

Early nesting biology of the wood-nesting adventive bee, *Lithurgus chrysurus* Fonscolombe (Apoidea: Megachilidae: Lithurginae)

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ABSTRACT

This, the second study of the nesting biology of *Lithurgus chrysurus* Fonscolombe found at Palmerton, Carbon Co., Pennsylvania, describes its nest construction, provisioning, egg deposition, and larval development. The first study (Rozen, 2013) was based on observations on the late-stage nesting biology in early fall, when these activities were no longer being performed. Comparisons are made with activities of the native *Lithurgopsis apicalis* (Cresson); in general, the two species have similar, but not identical, nesting biologies. Because *Lithurgus chrysurus* is an adventive bee native to the Mediterranean regions and is capable of constructing nests in both soft wood as well as firmer wood, it is unclear why it has not expanded its range to any great extent in the New World.

INTRODUCTION

The nesting biology of *Lithurgus chrysurus* Fonscolombe was recently described based on observations gathered in October 2012 from infested firewood logs, horizontally stacked in the open, in Palmerton, Carbon Co., Pennsylvania (Rozen, 2013: fig. 1). Although adult bees were first seen there in midsummer, that study was undertaken well after the nesting season, when bees were no longer flying and provisioning nests. Consequently, information on the nature of the provisions, early larval development, egg and larval anatomy, as well as

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the processes of provisioning and egg deposition was missing. The purpose of the current study is to fulfill our understanding of these matters to the extent possible. This species is native to the circum-Mediterranean region of the Old World (Ascher and Pickering, 2013). It was accidentally introduced into the United States, probably around the mid 1970's, and discovered in Phillipsburg, Warren Co., New Jersey, in 1977, as reported by Roberts (1978), who first described its nesting biology, which was later also treated by Rust et al. (2004) from a nest site within its native range in France.

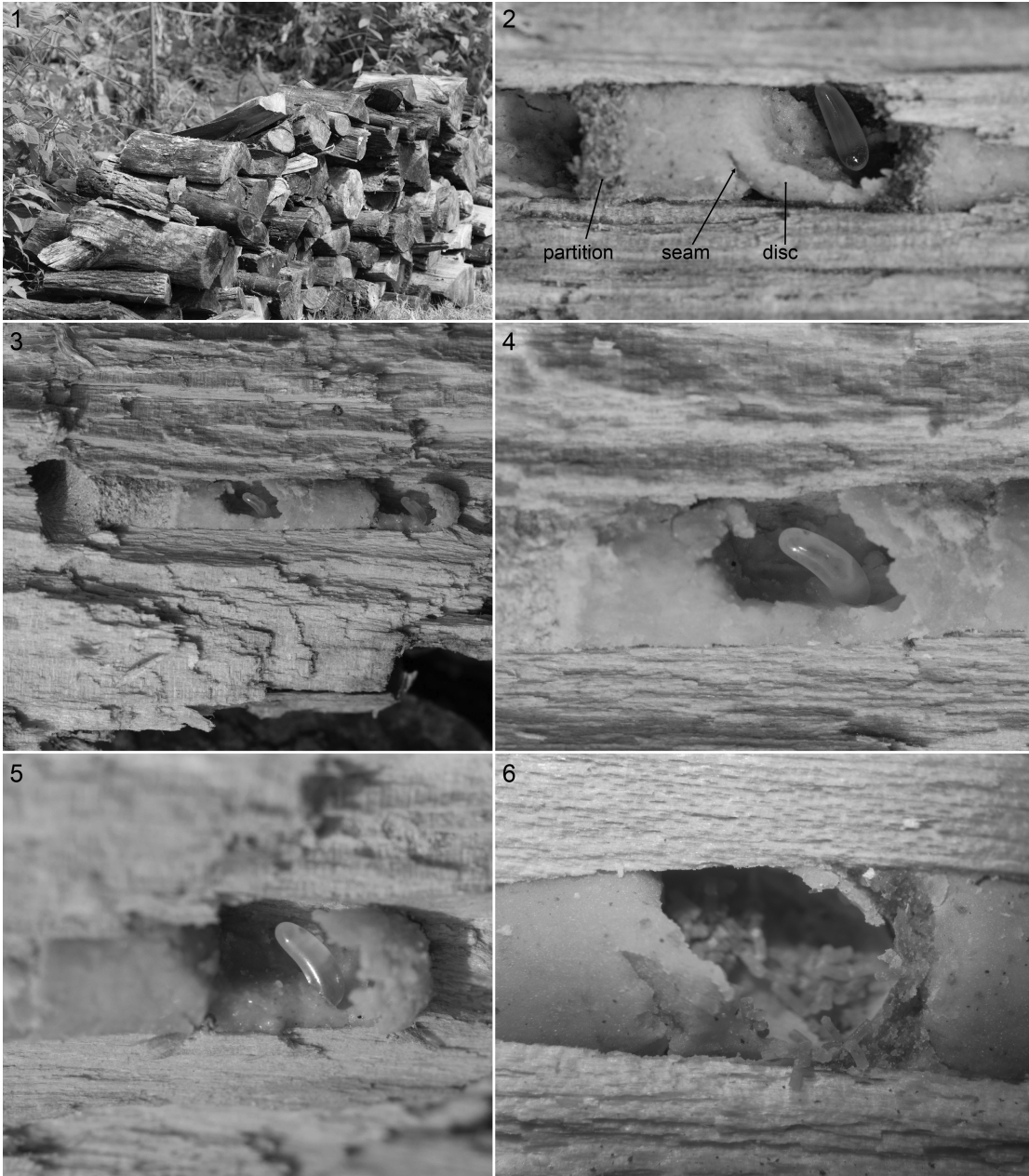
After completion of the first investigation of this species, J.G.R. and H. Glenn Hall undertook a study of the nesting biology of *Lithurgopsis apicalis* (Cresson), a North American genus that had formerly been considered a subgenus of *Lithurgus* (Rozen and Hall, 2014). This now permits a close comparison of nesting biologies of representatives of both genera throughout the following account.

