

American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N. Y. 10024

NUMBER 2265

AUGUST 18, 1966

Preliminary Systematic Study of the Pupae of Andrenid Bees (Hymenoptera, Apoidea)

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The purpose of the present paper is to describe the known pupae of the bee family Andrenidae and to elucidate, insofar as possible, the phylogeny and taxonomy of the family on the basis of characteristics of the pupae. As with most insects, the adults of bees have been studied systematically far more than have the immature stages. Pupae have been particularly neglected because the pupal stage is not easily found owing to the fact that bee nests are hidden and the external evidence of a nesting site is usually obliterated by the time larvae begin to pupate. Furthermore, the pupal stadium is usually short in comparison with that of the adult or larva, so that an investigator is far more likely to uncover larvae or to collect adults. Last, specimens of pupae do not preserve well, a situation that discourages taxonomic study.

Though pupae are occasionally collected and described, most descriptions are of little taxonomic meaning; many important taxonomic features are overlooked when an author has had no opportunity to compare his specimens with those of related taxa. Michener's paper (1954) on the pupae of bees, an outgrowth of his study of bee larvae, was exceptional in that he had pupae of 20 species, and in that he contrasted one species with another. Unfortunately, only one of his species belonged to the Andrenidae. The present investigation is based on 17 species in six genera.

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We wish to thank the following people for the loan of material used in this study: Dr. George E. Bohart and Mr. P. F. Torchio, Entomology Research Division, United States Department of Agriculture, Logan, Utah; Dr. Paul D. Hurd, Jr., California Insect Survey, Berkeley, California; and Dr. Charles D. Michener, the University of Kansas, Lawrence.

DISCUSSION

As mentioned by Michener (1954), the differences between bee pupae can be of two kinds. First, there are those features that have a counterpart in the adult; for example, the long pupal mouth parts of *Nomadopsis zonalis sierrae* (fig. 8) and the short ones of *helianthi* (fig. 4) reflect the mouth parts of the adults in length. The other set of features are those (usually tubercles and spines) that are expressed in the pupae alone. Only the latter are treated in this study.

It is obvious from the present investigation that numerous consistent differences exist among the pupae of andrenids. The known pupae of no two genera treated here are alike. Dissimilarities in pupae also occur at the species level, at least in some *Nomadopsis*, the only genus for which many pupae have been collected. For example, *N. scutellaris scutellaris* and *personata* can be distinguished from other species in the genus by the absence of scutal tubercles.

The adaptive significance of pupal characteristics, first discussed by Michener (1954), remains a partial mystery. Some of the tubercles allow for the development of setae of the adult, but other tubercles, such as those on the vertex of *Perdita*, and the terminal spine of *Perdita*, *Nomadopsis*, and others, do not serve this function. If anything, the problem is more inexplicable than it was 10 years ago, because we now know that all the pupae used in this study live in horizontal or slightly tipped cells, which presumably provide nearly identical environments. It is difficult to understand, therefore, what selective factors have been responsible for modifying the anatomy of these pupae. Such factors, however, are almost certainly present, and their detection will require more intensive studies of the biology of bee pupae. As a point of departure for such investigations, we believe that the elongate terminal spine found in a number of genera may be a device that allows the pupa to rotate on its long axis in the cell; however, the function of the movement is a moot question.

This study substantiates the presumed phylogenetic interrelationships of the family to some extent. For example, the Andreninae (*Andrena*) seem to be separated by a considerable gap from the Panurginae on the basis of pupal features, and, within the Panurginae, *Perdita* pupae are unquestionably distinctive. However, the pupae of the panurgines, al-

though differing from one another, do not demonstrate patterns of relationship. The fact is not surprising, because the various genera are few in number, and most are not considered closely related as judged by adult characteristics (Rozen, 1951). It is interesting that *Nomadopsis* and *Calliopsis*, presumed near relatives on the basis of adult (Rozen, 1958) and larval (Rozen, 1966b) features, have pupae that exhibit a number of dissimilarities.

