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Biology and Immature Stages of the Panurgine Bee Genera *Hypomacrotera* and *Psaenythia* (Hymenoptera, Apoidea)

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Of the nine genera of North American panurgine bees, the biologies of six and larvae of five have been described (Rozen, 1966, 1967). The present paper treats, for the first time, the bionomics, larva, and pupa of the North American genus *Hypomacrotera* Cockerell and Porter, gives the first description of the larva and pupa of the New World genus *Psaenythia* Gerstaecker, and includes new biological data concerning *Psaenythia*. The phylogenetic relationships of the two genera to other panurgines are discussed in light of the information reported here. Life histories and immature stages of *Xenopanurgus* Michener and *Metapsaenythia* Timberlake have yet to be studied.

I wish to thank Mrs. Marjorie Favreau for her untiring assistance in excavating nests on a hot desert in August and a cold desert in May. Mrs. Rose Ismay typed and edited the manuscript. The research was supported by National Science Foundation Grant GB-5407.

BIOLOGY OF *HYPOMACROTERA*

On the basis of adult anatomy, *Hypomacrotera* is a member of a large complex of New World panurgine bees including *Nomadopsis* and *Cal-*

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liopsis from North America. The genus contains two nominal species, *callops* Cockerell and Porter, and *subalpinus* (Cockerell). However, because the genus has never been revised, unrecognized species may exist. Each species consists of two subspecies, the non-nominate forms being *subalpinus andradensis* Cockerell and *callops persimilis* Cockerell. Specimens of *H. subalpinus* in the American Museum of Natural History collection are variable, especially with respect to size and to light color markings, and suggest therefore that the races of the species need further study before they can be properly delimited. Consequently, the adults of *subalpinus* collected in connection with the present study are not assigned to subspecies.

Except for a somewhat less-produced wing apex, the male specimens of *H. callops* involved in the present investigation agree closely with the male type of the nominate subspecies in the collection of the American Museum of Natural History and are therefore assigned to *H. callops callops*. However, other adult specimens from southeastern Arizona in the collection of the American Museum of Natural History agree closely with the description of *callops persimilis*, the type of which I have not examined. If the latter specimens are indeed *persimilis*, then *persimilis* and *callops* are sympatric and distinct, and must be assigned separate species status. Not only do the two forms differ in the features listed by Cockerell (1900), but also the females of *persimilis* before me have a long middle basitarsus and a dark basitibial area on the midleg; the female of *callops* possesses an unusually short middle basitarsus and the basitibial area of the midleg is whitish.

DESCRIPTION OF NESTING SITE: Both *H. callops callops* and *subalpinus* nested along the slightly sloping shoulders of a paved, east-west running road, Tenth Street, on the outskirts of Douglas, Cochise County, Arizona (fig. 1). First found on August 22, 1968, when the adults were fresh, the two species were much less abundant by August 31, 1968, when many of the adults were frayed. Creosote bushes (*Larrea*) dominated the land adjacent to the road in former years, but are now replaced by newly constructed houses. The road shoulders (fig. 1) were occasionally graded and the vegetation was moderately sparse and low; none of the discovered nest entrances was shaded. *Physalis*, the pollen plant of *H. callops callops*, and *Sphaeralcea*, that of *H. subalpinus*, grew moderately for a distance of about a tenth of a mile along the shoulders. The nests of *H. callops callops* were found sparsely and widely distributed along both sides, whereas the burrows of *H. subalpinus* seemed to be restricted to one section of the south side of the road. So far as is known, the nests of the two species were not interspersed although all areas seemed super-

ficially identical. The soil was moderately hard, contained small stones, and at the cell level was moist because of summer thunderstorms.

NESTING HABITS OF *H. subalpinus*: Although adults of *H. subalpinus* were common on the pollen plant, we located only four nests. Although not closely spaced, all were along one section of the road where occasional females of a species belonging to the parasitic bee genus *Oreopasites* searched for burrow entrances. Three entrances were on moderately sloping ground; the other was on a nearly horizontal surface. The latter en-



FIG. 1. Nesting area of *Hypomacrotera* along Tenth Street, Douglas, Arizona.

trance had a tumulus on one side, whereas another entrance had a tumulus on the downhill side. In all cases the entrances were not obscured by tumuli. The main tunnels were 4.5 mm. in diameter, and, except for one tunnel, which was open most of its length, all were loosely filled with soil below the entrance. All the main burrows descended in a tortuous fashion.

Four cells were situated at depths of about 5 to 7 cm. One nest had two cells, whereas another had none as yet. As the season seemed early at the time of excavation, completed nests possibly have a number of cells. Laterals seemed nearly horizontal and did not dip and then rise before connecting to cells. Two cell openings were respectively 3.50 and 3.25 mm. in diameter. The cells were nearly horizontal, with their rear

end slightly lower than the front. The cells possessed a somewhat shiny, waterproof lining over rather uneven walls which, here and there, bore impressions of the pygidial plate of the female. In several cells the wall was about 0.5 mm. thick and possibly could have been plastered with a soil lining, although it may only have been kneaded by the pygidial plate of the female. Cell dimensions are given in table 1.