Lithurgus chrysurus is of considerable interest because of its destructive potential. When first discovered in the United States, it was found nesting in compressed-wood fiber backing of asphalt shingles in Phillipsburg (Roberts, 1978). It not only dug nesting tunnels in the backing of shingles but also invaded the supporting wood structures. Although not appearing to be a serious problem in its native Old World range (but see Rust et al., 2004), might it become a pest in a new environment that may lack its natural enemies? Perhaps not, since it presumably has existed for 35 years without being noticed (Michener, 2007). However, on July 2, 2013, we observed numerous males searching for females emerging from the log façade of a seven-year-old home in Schnecksville, Lehigh Co., Pennsylvania, and from the newly installed roof of a covered bridge in Slatington, Lehigh Co., Pennsylvania.

METHODS AND TERMINOLOGY

Since the discovery of the site in Palmerton in 2012, firewood logs containing nests remained unmoved until a small number of them were brought to Lehigh Gap Nature Center (LGNC) for the first study in October 2012. Then, a few days before the inauguration of the current endeavor on July 24, 2013, all of the remaining logs in the woodpile were brought to LGNC where they were stored outside (fig. 1). Some were dissected then and others were transported to the American Museum of Natural History and dissected thereafter for two days. It is unknown how far the original storage area was from the source of provisions, and no observations of bees visiting flowers were conducted. Since provisions found in the nest were of only one pollen type, they are presumed to be *Centaurea* (Asteraceae) to which the bee has been reported to be restricted (Roberts, 1978).

Most logs were roughly 45–50 cm long, though several were considerably longer, and of various diameters. Some were split, but smaller ones remained whole. The wood ranged from being soft and degraded to being surprisingly firm and hard. While logs were probably various tree species, the firm logs were tentatively identified as that of a soft red maple that had undergone some bacterial degradation. Even the soundest wood contained fresh nests with live immatures, indicating the females were capable of excavating tunnels through such substrates.



FIGURES 1– 6. Photographs of nests of *Lithurgus chrysurus*. 1. Woodpile of restacked firewood logs containing nests at Lehigh Gap Nature Center in Slatington, Lehigh Co., Pennsylvania. 2. Cell containing single egg from a series of cells, defined by partition of wood chips (egg accidentally detached from provisions presumably resulting from jarring of wood as we attempted to split it). Note seam indicating division of disc from anterior cylinder of provisions. 3. Cell containing two eggs; note lack of partition between them. 4, 5. Close-ups of front and rear cells, respectively. 6. Cell from which fifth instar had been removed showing fecal pellet adhering to larval chamber and not mixing with provisions as in *Lithurgopsis apicalis*.

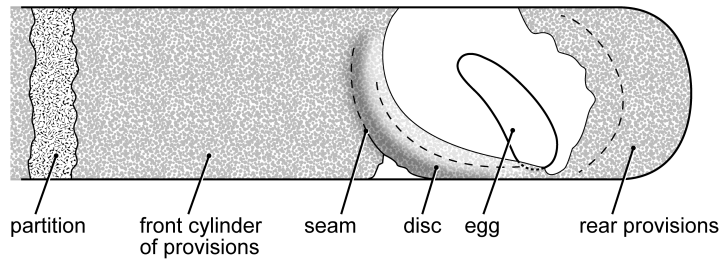


FIGURE 7. Schematic diagram of a cell containing single individual of *Lithurgus chrysurus* showing arrangement of provisions and position of egg, cell front to left.

