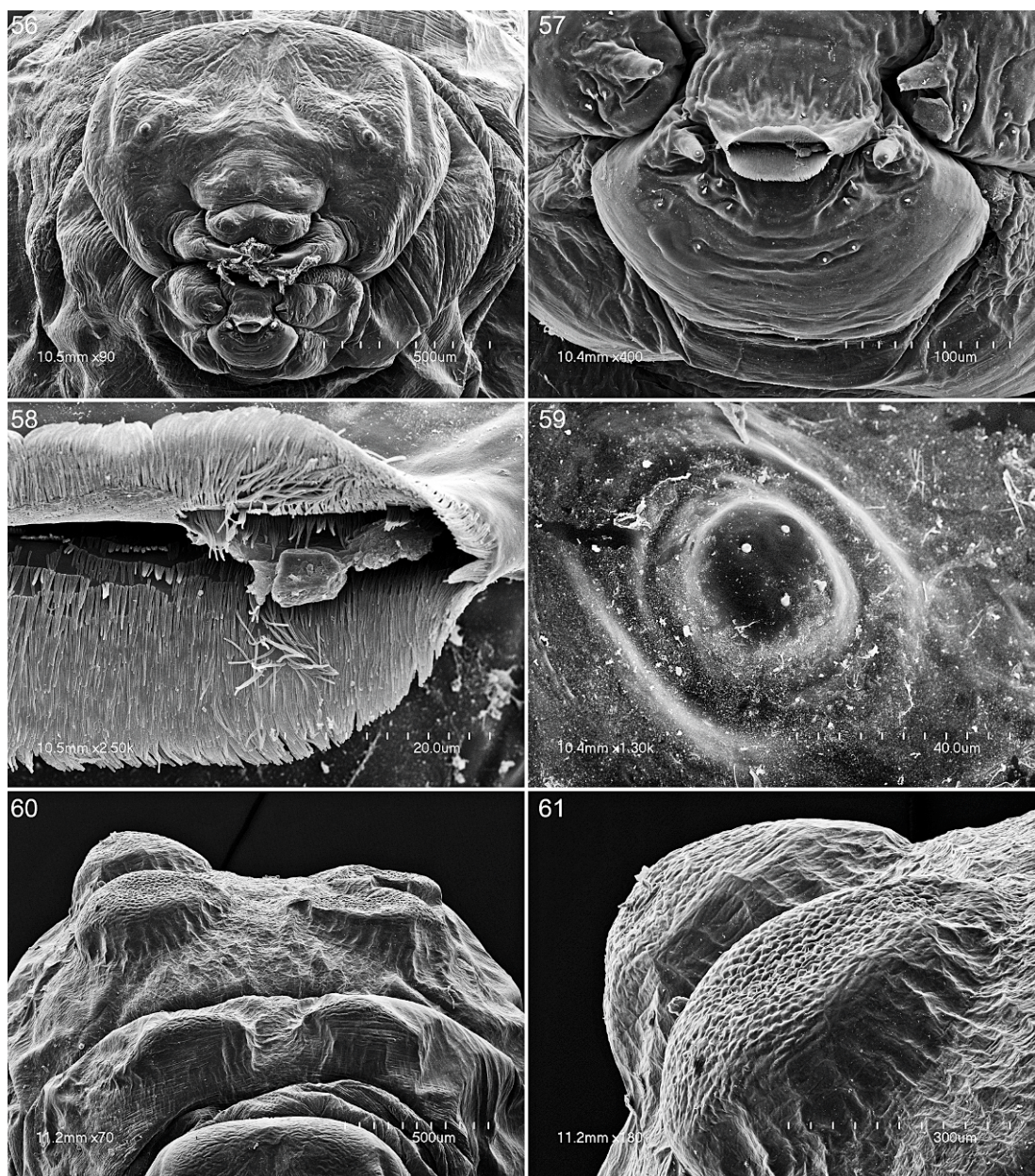
Figs. 50–55. *Rophites canus*. **50**. Postdefecating larva, lateral view. **51**. Apex of abdomen, lateral view. **52**. Head, frontal view. **53**. Head, lateral view. **54**. Right mandible, inner view. **55**. Spiracle, side view. Scale refers to figs. 50, 51.

to single cells were filled with soil after cell closure. Cells, with the long axis nearly horizontal, were encountered starting at the depth of approximately 10 cm with other cells appearing several centimeters lower (8–13 cm in the 2001 nest). We did not find cells to the depths of 25–30 cm reported by Enslin (1921), to the depth of 20 cm as reported by Malyshev (1925b), or to the depth of 23 cm according to Wilkaniec et al. (1985). However, our nests were in the early stages of construction. Cells were arranged variously: singly, in linear series of two, and in one case two cells each leading to another cell in front of them (two from the 2001 nest may have been in linear series). Cells were ovoid in shape; one measured 4.9 mm in maximum diameter and 5.5 mm in length (a single cell in 2001 measured 5.0 mm in maximum diameter and 6.5 mm long; Wilkaniec et al. (op. cit.) measured one cell 6 mm long and 5 mm in diameter; and Enslin (op. cit.) reported cells 6.0–6.5 mm in diameter). They were symmetrical around their long axis, without a flattened floor. Cell closures

(fig. 49) were distinct concave spirals in the inner surface with 5–6 coils to the radius. Cell walls were not noticeably harder than the substrate. Their surface was dull (i.e., without a shiny lining) but somewhat waterproof in that a water droplet placed on the surface took 2 min. to be absorbed, whereas a water droplet placed on the surrounding soil was instantaneously absorbed. The 2001 excavation demonstrated that the cell construction was progressive, with older larvae found above younger ones. Three cells were connected to the main burrow by laterals that were 1.2, 1.5, and 1.6 mm long.