ANDRENIDAE

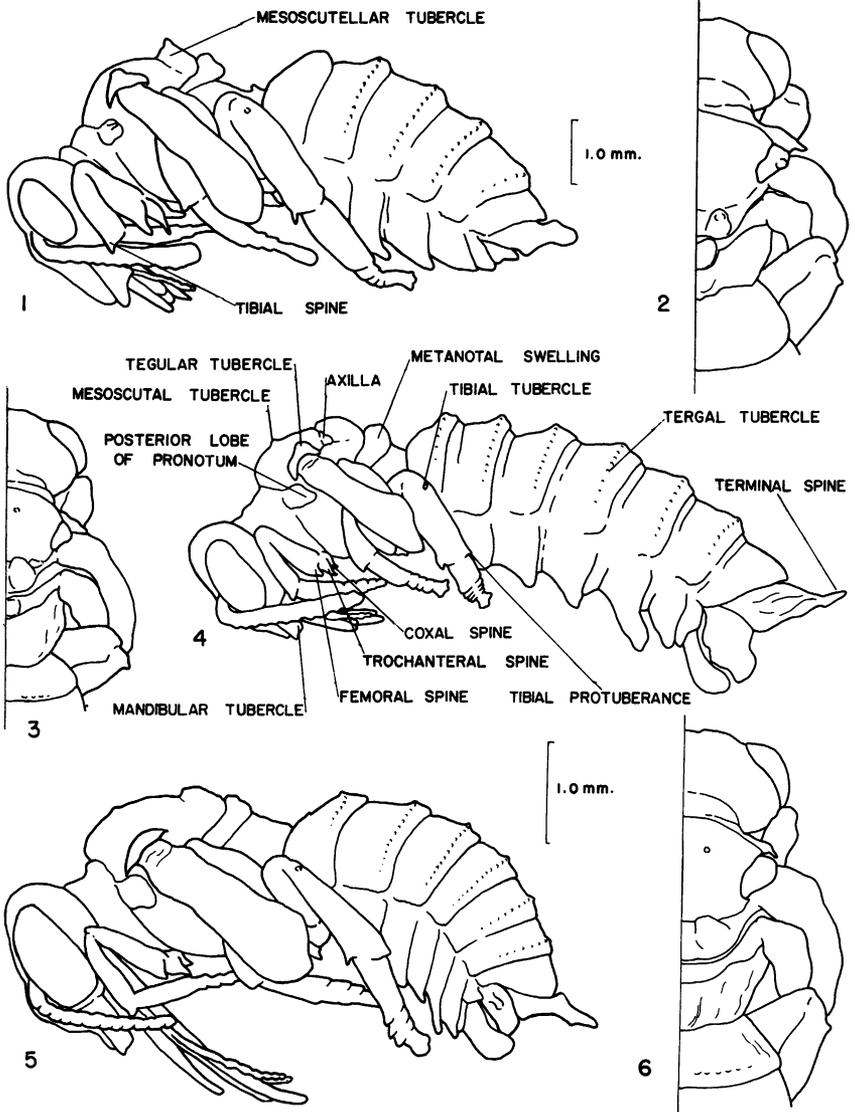
The pupae of this family seem to be distinguishable in some cases from those of other families of bees, of which the pupal characters have been studied by Michener (1954) or by us. The andrenids possess small but distinct apical tubercles on most metasomal terga, whereas known representatives of the Hylaeinae, Colletinae, and Diphaglossinae either lack such tubercles entirely or have, at best, minute tubercles or only irregularities. The andrenids do not exhibit a tubercle on the forewing and have at most a small tubercle at the base of the hind tibia, in contrast with halictids which have a large wing tubercle and a large spine at the base of the hind tibia. Further, andrenids do not have long setae as do most megachilids (Rozen, 1966a). The Andrenidae (except for *Perdita*) possess mesoscutal, mesoscutellar, and metanotal tubercles, or all three, and therefore can be distinguished from the Apidae which consistently lack such tubercles. The Anthophoridae are a large, diverse group the pupae of which have not been adequately studied. They will be treated in a subsequent paper, in which they will be compared with those of the Andrenidae. The pupae of the Fideliidae, Oxaeidae, and Melittidae are unknown.

GENERAL DESCRIPTION

Body without setae.

HEAD: Scape and frons without tubercle; vertex without tubercle, except in *Perdita*; ventral surface of mandible without tubercle, except in *Nomadopsis*, *Perdita*, and *Andrena*.