Some of the wood was wet; other pieces were dry. Since logs had been restacked after being shipped to LGNC, possible patterns of nest-site preferences within the stack were not detectable. Logs were split with chisels, axes, and knives, and at the AMNH cells were examined by stereomicroscope. Firm logs were difficult to open, requiring considerable pounding to be split, unfortunately often resulting in dislodging of cell contents (e.g., fig. 2).

Photographs were taken with a Canon EOS 50D in the field and in the laboratory with a Canon PowerShot A2300, 16.0 megapixels. The latter camera, handheld, was also used to take microphotographs through one lens of a Leitz Wetzlar stereomicroscope.

With larvae to be cleared for study, the head was removed from the body, and both parts were boiled in an aqueous solution of sodium hydroxide, washed, transferred to 75% ethanol, stained with Chlorazol Black E, and placed in glycerin on a well slide for examination and storage. Eggs and larvae examined with a Hitachi S-5700 scanning electron microscope were first critical-point dried and then coated with gold/palladium.

Preserved immature stages, and samples of cocoons, cells, and tunnels are preserved in the collection at the AMNH.

OBSERVATIONS

DESCRIPTION OF NESTS: All nests of *Lithurgus chrysurus* discovered conformed to the description presented by Rozen (2013), with cells arranged in linear series running with the wood grain. All cells and burrows were uniform with diameters ranging 5–6 mm. Cells (fig. 2) containing one immature ranged 12–14 mm in length. All cell partitions were constructed of wood chips and tended to be flat to faintly convex on the posterior side and distinctly concave on the anterior side. No soil or substance other than wood chips was used.³ Although cells containing single immatures appeared to be the most common, cells nearly double in length and containing two immatures were not uncommon (fig. 3), and some very long ones contained three immatures.

³ Interestingly, another kind of megachilid nest was found in some of these logs. They could easily be recognized because cells were smaller and lined with mud. Their cocoons were smaller and more oval than those of *Lithurgus chrysurus*, and contained a nipple at the front end. Larval body integument was more yellow tinged, and the vestiture appeared far more “hairy.”

Thus the nest pattern was similar to that of *Lithurgopsis apicalis* with cells of various lengths proportional to the number of inhabitants. Although cells of *Lithurgus chrysurus* tended to be horizontal whereas those of *L. apicalis* were vertical, this difference is a consequence only of the orientation of the piece of wood in which they occurred, since cells of both generally run parallel to the wood grain.

PROVISIONS: The stored provisions of these two species were remarkably different in color, texture, moisture content, and pollen grain size as well as pollen source. Although rigorous pollen analyses were not performed on the stored food of either species, both bee species appear to be monolectic: *Lithurgus chrysurus* on *Centaurea* (Asteraceae) (pollen grain an oblong oval, with the longest dimension = 40 μm , fig. 15) and *Lithurgopsis apicalis* on *Opuntia* (Cactaceae) (pollen grain a multifaceted sphere = 100 μm in diameter, fig. 16). The provisions of *L. chrysurus* were light gray to pale tan, mealy moist, pasty with a fine texture owing to a relatively small pollen grain size. Those of *L. apicalis* were yellow, loose to almost fluffy, lacking moisture, and coarsely textured because of large pollen grain size.

Despite these differences in provisions, the two bee species seem to shape them in a similar fashion. (To simplify the following explanations, they are based on cells that are assumed to hold a single developing individual.) In the case of *Lithurgopsis apicalis* (see Rozen and Hall, 2014), the female brings in a small amount of pollen and deposits it against the rear of the cell. She then somehow accomplishes the following: she brings in more provisions, forms it into somewhat firmer, perhaps more moist, posteriorly concave dish-shaped structure (termed “disc” in Rozen and Hall, 2014: fig. 11) and deposits her egg by firmly attaching its posterior end to the edge of the disc. Thus, the egg is positioned behind the disc and is enclosed in a small open space (“egg chamber” in Rozen and Hall, 2014: fig. 12). She then completely fills in the front of the cell with soft pollen, so that most of the provisions are in front of the egg. Because the egg chamber is small, an entire, newly provisioned cell appears to be filled with provisions when first examined (Rozen and Hall, 2014: figs 12, 13), although after the larva feeds, the former egg chamber, now a larval chamber, enlarges.