Completed provisions were spherical, pale yellow, with a smooth surface, and without a waterproof coating (they "melted" when placed in water in both the 2001 and 2004 studies). Such a coating has been reported for *Sphecodosoma dicksoni* (Rozen, 1993) and *Dufourea novaeangliae* (Eickwort et al., 1986). A sample of eight provisions had a median diameter of 3.3 mm with a range of 2.8–3.6 mm (one from the 2001 study was

Figs. 56–61. SEM micrographs of postdefecating larvae of *Rophites canus*. **56**. Head, frontal view. **57**. Labiomaxillary region, frontal view. **58**. Close-up of salivary lips, frontal view. **59**. Left antenna, showing four sensilla. **60**. Paired dorsal thoracic tubercles. **61**. Close-up of meso- and metathoracic tubercles, right side, showing texture of flattened apices.

3.5 mm in diameter). Malyshev (1925b) measured them at 3.0–3.25 mm in diameter, and Wilkaniec et al. (1985) claimed they ranged 3.0–3.5 mm in diameter. Enslin (1921) stated that the food masses were 6 mm in diameter, a questionable measurement since it is approximately the same as the diameter of the cells that he had measured.

Figs. 62, 63. *Rophites canus*. **62**. SEM micrograph of spiracle. **63**. Nesting site (in foreground) at the soccer field on the campus of Atatürk University, Erzurum, Turkey. This is the same soccer field where nests of *Systropha planidens* were excavated.

The postdefecating larvae, when extracted from their cocoons, were completely covered with a shiny, clear, dry coating that, on first glance, seemed to (but did not actually) glue the posterior end of the abdomen to the ventral surface of the labium, pro-, and mesothorax. The source of the coating is presumably glandular but from what glands is unknown. It was obviously deposited after cocoon construction. The coating perhaps functions to prevent water loss. JGR has observed similar larval coatings among numerous taxa of solitary and cleptoparasitic bees.

Three cocoons from which live larvae were taken had a median length of 7.5 mm (range of 7.0–8.0 mm) and a median diameter of diameter of 6.1 mm (range of 5.6–6.6 mm). Their shape was roughly the shape of the cell. Each cocoon consisted of an outer layer composed of soil to which the feces and silk adhered closely. The soil was obviously the cell wall to which the silk and feces were glued. A layer of feces was thinly spread over the posterior 2/3 to 3/4 of the inner surface of the cell before silk was applied. The inner layer was composed solely of thin sheets of silk closely but loosely applied to one another. The entire layer was semitransparent, so that one can vaguely see the distribution of the darker fecal layer contrasting with paler cell wall where the feces were not applied. Also seen was a white blotch at the posterior end of the cocoon representing the final pale meconial discharge. The inner surface of the cocoon was pale to medium tan. It appeared to consist of a continuous thin, shiny sheet of silk. Its individual threads, while fused with one another to form the sheet, still maintained their outline, thereby imparting a sheen to the reflective surface. No special external construction, or ''nipple'', was evident at the front end of the silken cocoon as observed in many megachilid cocoons. The cocoon described and pictured by Enslin (1921: figs. 2–4) appears to be identical to these.

Last Larval Instar of *Rophites* (*Rophites*) *algirus trispinosus* Pérez
Rozen, 1993: figs. 41–45

DIAGNOSIS: The very narrow salivary lips and projecting labral tubercles will enable the larva of this species to be distinguished from that of *Rophites canus*.

DESCRIPTION: Rozen (1993) described a larva of this species that was not fully mature, although it was a last larval instar. The paired midbody dorsal tubercles were rounded as depicted (ibid.: figs. 21, 22) but only questionably with a finely wrinkled apical surface. The nesting site from which it was collected was being attacked by adults of the cleptoparasite *Biastes emarginatus* (Schenck) (Apidae: Nomadinae: Biastini). No additional material has become available.

REMARKS: Stöckhert (1922) described the larva of the related *Rophites* (*Rophites*) *quinquespinosus* Spinola as being exactly like that of *Rophites canus* except for size.

Mature Larvae of *Conanthalictus*

DIAGNOSIS: The mature larvae, as non–cocoon spinners, lack projecting labiomaxillary regions, and paired dorsal prothoracic tubercles are absent, characters found in other rophitine taxa. The characters presented in the key can separate the two species treated here.

Mature Larvae of *Conanthalictus* (*Conanthalictus*) *conanthi* (Cockerell) Rozen, 1993: figs. 35–39

DIAGNOSIS: The apically more pointed dorsal body tubercles of this species (Rozen, 1993: fig. 37) distinguish it from the more rounded body tubercles of *Conanthalictus bakeri* (figs. 64, 65).

DESCRIPTION: The reader is referred to the previous description and illustrations of the larva of this species (Rozen, 1993).

REMARKS: Rozen and McGinley (1976) briefly described the nesting site of this species, and Rozen (1993) subsequently gave a more complete account of the nesting biology.

Mature Larvae of *Conanthalictus* (*Phaceliapis*) *bakeri* Crawford Figures 64–69

DIAGNOSIS: The rounded body tubercles of this species easily separate it from the more pointed tubercles of *Conanthalictus conanthi*.

The larval mandibles of the two species of *Conanthalictus* treated here differ from those of all other rophitines in that the mandibles are interpreted as having a conspicuous subapical tooth in addition to smaller teeth extending along the apical dorsal edge both proximal and distal to the subapical tooth. We have re-examined specimens of both and think that this interpretation is still appropriate since the subapical tooth is substantially larger than all other teeth along the dorsal edge in the two species. Interestingly, when the mandible of the predefecating larva of *C. bakeri* was re-examined with a compound microscope, it, like that of *C. conanthi*, appeared to have no teeth along the ventral apical edge. Yet, the SEM micrograph (fig. 68) of the predefecating larva clearly has two teeth along this edge.

In the following, comparisons with *Conanthalictus conanthi* refer to the description presented by Rozen (1993).