MESOSOMA: Posterior lobe of pronotum produced in varying degrees, except in *Perdita*; mesepisternum with tubercle only in *Perdita lingualis*; mesoscutum with pair of very small tubercles in *Calliopsis* and many *Nomadopsis*; mesoscutellum with pair of tubercles of varying size and shape; axillae usually not produced; metanotum in some species produced; propodeum with protuberance in *Andrena bisalicensis*; tegula bearing tubercle in *Andrena*, *Melitturga*, and *Calliopsis*; wing without tubercle;



FIGS. 1, 2. *Andrena bisalicensis* Viereck, lateral and dorsal views.

FIGS. 3, 4. *Nomadopsis helianthi* (Swenk and Cockerell), dorsal and lateral views.

FIGS. 5, 6. *Nomadopsis hesperia equina* (Cockerell), lateral and dorsal views. Scale same as *N. helianthi*.

coxae with spines; fore and mid trochanters and fore femora usually with spines; hind trochanter with spine, except in *Melitturga* and *Calliopsis*; *Calliopsis* without any trochanteral or femoral spines; *Perdita* with long coxal and trochanteral spines; those of Andreninae longer than those of Panurginae; only *Andrena* with spine on fore tibia; base of hind tibia with small tubercle, except in *Perdita* and *Melitturga*; outer apex of hind tibia in some species produced.

METASOMA: Terga with small tubercles, beginning on tergum 1 in Panurginae, on tergum 2 in Andreninae; *Perdita* with small sternal tubercles; terminal spine of various lengths.

ANDRENINAE

ANDRENA FABRICIUS

Andrena (Thysandrena) bisalicyis Viereck

Figures 1, 2

Length, 9.5 mm. Mandible with large tubercle on ventral surface; vertex without tubercles. Posterior lobe of pronotum produced; mesoscutum without tubercles; mesoscutellum with pair of large tubercles; axilla not produced; metanotum with very large median swelling; propodeum with posterior protuberance; mesepisternum without tubercle. Tegula with tubercle. Each coxa with long apical spine; each trochanter with long apical spine; fore and mid femur with long basal spine; fore tibia with outer apical spine; hind tibia with small tubercle near base and small, outer, apical protuberance. Metasomal terga 2-6 (male) and 2-5 (female) with one subapical row of small tubercles; metasomal sterna without tubercles; terminal spine short, and broadly rounded apically.

MATERIAL STUDIED: One male and one female pupa, Alpine, Bergen County, New Jersey, July 7, 1965; pupated in laboratory, August 12, 1965 (M. Favreau, O. Hamill), in the collection of the American Museum of Natural History. Associated adults identified by Wallace E. LaBerge.

Andrena (Leucandrena) erythronii Robertson

Length, 12.0 mm. As described for *A. bisalicyis*, except as follows: mandible apparently without tubercle; propodeum without protuberance; spines on coxae, trochanters, and femora longer.

MATERIAL STUDIED: One male pupa, Potter's Lake, Lawrence, Douglas County, Kansas, nest B-4, September 18, 1954 (C. D. Michener), on loan from the University of Kansas. Associated adults identified by C. D. Michener.

Andrena (Mimandrena) imitatrix Cresson

Length, 9.5 mm. As described for *A. bisaliciis*, except as follows: posterior lobe of pronotum only slightly produced; propodeum without protuberance.

MATERIAL STUDIED: One male pupa, Lewisboro, Westchester County, New York, August 9, 1965 (M. Favreau), in the collection of the American Museum of Natural History. Associated adults identified by Wallace E. LaBerge.

PANURGINAE

NOMADOPSIS ASHMEAD

Nomadopsis (Micronomadopsis) helianthi (Swenk and Cockerell)

Figures 3, 4

Michener (1954) described the pupa of this species under the name *N. euphorbiae* (Cockerell).