In the case of *Lithurgus chrysurus* the arrangement of the provisions appears to be similar, but dimensions are different. With this species, the female first brings in a limited (but perhaps quite variable) amount of provisions (which are pasty, paler, and more moist than those of *Lithurgopsis apicalis*) and deposits them against the rear of the cell. She then somehow⁴ constructs a very large, posteriorly concave dish-shaped disc that stretches diagonally across the lumen of the cell (fig. 2, “disc”) and affixes the posterior end of her egg to the edge of the disc. The disc pollen is perhaps somewhat more cohesive and apparently slightly moister than the provisions in front of it. The egg chamber is much larger than that of *L. apicalis*, so that the provisions deposited at the rear rarely, if ever, meet the large disc above the anterior end of the egg. After depositing her egg, the female then completely fills in the front of the cell with a

⁴ With both of these species, eggs are deposited on the posterior disc surfaces, but how this is accomplished is unknown since almost certainly discs must be constructed before eggs are attached. Slanting of the egg toward the cell opening dictates that the depositing female faces the opening since eggs are always deposited posterior ends first. Observations of cells undergoing provisioning may lead to a better understanding of this matter.

large quantity of pasty, firmly packed provisions. However, because these provisions are not soft and fluffy, the seam between the convex front of the disc and the anterior cylinder of provisions is often visible (see fig. 2).

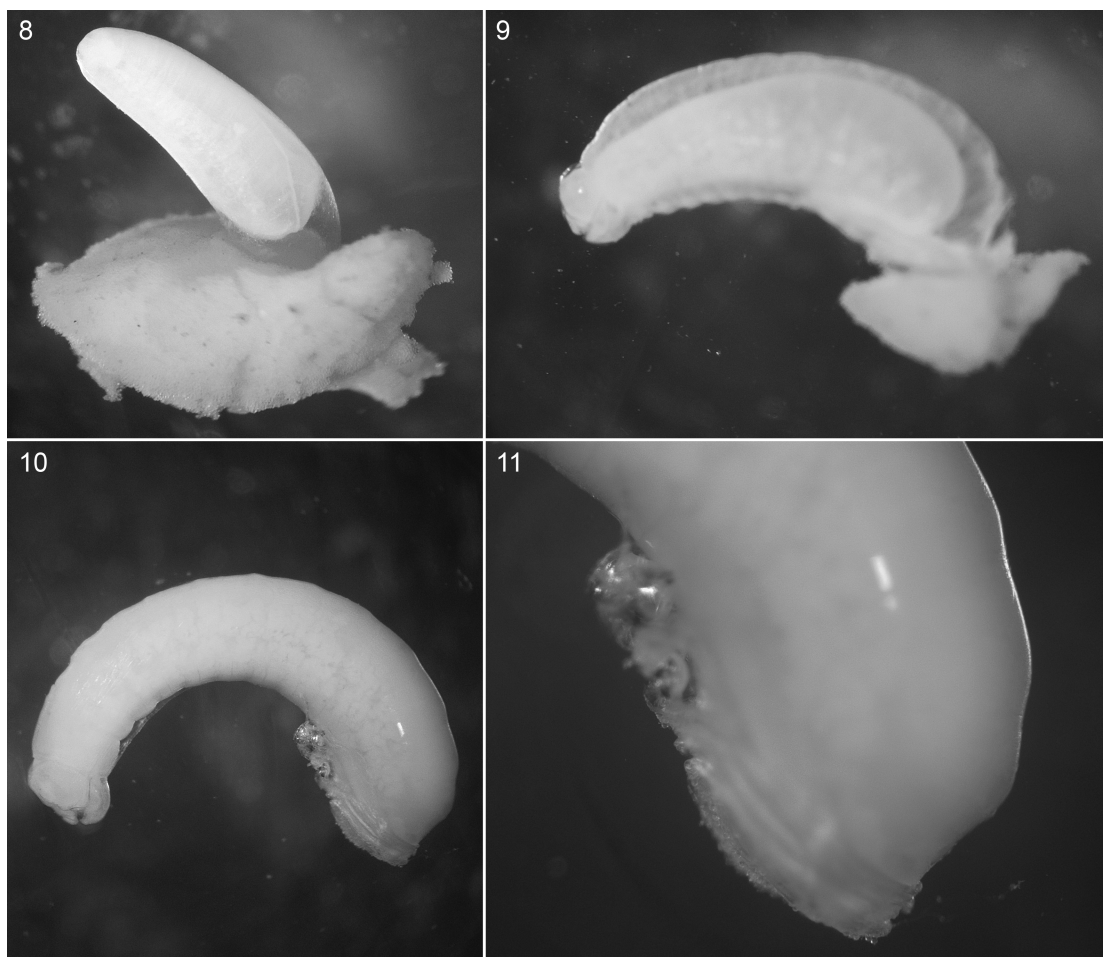
The assumption here is that behaviors leading to the formation of the discs of the two species and attachment of the eggs to the discs are homologous. Although we think that this is reasonable, it needs further support, which might come from (1) a more complete study of the biology of one or both of the species, particularly if cells can be examined in various stages of being provisioned, and/or (2) an examination of the biology of other species, which could provide new data to broaden our interpretation.