HEAD (figs. 66, 67): Integument of head capsule with scattered small sensilla that are not obviously setiform. Integument unpigmented except for mandibular apices.

Head size (figs. 64, 65) moderately small compared with body size; head capsule much wider than length measured from top of vertex to lower clypeal margin in frontal view. Unlike that described for *Conanthalictus conanthi*, tentorium complete, including dorsal arms. As in *C. conanthi*, anterior tentorial pit close to anterior mandibular articulation; posterior tentorial pits in normal position; postoccipital ridge weak, evident only near posterior tentorial pit, vanishing dorsally (perhaps more quickly in postdefecating larva than in predefecating larva); median longitudinal thickening of head capsule absent; hypostomal ridge moderately developed; pleurostomal ridge well developed; epistomal ridge laterad of anterior tentorial pit extremely short because of closeness of pit to anterior mandibular articulation; ridge between pits either absent (postdefecating larva) or present but fading well before median line (predefecating larva). Parietal bands evident both as integumental scars and as subcutaneous white imaginal discs on uncleared specimens, unlike those of *C. conanthi*. As in *C. conanthi*, antennal prominence large, globose, occupy-
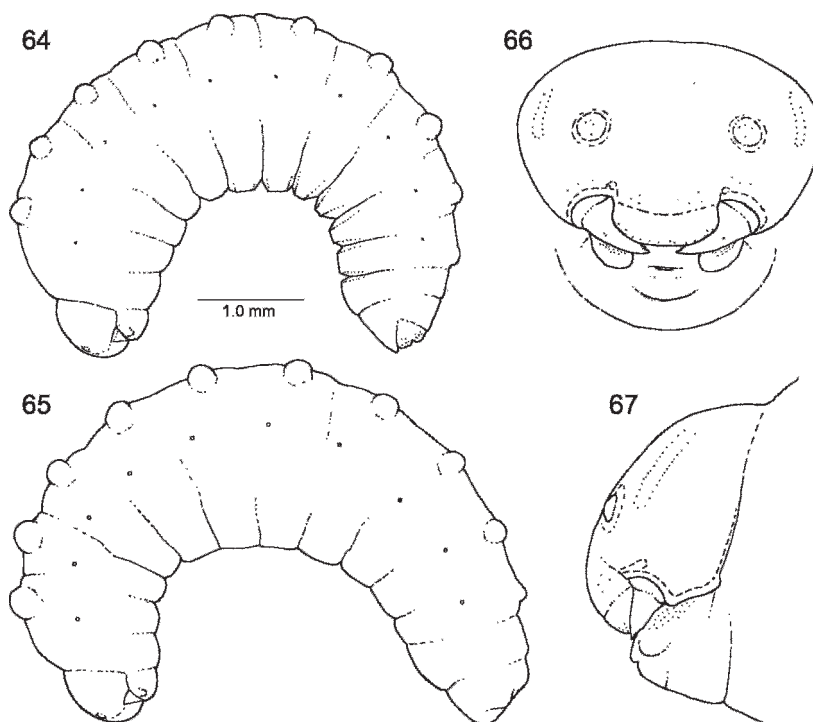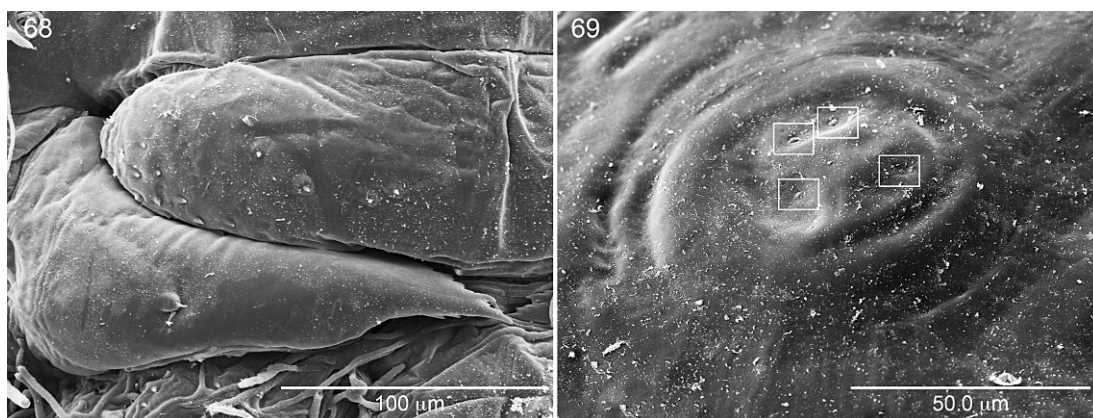
Fig. 64. Postdefecating larva of *Conanthalictus bakeri*? (specimen not certainly identified to species; see text). Fig. 65. Predefecating larva of *C. bakeri* (specimen certainly identified to species). Figs. 66, 67. Head of postdefecating larva of *C. bakeri*?, frontal and lateral views, respectively. Scale refers to figs. 64, 65.

ing much of anterolateral area of parietal, though not strongly projecting; antennal disc and papilla moderately large; papilla projecting slightly, bearing 3–4 sensilla. Vertex evenly rounded as seen from side, without projections. Labrum not projecting as far as clypeus in lateral view (fig. 67), very short in frontal view (figs. 66, 68); labrum and epipharynx apparently without spicules.