Length, 6.0–8.0 mm. Mandible with tubercle on ventral surface; vertex without tubercles. Posterior lobe of pronotum produced somewhat postero-ventrally; mesoscutum with pair of very small tubercles slightly anterior to middle; mesoscutellum with low, paired swellings; axilla somewhat swollen; metanotum with median swelling; mesepisternum without tubercle. Tegula not produced. Each coxa with apical spine; fore and mid trochanter with apical spine; fore femur with basal rounded spine; hind tibia with small tubercle near base and no outer apical protuberance. Metasomal terga 1–6 (male) and 1–5 (female) with one subapical row of very small tubercles; metasomal sterna without tubercles; terminal spine elongate, and slightly rounded apically.

MATERIAL STUDIED: Twelve male and eight female pupae, 16 miles northeast of Douglas, Cochise County, Arizona, August 24, 1962 (J. G. Rozen, S. Hessel, M. Statham), in the collection of the American Museum of Natural History; two male and two female pupae, Artois, Glenn County, California, August 12, 21, 1953 (Rozen), on loan from the California Insect Survey; one male and one female pupa, Newport Ranch, 2 miles southwest of Romoland, Riverside County, California, August 17, 1946 (J. W. MacSwain), on loan from the California Insect Survey. Associated adults identified by J. G. Rozen.

Nomadopsis (Micronomadopsis) hesperia equina (Cockerell)

Figures 5, 6

Length, 5.5–6.25 mm. As described for *N. helianthi*, except as follows: posterior lobe of pronotum in some produced more strongly; axilla not

produced; metanotum without median swelling; mid femur with basal rounded protuberance; terminal spine pointed apically.

MATERIAL STUDIED: Two male pupae and one female pupa, San Lorenzo, Alameda County, California, September 16, 18, 1954 (J. G. Rozen and P. D. Hurd), on loan from the California Insect Survey. Associated adults identified by J. G. Rozen.

Nomadopsis (Micronomadopsis) scutellaris scutellaris (Fowler)

Length, 6.5 mm. As described for *N. helianthi*, except as follows: posterior lobe of pronotum somewhat more produced; mesoscutum without tubercles; metanotum only slightly swollen medially; mid femur with short basal spine; terminal spine pointed apically.

MATERIAL STUDIED: One male pupa, Turlock, Stanislaus County, California, June 3, 1955 (P. D. Hurd, J. G. Rozen, R. Snelling), on loan from the California Insect Survey. Associated adults identified by J. G. Rozen.

Nomadopsis (Micronomadopsis) personata (Cockerell)

Length, 5.5–6.5 mm. As described for *N. helianthi*, except as follows: posterior lobe of pronotum somewhat more strongly produced; mesoscutum without tubercles; axilla not produced; metanotum not produced; mid femur with basal spine; tergum 1 with very few subapical tubercles; terminal spine pointed apically.

MATERIAL STUDIED: Two male pupae and one female pupa, Wallace Ranch, 5 miles southeast of Umapine, Umatilla County, Oregon, January, 1963, pupated in March, 1963 (P. F. Torchio), on loan from P. F. Torchio. Associated adults identified by J. G. Rozen.

Nomadopsis (Micronomadopsis) scitula (Cresson)

Length, 7.5 mm. As described for *N. helianthi*, except posterior lobe of pronotum more strongly produced.

MATERIAL STUDIED; One male pupa, Hidden Valley, Wyoming, August 8, 1955 (G. E. Bohart and E. A. Cross), on loan from the California Insect Survey. Associated adult identified by J. G. Rozen.

Nomadopsis (Nomadopsis) zonalis sierrae Rozen

Figures 7, 8

Length, 8.5–9.0 mm. As described for *N. helianthi*, except as follows: mesoscutellum with larger swellings; axilla not produced; metanotum only slightly swollen medially.

MATERIAL STUDIED: Three male pupae, Tuolumne, Tuolumne County, California, July 3, 1961 (J. G. Rozen), in the collection of the American Museum of Natural History. Associated adults identified by J. G. Rozen.

Nomadopsis (Nomadopsis) puellae (Cockerell)

Length, 9.5–10.0 mm. As described for *N. helianthi*, except as follows: posterior lobe of pronotum only very slightly produced; metasomal tergum 6 (male) and 5 (female) without tubercles; terminal spine shorter, and broadly rounded apically.