The above description of the provisions of *Lithurgus chrysurus* attempts to compare them in light of the interpretation of those of *Lithurgopsis apicalis*. Rust et al. (2004) provided a somewhat different interpretation. They regarded the provisions at the rear of the cell as extending forward along the bottom surface and to serve as the surface for egg attachment, calling it the “inner layer” with “both its anterior and the posterior ends slightly elevated.” Hence, they considered the provisions at the rear to be a part of the herein so-called disc. Both interpretations agree that the disc (“inner layer”) tends to be composed of more moist provisions compared with those at the front part (“outer layer”) of the provisions, which is drier. They also noted in some cases a gap existed “between the inner and outer layers of the provisions on the bottom surface”; this is presumably the seam noted above between the disc and front cylinder of the provisions.

DESCRIPTION OF EGG: Eggs of both species are nearly identical, with the long axis slightly curved and with the posterior end enlarged compared with the anterior end (compare fig. 8 with that of Rozen and Hall, 2014: fig. 21). Two eggs of *Lithurgus chrysurus* were 3.8 and 4.1 mm long and had maximum widths in the lower half of 1.3 and 1.4 mm, respectively. The chorion is transparent, reflective, and with no chorionic sculpturing when viewed with stereomicroscope. On SEM examination, the chorion appears smooth and featureless except for a network of fine ridges leading to the micropyle, a tight cluster of pores at the front end of the egg (fig. 17), perhaps not too unlike the micropylar area of *Lithurgopsis apicalis* (Rozen and Hall, 2014: fig. 24).

LARVAL DEVELOPMENT AND BEHAVIOR: While attached to the provisions, the anterior end of the curved egg of *Lithurgus chrysurus* bends toward the disc (fig. 8). After hatching, terminal abdominal segments of the larva are encircled by a ring of tightly folded chorion (fig. 9), accumulated there as part of the hatching process. Because the posterior end of the chorion in turn is still affixed to the lower end of the disc, the feeding young larva is firmly anchored at its posterior end to the disc. The larva's long agile body loops forward so that its head can reach and consume various parts of the disc in front of it (fig. 10). As with *Lithurgopsis apicalis*, the first four larval stadia of *L. chrysurus* are passed while the larva is so attached (figs. 9, 10). It detaches presumably as it molts to become the fifth (final) larval instar, after which it immediately starts defecating. The early cast exoskeletons as well as the chorion remain affixed to the larva's posterior end (fig. 11) until the start of the fifth stadium.

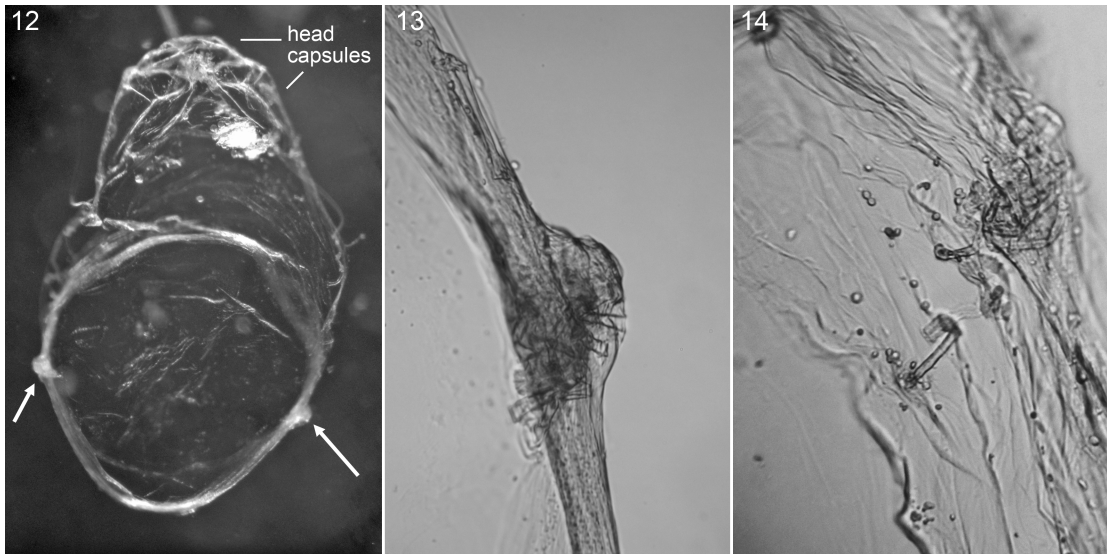
In some circumstances, the exuviae of the early larval stages can be carefully separated after they are removed en masse from a preserved fourth instar. Afterward, the exoskeleton of the