Mandible similar to that of *Conanthalictus conanthi* (Rozen, 1993: figs. 38, 39) with conspicuous, sharply pointed subapical tooth and with series of sharp teeth along dorsal apical edge (see "Remarks" for further explanation of mandibular apex); ventral apical edge with one or two minute teeth; cusp not developed; apical concavity scarcely developed, a flattened area near mandibular apex; outer mandibular surface with one or two, small, inconspicuous tubercles, each bearing single short sensillum. Labiomaxillary region greatly recessed, as in *C. conanthi*. Maxilla

with dorsal surface spiculate; cardo, stipes, and articulating arm of stipital sclerite not evident; maxillary palpus recognizable only by several sensilla at maxillary apex. Labium (unlike that described for *C. conanthi*[7]) weakly divided into prementum and postmentum,

[7] Examination of the postdefecating larva of *Conanthalictus bakeri* raises the possibility that the prementum/postmentum boundary of *C. conanthi* was confused with the posterior boundary of the postmentum (Rozen, 1993: fig. 35). Reexamination of the head of *C. conanthi* in the collection of the AMNH confirms that there is a ventral line approximately in line with an imaginary line drawn from the vertex through the posterior tentorial pit, as illustrated (loc. cit.). However, in *C. bakeri*, the posterior margin of the postmentum is clearly behind this imaginary line; another transverse ventral line anterior to it is considered to demark the prementum/postmentum boundary. In other rophitines, the posterior margin of the postmentum falls behind this imaginary line. At the same time, if the labial length depicted in (loc. cit.) is actually only the length of the prementum, then it is disproportionately long compared with that shown in fig. 67 for *C. bakeri*.

Figs. 68, 69.   SEM micrographs of predefecating larva of *Conanthalictus bakeri*? **68**. Labrum, right side, and right mandible, frontal view, showing tubercle on outer surface and bifid apex of mandible. **69**. Right antenna, with sensilla identified by rectangles.

moderately long; labial palpus not evident except for several sensilla. Salivary lips absent; opening of salivary duct a transverse slit, narrow on postdefecating specimen but wide on predefecating specimen. Hypopharynx nonspiculate, not longitudinally grooved; hypopharyngeal groove absent (alternatively the wide salivary opening may possibly be the median remnant of the hypopharyngeal groove, with the salivary duct opening into it).

BODY: Integument with fine scattered non-setiform sensilla; many areas with fine, widely and evenly spaced spicules; dorsal body tubercles faintly wrinkled apically. Body form (figs. 64, 65) moderately robust; intersegmental lines moderately weakly incised on predefecating form; on postdefecating form ventral intersegmental lines modified as explained under "Remarks", below; as in *Conanthalictus conanthi*, paired prothoracic dorsal tubercles absent; mesothorax, metathorax, abdominal segments 1–8 with paired dorsal tubercles (figs. 64, 65), which are conical rather than transverse; venter of abdominal segment 9 scarcely produced ventrally; abdominal segment 10 oriented apically on 9, with dorsal surface shorter than ventral surface, so that anus directed somewhat dorsally; venter of 10 of postdefecating larva with faint transverse line. Spiracles very small, without sclerites, not on tubercles; peritreme present, narrow; atrium projecting slightly beyond wall, with rim, globose; atrial wall smooth; primary tracheal

opening with collar; subatrium normal in length, consisting of about 10 chambers. Male with distinct median, transverse, integumental scar ventrally near posterior margin of segment 9; female sexual characters unknown.

MATERIAL STUDIED: 1 postdefecating larva, USA: Arizona: Pima Co.: Organ Pipe Cactus National Monument, August 15, 1995 (J.G. Rozen and S. Budick); 1 probably early last larval instar, same, except April 1, 1995 (J.G. and B.L. Rozen).

REMARKS: JGR discovered a nest of *Conanthalictus bakeri* (adult collected and identified) on March 25, 1995, at Organ Pipe Cactus National Monument, Pima County, Arizona, and excavated it the next day. Two immature larvae from it were reared for several days after excavation but were preserved on April 1, 1995, because they were not faring well. At least one of these appeared to be an early-stage last larval instar; it is described here, its identity certain. Later the same year, JGR again visited the National Monument and retrieved a single mature *Conanthalictus* larva from a nest marked in the spring. No adult voucher specimen was associated with the nest. Although the larva appears to be that of *C. bakeri*, adults of *C. deserticola* Timberlake were also common in the spring. Thus, the postdefecating larva described here is possibly *C. deserticola*. The differences between these two larvae are discussed under "Remarks", below.

Michener's statement (2000) that *Conanthalictus* has a fused prementum and postmentum was based on only *C. conanthi* as reported by Rozen (1993). The prementum is weakly separated from the postmentum in *C. bakeri*.

Although the postdefecating and predefecating larvae described here are nearly identical, they do differ beyond what one usually sees between these two life phases. The peculiar, accordion-like ridges nearly paralleling the ventral intersegmental lines on many of the abdominal segments of the postdefecating form (fig. 64) are without precedent among bee larvae and probably resulted from a postmortem change, the specimen having expanded in the preservative. Presumably the intersegmental lines would be concealed in life, a coarctation that perhaps serves as a defense mechanism to protect a diapausing individual from attack or dehydration. It seems unlikely that an active, functioning bee larva would have such ridges, and they certainly are not present on the predefecating larva (fig. 65). The ridges are integumental in nature since they persisted even after the specimen was cleared in an aqueous solution of sodium hydroxide.

The apices of the 10th abdominal segments of the postdefecating (fig. 64) and predefecating (fig. 65) larvae appear dissimilar. However, while clearing the predefecating larva in an aqueous solution of sodium hydroxide, we discovered that the anus is very large, and the soft, perhaps rectal integument surround the anus appears capable of everting during defecation. The roughened area surrounding the wide, slitlike anus on the postdefecating larva is thus interpreted to be the shriveled soft rectal integument.

The labiomaxillary regions of the two larvae also appear different, but this may be due to postmortem modifications of the more pliable integument of the feeding larva.

Two differences appear to be unrelated to larval stage. The predefecating larva has three sensilla on each antenna, and the postdefecating larva has four sensilla on each. The predefecating larva shows the internal epistomal ridge advancing part way mesad of the anterior tentorial pit, while the median section of the internal epistomal ridge is completely

absent in the postdefecating larva (fig. 66), as in *Conanthalictus conanthi* (Rozen, 1993: fig. 36). More larval specimens of *C. bakeri* and *C. deserticola* are needed to determine whether these differences are intraspecific or interspecific.