MATERIAL STUDIED: One male and one female pupa, 2 miles east of Apache, Cochise County, Arizona, September 22, 1963, pupated in laboratory, April 5 and March 7, 1964 (J. G. Rozen), in the collection of the American Museum of Natural History. Associated adults identified by J. G. Rozen.

Nomadopsis (Macronomadopsis) anthidia anthidia (Fowler)

Figures 9, 10

Length, 8.0–10.0 mm. As described for *N. helianthi*, except as follows: posterior lobe of pronotum only very slightly produced; mesoscutellum with swellings directed anteriorly; mid femur with basal spine; terminal spine shorter, and more broadly rounded.

MATERIAL STUDIED: One male pupa and three female pupae, Tuolumne, Tuolumne County, California, spring, 1953 (J. G. Rozen), on loan from the California Insect Survey. Associated adults identified by J. G. Rozen.

Nomadopsis boharti Rozen

The only available specimen of this species was poorly preserved, so that a complete taxonomic description is not possible. All characters that are present, however, were as described for *N. helianthi*, except that the posterior lobe of the pronotum was somewhat more strongly produced.

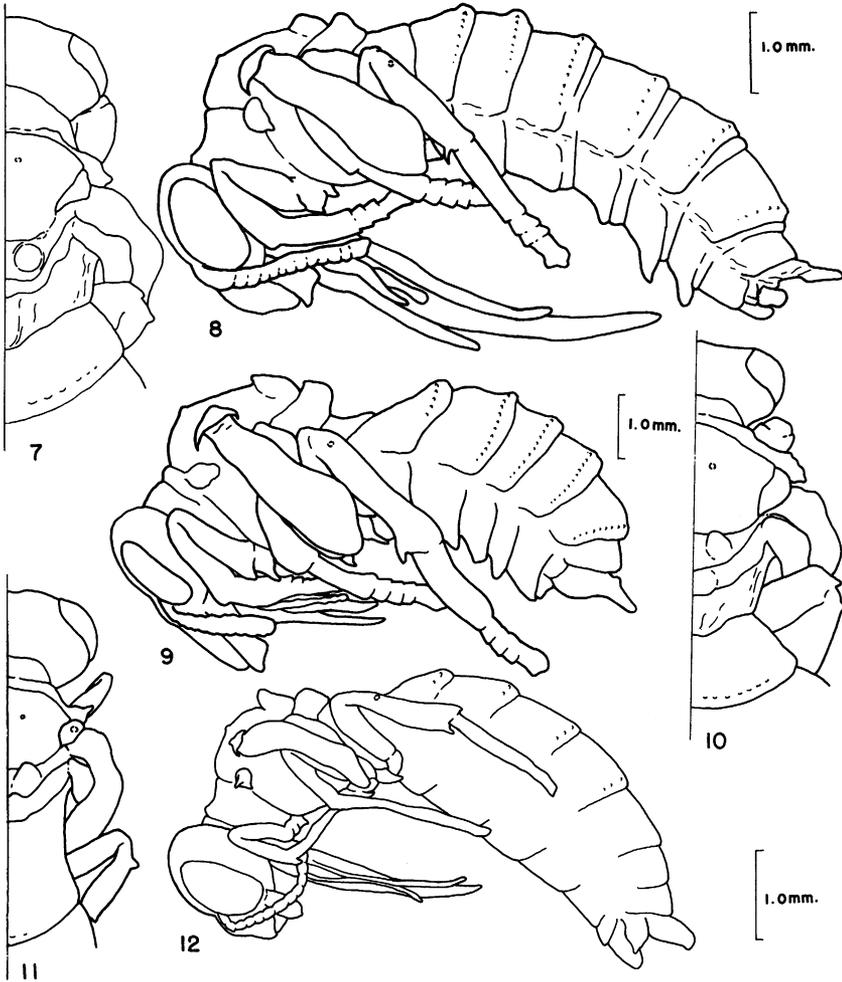
MATERIAL STUDIED: One male pupa, Tuolumne, Tuolumne County, California, June 8, 1953 (J. G. Rozen), on loan from the California Insect Survey. Identified by J. G. Rozen.