FIGURES 8–11. Microphotographs of immatures of *Lithurgus chrysurus*. **8.** Egg attached to scrap of disc. **9.** Second instar attached to scrap of disc. **10.** Fourth instar, with disc removed, showing accumulation of chorion and exoskeletons of previous instars at rear. **11.** Close-up of rear.

third instar can sometimes be teased from the earlier stages, and less frequently the second instar skin can also be removed intact. Both of these instars can be identified by their somewhat sclerotized head capsules. As is the case with *Lithurgopsis apicalis*, the head capsule of the first instar is not sclerotized (probably a good indication that first instars do not ingest pollen), so that its exoskeleton cannot be identified as easily as those of subsequent instars, in which vacated head capsules are easily seen adhering to the fourth instar's rear venter (fig. 11). A clue to the presence of the first instar skin is the presence of a cluster of spiracular atria and subatria on each side of a skin for each of the first three instars as demonstrated in figures 12–14.

In a recent paper Rozen and Hall (2012) hypothesized that body surface vestiture (combination of setae and elongate spicules) and certain body tubercles may enable the last larval instar to move about in the brood chamber in the case of *Trachusa larreae* (Cockerell). Early instars of that species lacked such body vestiture and are incapable of moving, suggesting that this vestiture

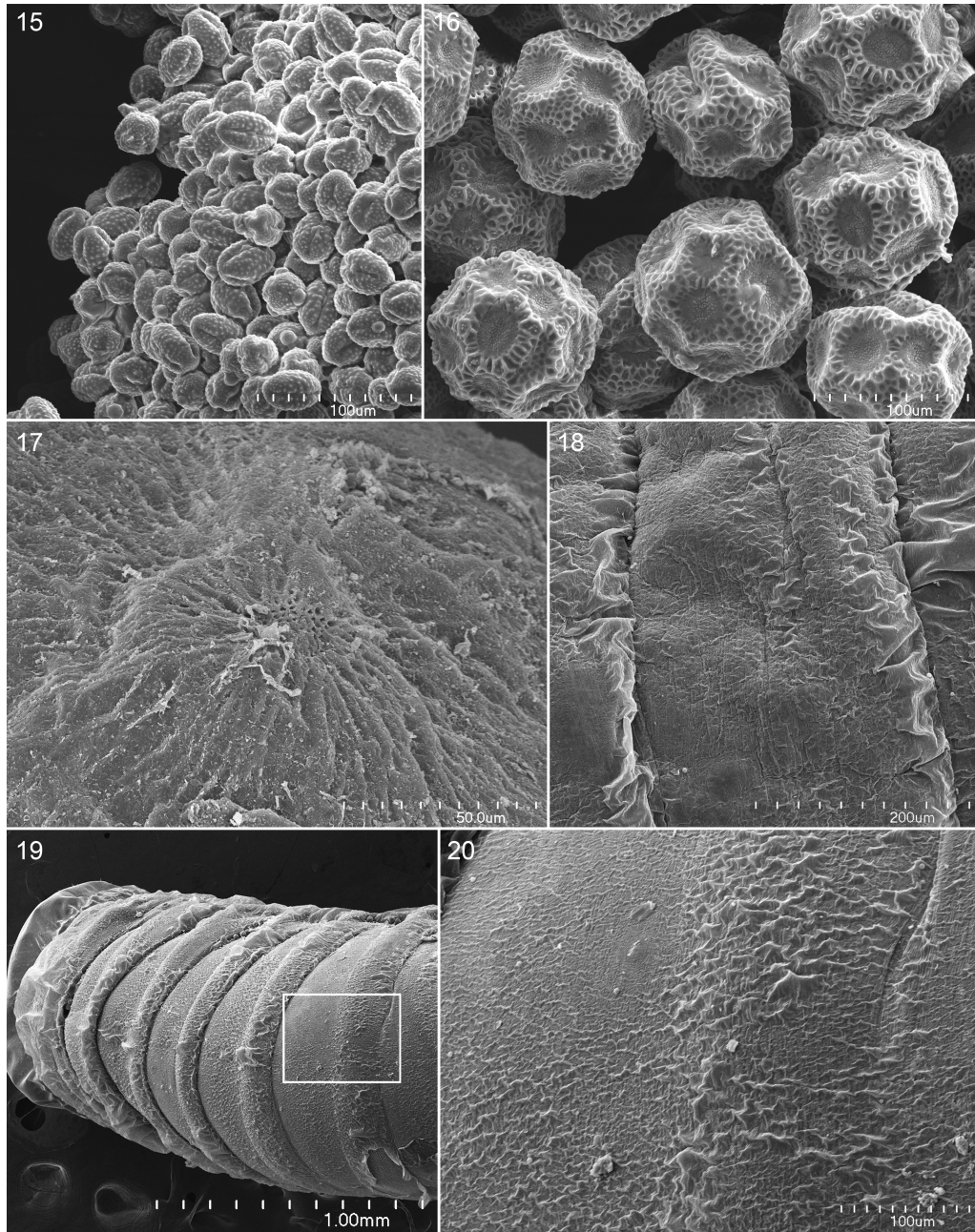