PUPAE OF THE ROPHITINAE

As pointed out by Rozen (2000), terminology referring to pupal tubercles is confusing since it is often difficult to distinguish between a swelling, protuberance, tubercle, spine, spicule, etc. Even a seta, normally identified by a distinct alveolus, can be confused with a long, tapering, hairlike extension at the apex of a tubercle. Furthermore, a structure called by one term on one species might on another species be more appropriately called by another term even though the two structures are indeed homologous. For example, Michener (1954) used the term *spicules* for projections forming apical transverse rows on metasomal terga, but when they are relatively large and rounded as they are in some rophitines, *tubercles* seems a better choice. This choice is also supported by the peculiar apical metasomal tubercles of questionably identified *Osiris pallidus* Smith, each of which is surmounted by a patch of densely set spicules (Rozen, 2000).

Almost all of the truly pupal features (in contrast to adult features that appear in the pupal stage) pertain to the position and size of tubercles. As Michener (1954) implied, these tubercles are of two sorts: those that accommodate developing adult setae and others that clearly do not. We suspect that the latter serve as contact points cushioning the pupa from the substrate or from other objects. This is suggested by that fact that these blisterlike protuberances are positioned at the outermost places on the body (e.g., vertex, outer edge of scape, middle of the wing pad, tegula, etc.) or where one part of the body touches another part (as for example, where the flagellum rubs against the compound eye). It is unclear why this might be of importance to the pupa since pupae of many bees are in cocoons and thereby seemingly protected from abrasion by soil particles in the cell wall. (However, it is interesting that the pupal setae of Mega-

chilidae might serve a similar function.) Although some tubercles accommodate developing adult structures such as tufts of setae whereas others do not, there are a number of tubercles observed in this study where both functions are performed by a single structure, as, for example, when a tubercle is substantially larger than the resulting adult structure.

Tubercles, particularly those with pointed apices, also may have another function, i.e., assisting the pupa to rotate in its chamber, either by providing traction when a pupa rotates its metasoma, or by serving as pivot points on the vertex and metasomal apex, or by a combination of both actions. One also wonders if sharp-pointed tubercles or stout setae when rubbed against the cell or cocoon wall might also function to scour the chamber, killing ectoparasites that might be present.

To the extent they are known, pupae of this subfamily vary considerably in size but little in structure. To facilitate comparison, all pupae are diagnostically treated in the "Diagnosis" section of "Pupa of *Dufourea holocyanea*" rather than separately at the start of each description. The descriptions presented below are patterned after that of *Sphecodosoma dicksoni* (Rozen, 1993).

Pupa of *Dufourea holocyanea* (Cockerell)
Figures 70–72

DIAGNOSIS: This is the largest rophitine species (length > 8 mm) for which we have pupae, but structurally it is almost identical to pupal *Dufourea a. australis* (length < 7 mm). In addition to a somewhat larger body, the pupa of *D. holocyanea* (fig. 70) has a proboscis that is shorter relative to its body size than does *D. a. australis* (fig. 73). The most reliable pupal character (as opposed to characters listed above that are also features of adults) to distinguish between these two species relate to the bilobed apical edge of S6, which in *D. holocyanea* (fig. 72) has the lobes slightly more distinctly separated than are those of *D. a. australis*.

The pupa of *Dufourea holocyanea* is also similar to that of *Sphecodosoma dicksoni* (Rozen, 1993: fig. 33), which, however, has a substantially smaller body (length < 4 mm) and much longer mouthparts in relation to its

body size. The condition of the apical edge of the male S6 of *S. dicksoni* is unknown.

The pupa of *Rophites canus* (length < 6.5 mm) can best be distinguished from others treated here by its much reduced paired vertical tubercles, by its more robust overall appearance, by the sharply pointed, hind tibial tubercle, and by the sharply pointed, forward-directed tubercles on T1 (fig. 72).

HEAD: Integument without setae. Scape with outer surface bearing several low indistinct swellings and moderately large, rounded apical tubercle; pedicel without tubercle; most basal flagellomeres with small but pronounced tubercle next to eye (not visible in fig. 70); all flagellomeres of both sexes with tuberclelike swelling on outer surface. Vertex with large tubercle immediately mesad of each adult lateral ocellus; each adult ocellus covered with small, low convexity; genal tubercle below eye absent; frons with low varicosities on each side; clypeus without tubercles; labrum unmodified.

MESOSOMA: Integument without setae. Lateral angle of pronotum swollen, especially laterally; lateral pronotal lobe swollen; mesoscutum with dorsal surface swollen and indistinctly varicose on each side, leaving a deep longitudinal trough along midline and lesser furrows along parapsidal lines; axilla small but produced dorsally; mesoscutellum with pair of strongly produced, somewhat forward-projecting tubercles; metanotum produced medially, indistinctly bilobed. Tegula with strongly projecting tubercle; forewing with outer surface irregular but without tubercles (including large tubercle one-third distance from apex as in Halictinae, Rozen, 2008). Each coxa with pointed apicoventral tubercle; fore- and mid-trochanters each with pointed apicoventral tubercle; hind trochanter with rounded swelling; fore-, mid-, and hind femora each with basal swelling; hind femur with two small rounded apical tubercles; hind tibia with elongate basal tubercle on outer surface; all tibiae each with apical rounded tubercle on outer surface.

METASOMA: Integument without setae; T1–6 (male) or T1–5 (female) with posterior transverse row of moderate-size, acutely rounded, non-seta-bearing tubercles, these rows narrowly interrupted along midline and

with largest tubercles in each row found sublaterally; rows on T1 and T6 (male) and T1 and T5 (female) consisting of fewer tubercles relative to other rows; apex of metasoma rounded, not produced as elongate apical spine. Male S1–5 apically flared with sublateral apical edges more or less produced, almost tuberclelike; S6 apically bifurcate; female S1–5 sublaterally apically flared, but questionably not as strongly so as in male.