CALLIOPSIS SMITH

Calliopsis (Calliopsis) andreniformis Smith

Figures 11, 12

Length, 7.5 mm. Mandible without tubercle on ventral surface; vertex without tubercles. Posterior lobe of pronotum produced; mesoscutum



FIGS. 7, 8. *Nomadopsis zonalis sierrae* Rozen, dorsal and lateral views.

FIGS. 9, 10. *Nomadopsis anthidia anthidia* (Fowler), lateral and dorsal views.

FIGS. 11, 12. *Calliopsis andreniformis* Smith, dorsal and lateral views.

with pair of very small tubercles anterior to middle; mesoscutellum with pair of anteriorly directed tubercles; axilla not produced; metanotum somewhat swollen medially; mesepisternum without tubercle. Tegula with small but distinct tubercle. Each coxa with very small spine; trochanters without spines; fore femur without spine; hind tibia with small tubercle

near base and small outer apical protuberance. Metasomal terga 1-4 (5, 6, and 7 destroyed) (male) with few, very small tubercles; metasomal sterna without tubercles; terminal spine elongate, and broadly rounded apically.

MATERIAL STUDIED: One male pupa, 11 miles east of Brookville, Jefferson County, Pennsylvania, August 11, 1964 (A. Moldenke), in the collection of the American Museum of Natural History. Associated adults identified by J. G. Rozen.

PANURGINUS NYLANDER

Panurginus Species A

Figures 13, 14

Length, 6.5-7.0 mm. Mandible without tubercle on ventral surface; vertex without tubercles. Posterior lobe of pronotum scarcely produced; mesoscutum without tubercles; mesoscutellum with pair of pointed, anteriorly directed tubercles; axilla not produced; metanotum not produced; mesepisternum without tubercle. Tegula not produced. Each coxa with long apical spine; each trochanter with long apical spine; fore femur with basal spine; hind tibia with small tubercle near base and small outer apical protuberance. Metasomal terga 1-6 (male) and 1-5 (female) with scarcely noticeable tubercles; metasomal sterna without tubercles; terminal spine elongate, and rounded apically.

MATERIAL STUDIED: One male pupa and three female pupae, Preston Spring, Cub River Canyon, Franklin County, Idaho, May 6, 1949 (G. E. Bohart), on loan from G. E. Bohart.