FIGURES 12–14. Microphotographs of cast exoskeletons from the same fourth instar of *Lithurgus chrysurus* in figures 10, 11. **12.** Third instar exoskeleton with chorion, and first and second instar exoskeletons removed showing position (arrows) of cluster of 10 spiracles on each side. **13.** Close-up of spiracles on right side figure 12. **14.** Close-up of spiracles on the right of the first instar with exoskeletons of second and third instars removed.

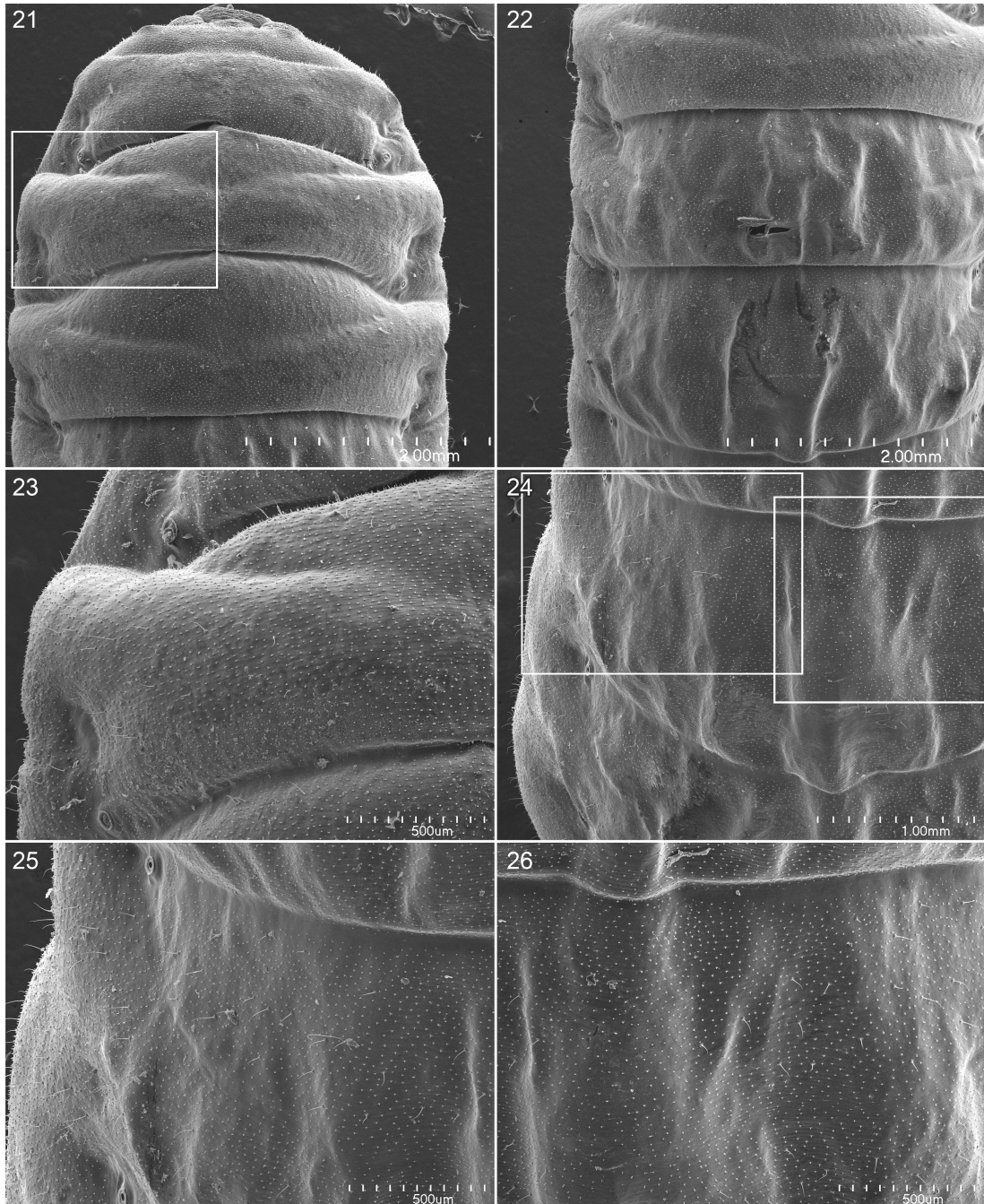
may function to enable movement. Then as Rozen (2013) stated in a paper describing the nesting biology of *Lithurgus chrysurus* from Palmerton, Pennsylvania “since ‘hairy’ mature larvae are characteristic of most Megachilidae, this hypothesis can and should be tested broadly within the family.” In the current study we continue the test by documenting that the first four larval instars of *L. chrysurus* are sedentary, with their posterior ends fastened to the provisions, while the fifth instar is no longer attached. Recovery of the earlier instars enables us to document that the integument of the third (fig. 18) and fourth instars (figs. 19, 20) (and no doubt first and second) lack setae and spicules, whereas fifth instars (figs. 21–25) are clearly spiculate and bear fine setae. However, it is noteworthy that, while this supports the hypothesis, the vestiture on this species is far less pronounced than that observed on *Trachusa larreae* (Rozen and Hall, 2012: figs. 44–51). We suppose that this may be correlated with either less activity or some different activity of *L. chrysurus* compared with that of *T. larreae*. Observations of the last larval instar of *L. chrysurus* showed it to be an elongate larva, always partly curled, primarily moving only the anterior part of its body to obtain food from the walls of the larval chamber. We were unable to observe any larvae toward the end of the feeding period or while cocoon spinning.