MATERIAL STUDIED: 1 male and 5 female pupae USA: Washington: Kittitas Co.: 17 km NNE of Selah, Yakima River Canyon, Highway 821 at mile 10, April 2005, excavated as prepupae (E. Miliczky).

Pupa of *Dufourea australis australis* Michener
Figure 73

DIAGNOSIS: See "Diagnosis" of the pupa of *Dufourea holocyanea*.

DESCRIPTION: As described for male of *Dufourea holocyanea*.

MATERIAL STUDIED: 1 male pupa, USA: Arizona: Pima Co.: Desert Station, E side of Tucson Mts., collected as postdefecating larva May 1, 1993, preserved as pupa June 25, 1993 (J.G. Rozen); 1 male pupa, same except preserved as pupa, August 21, 1998.

Pupa of *Sphecodosoma* (*Sphecodosoma*) *dicksoni* (Timberlake)
Rozen, 1993: figs. 33, 34

DIAGNOSIS: See the "Diagnosis" of the pupa of *Dufourea holocyanea*.

DESCRIPTION: The reader is referred to the previous description of the pupa of this species (Rozen, 1993). The placements of the major pupal tubercles are the same as described for *Dufourea holocyanea*, above, although the relative sizes of these tubercles differ from those of *D. holocyanea*.

Pupa of *Rophites* (*Rophitoides*) *canus* Eversmann
Figure 74

DIAGNOSIS: Please see the "Diagnosis" of the pupa of *Dufourea holocyanea*.

HEAD: As described for *Dufourea holocyanea* except for following: Paired vertical tubercles much reduced so as to be easily confused with lateral ocelli.

MESOSOMA: Axilla small, only slightly produced; paired mesoscutellar tubercles not forward projecting, smaller than those of *Dufourea holocyanea*. Tegula with strongly projecting but smaller tubercle than that of *D. holocyanea*. Each coxa with pointed apicoventral tubercle but that of hind coxa small; fore-, mid-, and hind trochanters each with pointed apicoventral tubercle; fore-, mid-, and hind femora each with basal swelling; hind femur with two, small, rounded, apical tubercles that appear more conspicuous than those of *D. holocyanea*; hind tibia with elongate basal tubercle on outer surface but this tubercle tapering to pointed apex from broad base.

METASOMA: T1–5 (female) with posterior transverse row of small, acute, non-seta-bearing tubercles, these rows narrowly interrupted along midline; row on T1 with tubercles tending to be forward-directed, longer than those in subsequent rows; each subsequent row tending to have tubercles that are smaller, less acute, and less forward directed than those of previous row.

MATERIAL STUDIED: 1 female pupa, Turkey: Erzurum: Atatürk University campus, June 2005 (H. Özbek).

PUPAL CHARACTERS OF HALICTIDAE

Over 50 years ago, Michener (1954) presented a comparative analysis of pupal characters of all bees whose pupae were available to him including exemplars of three halictine genera (*Augocholora*, *Halictus*, and *Lasioglossum*) and *Nomia*. Since then additional pupae have been described (see McGinley, 1989), but, considering the ephemeral duration of this stage and the difficulty in successfully preserving pupal specimens, we are not surprised that melittologists have largely ignored comparative studies of this life stage. Because of the gradual accumulation of pupal specimens, we can now consider pupal features that seem to characterize the Halictidae. In addition to the rophitine genera and the genera examined by Michener (1954), we have examined (determinations in
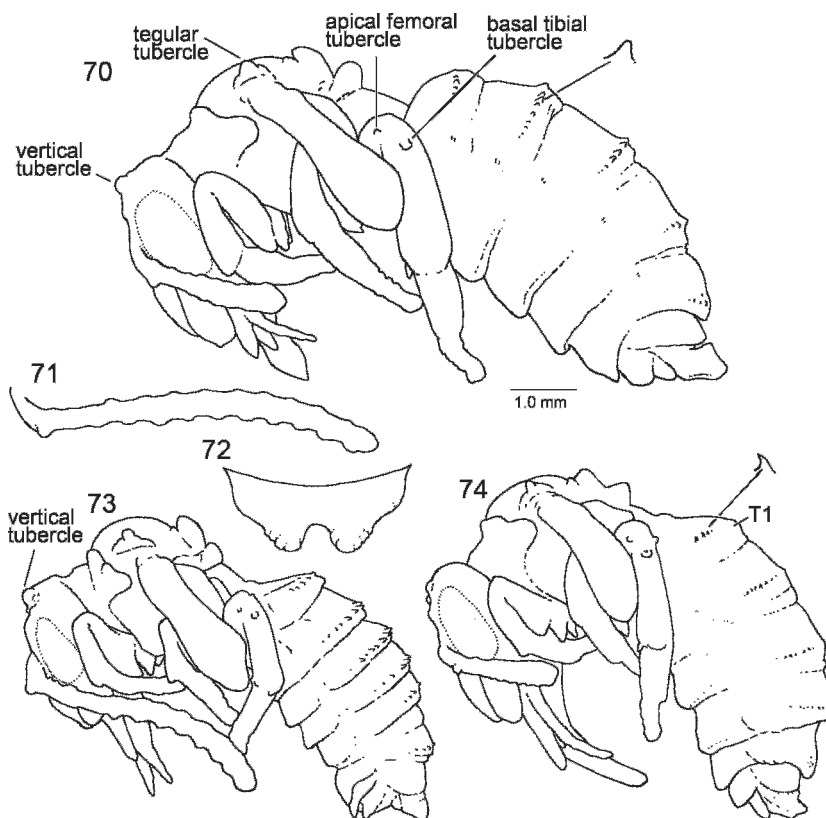
Figs. 70–74.   Pupae of rophitines bees. **70**. *Dufourea holocyanea*, female, lateral view. **71**. Male antenna of *D. holocyanea*, drawn to same scale as female. **72**. S6 of male of *D. holocyanea*, ventral view. **73**. *Dufourea a. australis*, male, lateral view. **74**. *Rophites canus*, female. Scale refers to figs. 70, 71, 73, and 74.