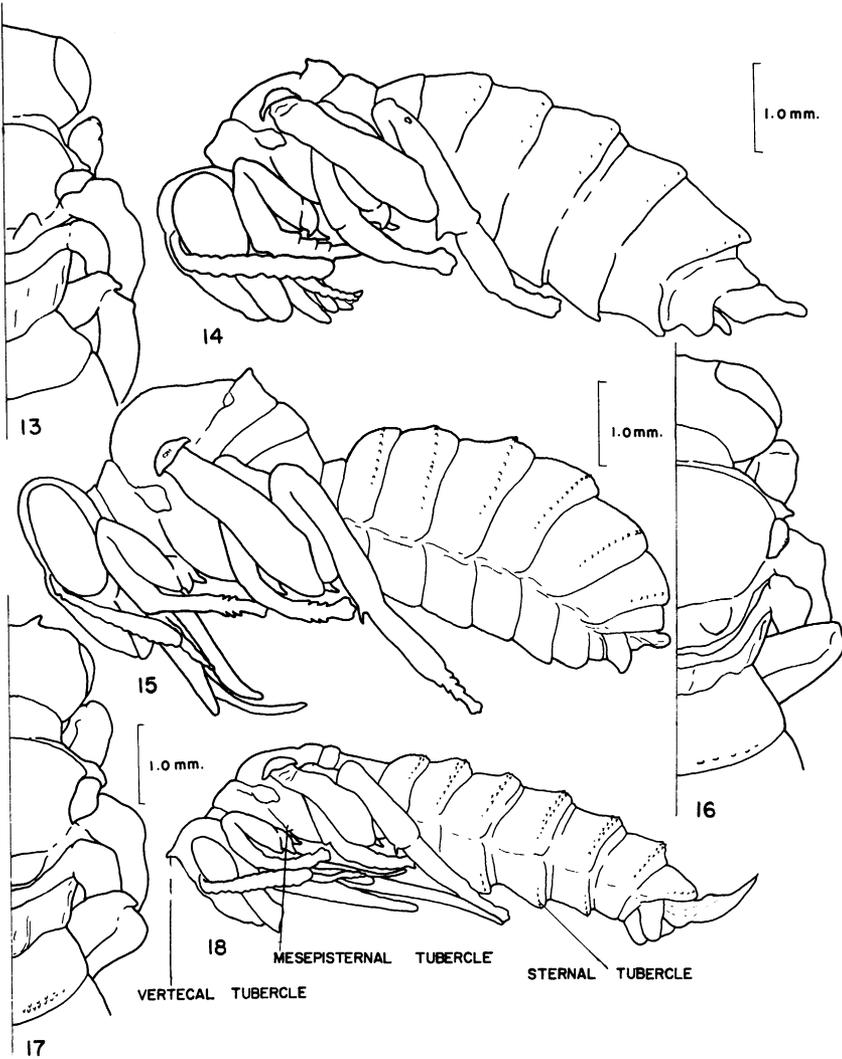
MELITTURGA LATREILLE

Melitturga clavicornis (Latreille)¹

Figures 15, 16

Length, 10.0-15.0 mm. Mandible without tubercle on ventral surface; vertex without tubercles. Posterior lobe of pronotum produced; mesoscutum without tubercles; mesoscutellum with pair of widely spaced tubercles; axilla somewhat swollen; metanotum not produced; mesepisternum without tubercle. Tegula with small tubercle. Each coxa with apical spine; fore and mid trochanters with small apical spine; fore femur with basal spine; hind tibia with no tubercle near base and no outer apical protuberance. Metasomal terga 1-6 (male) each with one subapical row of small, sharp-pointed tubercles; metasomal sterna without tubercles;

¹ The pupae of this species are unique in the Panurginae in that, when the eye darkens, the lower two-fifths is distinctly darker than the upper three-fifths.



FIGS. 13, 14. *Panurginus* species A, dorsal and lateral views.
 FIGS. 15, 16. *Melitturga clavicornis* (Latreille), lateral and dorsal views.
 FIGS. 17, 18. *Perdita lingualis* Cockerell, dorsal and lateral views.

terminal spine shorter than those of other genera, and broadly rounded apically.

MATERIAL STUDIED: Two male pupae, Sierre, Switzerland, collected as

larvae July 5, 1964, pupated February 20 and May, 1965 (J. G. Rozen), in the collection of the American Museum of Natural History. Associated adults identified by J. G. Rozen.

PERDITA SMITH

Perdita (Cockerellia) lingualis Cockerell

Figures 17, 18

Michener (1963) briefly compared the pupa of this species with that of *P. maculigera maculipennis*. The specimens used here are those studied by Michener.

Length, 8.0–9.5 mm. Mandible with swelling on ventral surface; vertex with pair of sharp-pointed, diverging spines, in approximate position of lateral ocelli. Posterior lobe of pronotum not produced; mesoscutum without tubercles; mesoscutellum without tubercles; axilla not produced; metanotum not produced; mesepisternum with moderate-sized tubercle anteriorly. Tegula not produced. Each coxa with long apical spine; each trochanter with long apical spine; fore femur with basal spine; hind tibia with no tubercle near base and no outer apical protuberance. Metasomal terga 1–7 (male) and 1–6 (female) each with several distinct subapical rows of small tubercles bearing long setae on their tips, most metasomal sterna with very small, subapical, setae-bearing tubercles; metasoma terminating in sharp-pointed spine that is more elongate than spines of other genera.

MATERIAL STUDIED: Four male and five female pupae, Lawrence, Douglas County, Kansas, September 1, 1955, sandy bank (C. D. Michener), on loan from the University of Kansas.

Perdita (Perdita) maculigera maculipennis Graenicher

Michener and Ordway (1963) described the specimens treated here.

Length, 6.5–8.0 mm. As described for *P. lingualis*, except as follows: tubercles of vertex more attenuate; sterna without tubercles; terminal spine more elongate.

MATERIAL STUDIED: Three female pupae, Lawrence, Douglas County, Kansas, May 28, 1958 (C. D. Michener and E. Ordway), on loan from the University of Kansas. Associated adults identified by P. H. Timberlake.

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