An interesting feature formerly overlooked was a difference in texture of the dorsal integument of the thoracic segments compared with the abdominal segments of the last stage larvae. As can be seen in figures 21 and 22, the thoracic segments appear much more planar and less rippled than the abdominal ones, though both have setae and spicules (figs. 23, 26).

Whereas the feces from the larva of *Lithurgopsis apicalis* intermixed with the uneaten loose *Opuntia* pollen in the cell, provisions in cells of *L. chrysurus* were more consolidated because



FIGURES 15–20. 15, 16. SEM micrographs of pollen of *Centaurea* sp. from larval provisions of *Lithurgus chrysurus* and of *Opuntia* sp. from larval provisions of *Lithurgopsis apicalis*, to same scale, respectively. 17. SEM micrograph of egg of *L. chrysurus*, showing micropyle. 18–20. Dorsal views of integument of abdominal segment 3 of various instars of *Lithurgus chrysurus* showing surface textures. 18. Third instar. 19. Entire anterior part of body of fourth instar showing projecting caudal annulets ringing thoracic and anterior abdominal segments. 20. Close-up of abdominal segment 3, identified by rectangle in figure 19.



FIGURES 21– 26. Dorsal view of integument of postdefecating fifth instar of *Lithurgus chrysurus*, showing integument and vestiture. **21.** Thorax of same. **22.** Metathorax and first two abdominal segments, showing contrast in integument between thoracic segments and abdominal segments of same. **23.** Close-up of integument of mesothorax, left side, as identified by rectangle in figure 21. **24.** Left side of abdominal segment 3 of same. **25.** Close-up of same, left rectangle of figure 24. **26.** Same, right rectangle of figure 24.

of small pollen size and greater moisture content, so that fecal pellets merely coated the exposed surface of the surrounding food mass (fig. 6).

The cocoon of *Lithurgus chrysurus* was described by Rozen (2013) and is being compared with that of *Lithurgopsis apicalis* by Rozen and Hall (2014).

DISCUSSION

Future studies of these two species and perhaps other species of *Lithurgus* and/or *Lithurgopsis* will be required to determine whether our interpretation of the arrangement of the provisions or that given by Rust et al. (2004) is more reasonable. Of greater interest, it is hoped these future studies will provide an understanding of how a female goes about arranging the provisions and attaching the egg to them in light of the fact that egg deposition must take place as the female faces the cell entrance while she affixes the egg to the disc.

When describing the original nest site, Roberts (1978) was impressed by the abundance of nests in the infested building, contrasting with their complete absence in adjoining buildings constructed of the exact same materials. He attributed this to a “highly gregarious” nesting behavior. He also noted that lithurgines as a group liked nesting in softwood, which is consistent with their nesting in soft compressed-wood fiber backing, and yet he also found and pictured them nesting in hardwood boards. In turn, we are impressed by the ever-growing number of lithurgine taxa reported nesting in soft cellulose materials (spring wood, degraded wood, horse dung, soft cactus tissue, compressed-wood fiberboard) (Michener, 2007; Roberts, 1978; Rozen, 1973, 2013; Sarzetti et al., 2012) and yet *Lithurgus chrysurus* burrows into firm wood that requires us to use axes, chisels, and hammers to penetrate.

Thus still unanswered: Why does this species seem to have such limited vagility? This bee appears capable of nesting in firm wood as well as soft or degraded wood; why then does it not spread its nesting range rather than build large, dense populations in areas that are so restricted and at the same time in regions where there is so much available dead wood?

ACKNOWLEDGMENTS

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