current usage, based on associated adults): HALICTINAE: HALICTINI: *Ruizantheda* (*Ruizanthedella*) *mutabilis* (Spinola) (det. Claude-Joseph) (on loan from Smithsonian Institution). AUGOCHLORINI: *Corynura chloris* (Spinola) (det. F. Claude-Joseph) Correo Nunoa, Chile, Transp. no. 163, T363 (F. Claude-Joseph) (on loan from Smithsonian Institution). NOMIINAE: *Pseudapis* (*Nomiapis*) *diversipes* (Latreille) (det. D.B. Baker), Pakistan: Baluchistan: Jalogir, 32 km N of Quetta, collected as larvae May 16, 1984, preserved May 25, 1984 (J.G. Rozen); *P.* (*Pseudapis*) *cinerea* (Friese) (det. J.G. Rozen), Rep. South Africa: Cape Province: 70 km E of Port Nolloth, November 26, 1974 (J.G. and B.L. Rozen); *Lipotriches* (*Macronomia*) *macropus* (Friese) (det. A. Pauly), Namibia: 22 km ESE of Seeis, March 16, 1976 (J.G. and B.L. Rozen). HALICTINAE: NOMIODINI: *Nomi-* *oides patruelis* Cockerell (det. Y.A. Pesenko), Pakistan: Sind: Gharo, 18 mi E. Karachi May 8, 1984 (J.G. Rozen, S. Lodhi, I. Stupakoff). We have also relied on the excellent descriptions (and often illustrations) of the pupae of *Agapostemon* (*Notagapostemon*) *nasutus* Smith (Eickwort and Eickwort, 1969); *Lasioglossum* (*Dialictus*) *umbripenne* (Ellis) (Eickwort and Eickwort, 1971); a number of species of *Augochlora* (Eickwort and Eickwort, 1972a, 1973a); *Neocorynura colombiana* Eickwort (Eickwort, 1979); *Augochlorella comis* (Vachal) (Eickwort and Eickwort, 1973b); and *Microsphecodes kathleenae* (Eickwort) (Eickwort and Eickwort, 1972b). Thus, exemplars of all halictid subfamilies and tribes (sensu Michener, 2000) are considered. The following is a description/discussion of the pupal features of the Halictidae to the extent they are now known.

INTEGUMENT: The body surface is without long, conspicuous setae, as is the case with all other families of bees except for the Megachilidae. However, the apices of some tubercles of the tergal transverse bands often have their apices more or less attenuated and therefore setalike.

HEAD: The outer apical tubercle on the scape found in the two genera of Nomiinae and in all of the Rophitinae appears in only *Augochlora* of the Halictinae. It is also absent in the single exemplar of the Nomioidini but seems to be replaced with a tuberclelike swelling of the first flagellomere. As indicated by Michener (1954), *Augochlora* also exhibits a low tubercle basally on the scape, and similarly placed but less distinctive swelling occurs sporadically among other taxa. Paired tubercles immediately mesad of the lateral ocelli are characteristic of most of the exemplars of the Halictidae but are reduced or absent in *Rophites canus*, *Pseudapis diversipes*, and *Nomia melanderi*. In most cases other tubercles are missing from the vertex, but one or more pairs of additional small tubercles are found in *Nomioides patruelis* and *Agapostemon* (*Agapostemon*) *sericeus* (Forster). Although none of the Rophitinae bear a pair of tubercles on the frons, they are found on many of the Halictinae, and two such pair occur on *Nomioides patruelis*. *Augochlora* (*Augochlora*) *pura* (Say) exhibits an erect tubercle on each galea, and the illustration of *Augochlorella comis* (Eickwort and Eickwort, 1973a: fig. 12) seems to indicate a similar tubercle.

MESOSOMA: The lateral angles and posterior lobes of the pronotum are often but not invariably more or less swollen. Interestingly, the mesoscutum is without tubercles except for *Nomioides patruelis*, which bears three small pairs of paramedian mesoscutal tubercles, and for *Corynura chloris*, which has a pair of small, low tubercles near the center. Conspicuous, paired, paramedian tubercles on the mesoscutellum are characteristic of all known pupal Halictidae. A small axillary tubercle occurs in a few genera including *Lasioglossum*, *Halictus*, *Corynura*, and *Nomioides* but is often difficult to detect, and a mesepisternal tubercle hidden under the forewing was noted in the case of *Agapostemon sericeus*. The metanotum is quite variable, in some cases strongly produced as a single median swelling as in *Rophites canus* and *Sphecodosoma dicksoni*, in other cases as a bilobed single swelling as in *Nomia melanderi* and many Halictinae, in still other cases as two distinct, closely adjacent tubercles as in *Lasioglossum umbripenne* (Ellis), and finally in the case of *Nomioides patruelis* as two well-separated tubercles not arising from a common swollen base. Pronounced tegular tubercles seem characteristic of all Halictidae except for the Halictinae, in which they are greatly reduced to nearly nonexistent. A conspicuous tubercle is found on the forewing pad of the Halictinae but not of the Rophitinae; in the Nomiinae, there is only a slight swelling in the appropriate position on the wing pad. Leg tubercles have not been systematically studied at this point, although apicoventral tubercles on coxae and trochanters and basal first femoral swelling appear to be generally present, accommodating developing adult setae. An invariable feature of all known Halictidae is the outer basal tubercle on the hind tibia; this appears to be the single uniform feature of the family but is not uniquely diagnostic since some members of the Andrenidae have similar tubercles as shown by Yager and Rozen (1966). In halictids, this tubercle varies in the extent of expression and shape from one taxon to the next but is always found close to but below the femoral-tibial joint.

METASOMA: In general, each tergum tends to have a posterior transverse row of small tubercles; this seems to be the basic ground plan. However, with *Nomia melanderi* the tubercles on T1 and T2 are absent and in the two species of *Pseudapis* and in *Nomioides patruelis*, they are absent on T1. In *Rophites canus* the band on T1 is reduced to only two short runs on the lateral edge of the tergum. In *Augochlora pura*, the band on T1 consists of two paramedian sets of two, very large tubercles whereas in rophitine bees tubercles on T1 tend to be a little smaller than those of the subsequent tergum. With most taxa, tubercles on anterior terga tend to be more rounded than those more posterior in position, although in *Rophites canus* tubercles on T1 are more pointed than the others. No doubt other arrangements will be discovered when more taxa are examined. The apex of the

metasoma immediately dorsal to the anus projects posteriorly to various degrees, although in the Rophitinae and Nomiinae its posterior projection is minimal. It is more obvious in the Halictini, especially in *Halictus* and *Lasioglossum*. In *Nomioides patruelis* the projection is even greater than in *Halictus* or *Lasioglossum* and tapers to a narrowly rounded but not pointed apex. In all species of *Augochlora* whose pupae have been observed and in *Augochlorella comis* the apex becomes very thin just before it suddenly expands at the end into a caudal knob (Eickwort and Eickwort, 1937b), from which the larval skin is hung.

DISCUSSION OF ROPHITINE NESTING BIOLOGY

Information on the biology of rophitine bees presented above is consistent with the previously published profile of the biology of the Rophitinae (Rozen, 1993: 16). The new data do not disagree with the previous understanding of the biological parameters of the subfamily, but they do highlight some interesting comparisons. (References to the following statements can be found under the taxon headings, above.) Thickness of the cell wall appears to vary from one taxon to the next. *Dufourea a. australis* constructs a strong, thick cell wall, possibly cemented with nectar, whereas the cell walls of *D. mulleri* and *D. malacothricis* are weaker and thinner, and the walls of *Sphecodosoma dicksoni* and *Rophites canus* appear to have no more strength than the surrounding substrate. Examining cells of these same species from different substrates might help identify whether such apparent differences result from biological phenomena or from edaphic conditions of the substrates.

Permeability of the cell lining to a water droplet applied as a test is surprisingly variable. The lining of *Dufourea novaeangliae* is highly waterproof; those of *D. mulleri*, *D. trochantera*, *Rophites canus*, and *Sphecodosoma dicksoni* are moderately water retardant; and those of *Protodufourea eickworti* and *Systropha planidens* are relatively permeable when so tested. Cell linings of *Conanthalictus conanthi* are permeable at first but become notably more retardant, presumably because of some action by the feeding larva. We have generally assumed that adult females were totally responsible for waterproofing cell walls, thereby assuring safe relative humidity for developing immatures, but the observations on *C. conanthi* suggest there may be exceptions.

Coating of larval food supplies, discovered relatively recently in rophitines, seems variable; it is found in *Dufourea novaeangliae*, *Sphecodosoma dicksoni*, and apparently *Conanthalictus conanthi* but absent in *Rophites canus*. If desiccation of the food sphere is the issue, we might expect that species with a waterproof covering of the food would not need a moisture-retardant cell lining and vice versa. The latter seems to be the case with *Rophites canus*; its food supply lacks a waterproof coating and its cell wall is quite waterproof. However, in *Dufourea novaeangliae*, which lives in the moist climate of the northeastern United States, the cell wall and the food coating are highly waterproof. Thus, the threat in this case would not seem to be possible desiccation of the food mass but rather the possibility of too much moisture entering both the cell and the food mass. As pointed out by Eickwort et al. (1986), feeding larvae of this species actively crawl around the food mass as they feed. The waterproof coating is thereby quickly removed, and the presumably hydroscopic food surface would come in contact with the cell surface.

So far as is known, all rophitine bees spin cocoons except for *Conanthalictus*; the two species whose larvae have been collected were not in cocoons and their labiomaxillary regions were recessed, without projecting salivary lips. The single larva of *Xeralictus timberlakei* exhibits features of a cocoon-spinning larva, but whether it was taken from a cocoon is unclear.

Among cocoon-spinning members of the subfamily, considerable variability exists in the sequence of silk production and defecation. In *Dufourea mulleri*, *D. novaeangeliae*, and presumably *D. trochantera*, the larva first spins a cocoon against the cell wall, then applies a layer of feces mostly against the posterior end of the cocoon, and, after finishing defecation, spins an inner layer of silk. *Protodufourea eickworti* and *Rophites*

canus first defecate against the cell wall and then spin their cocoons. The cocoon construction process of *D. a. australis* is not fully understood; before defecation, the larva deposits a glistening, brown material of unknown origin over the cell closure and frontal cell wall, then defecates over the rear cell wall, and finally spins a silken cocoon that covers the entire wall. Larvae of *Sphecodosoma dicksoni* are interesting because they spin two types of cocoon; larvae that do not diapause produce a thin cocoon made of a thin layer of silk over the entire cell surface and then deposit a thin layer of feces over the rear two-thirds of the cocoon. Larvae that subsequently diapause first spin an outer layer against the cell wall, then defecate over much of the cocoon surface, afterward spin an inner silken layer, and thus produce a more rigid cocoon.

Diapausing larvae found in cocoons tend to curl themselves into a tight circle so that their abdominal apex is appressed against the rear part of their labiomaxillary region and the venter of their prothorax (figs. 31, 50). Known exceptions are postdefecating larvae of *Dufourea novaeangliae* and *Protodufourea eickworti*, which, while tightly curled, do not have the abdominal apex reaching the venter of the head and prothorax.

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