The inside of the spiral cell closure was strongly concave and consisted of about four to five rows to the radius. The single pollen-nectar mass found was spherical, homogeneously moist, and coated with a thin, waterproof, transparent covering.

TABLE 1
DIMENSIONS (IN MILLIMETERS) OF NEST COMPONENTS OF *Hypomacrotera*
(Figures in Parentheses are Number of Measurements)

Species	Cell Length	Cell Diameter	Pollen Ball Diameter
<i>subalpinus</i>	8.0-10.0 (3)	5.0-6.0 (4)	3.0 (1)
<i>callops callops</i>	6.0-6.5 (7)	3.0-4.0 (9)	2.0-2.7 (4)

Adult males of *H. subalpinus* were collected at the nesting site in early May, a fact indicating that the species is probably multivoltine.

NESTING HABITS OF *H. callops callops*: Our knowledge of the biology of this species is more complete than is that of *H. subalpinus*. The five nests found were situated on slightly sloping ground. Tumuli surrounded and hid entrances of nests being provisioned. The main tunnels, two of which measured 2.75 and 3.25 mm. respectively in diameter, were otherwise essentially identical to those of *H. subalpinus*. They were partly to completely clogged with loose soil.

Cells, found singly (i.e., not in series) and between 5 to 11 cm. in depth, were essentially identical to those of *H. subalpinus* except for their smaller size (table 1) and in displaying more apparent pygidial embossings. The closures, identical on the inside to those of *H. subalpinus*, possessed a smooth, concave exterior surface against which the soil of the lateral burrow was piled; one closure was 2.0 mm. thick at the rim. The distances between four cells and the main burrows ranged from 5 to 10 mm.; laterals were filled with soil and led directly to the cells without dipping and rising again. The largest nest excavated contained four cells; the last (lowest) cell to be constructed was still open and empty. Completed pollen masses were spherical, homogeneously moist, variable in size (table 1), and coated with a thin, transparent, waterproof substance. Several incomplete provisions, also spherical, were smaller than the com-

pleted ones and lacked a coating. The completed spheres were not glued to the floor of the cell, and the eggs (one was 1.75 mm. long), supported by their anterior and posterior ends, rested on top of the provisions. The blunt anterior end of the shiny white egg was directed toward the front of the cell; the posterior end was more pointed. First instars fed while oriented in the same position as the eggs.

Three mature, postdefecating larvae were found resting on their dorsa, with their heads closest to the cell closures. The feces had been applied as a patch to the upper rear of the cell, as illustrated for *Meliturgula braunsi* Friese (Rozen, 1968, fig. 4). The larvae were quiescent or soon became so, and two were allowed to overwinter in the laboratory. This species, like *H. subalpinus*, is multivoltine, for adults were flying in early May, 1969.

MATING HABITS: Although the mating habits were not studied in detail, casual observations revealed that the premating patterns of the males of the two species were radically different. Males of *H. callops callops* flew swiftly back and forth low over the ground. This rapid flight and the fact that the males often returned to the same spot to rest suggest territoriality. Males of *H. subalpinus* were most commonly encountered sitting on flowers, presumably waiting for females to come to the plant. Occasionally, males flew swiftly from their resting places to other flowers, and several times two males were observed "fighting" on the same flower. Males of this species did not patrol the ground, as did males of *H. callops callops*.

Females of *H. callops callops* often flew from the pollen plant to the ground where they rested briefly before flying away. No copulations were seen on the flowers, but one pair copulated for two or three seconds as the female slowly descended into her burrow. Females of *H. subalpinus* were not noticed resting on the ground.

NEST ASSOCIATES: A cuckoo bee belonging to the anthophorid genus *Oreopasites* parasitized the nests of *H. subalpinus*. Males and females of the parasite were sparsely distributed over the restricted area of the host. In their search flight, the female *Oreopasites* flew close to the ground and made numerous stops, presumably at suspected nest entrances. One *Oreopasites* larva, probably a second instar, was encountered lying on top of a dead, young host larva. Remains of four first instar *Oreopasites* were recovered from the same cell, and the cell wall contained a number of pits, almost certainly egg deposition punctures. The wall also exhibited numerous rough, scraped areas, perhaps where the host female tried to dig out the parasite's eggs. No cuckoo bees were associated with the nests of *H. callops callops*.

BIOLOGY OF *PSAENYTHIA*

Psaenythia bicolor Timberlake, the biology of which has been treated briefly by Rozen (1967), nested two miles east of Apache, Cochise County, Arizona, where it was first discovered on August 28, 1968. Because the nesting season had just begun, a number of burrows were marked for later excavation which took place on May 2 and 6, 1969.

DESCRIPTION OF NESTING SITE: The site (fig. 2), a shallow cattle wallow, several hundred yards long and about 25 feet wide, in a nearly horizontal, grass-covered field, was dry both when found and when excavated. It was flooded with more than a foot of water in August, 1969 because of heavy summer rains. Clumps of a yellow-flowered *Solanum* grew in the wallow in late summer of 1968, and low clumps of a yellow composite occurred there the following spring, but extensive barren areas existed and the nest entrances were unshaded.

NESTING HABITS: The bees excavated their nests in the cracks of the dry and heavy soil, which contained much organic material but almost no stones, so that the entrances were inconspicuous. Nests were irregularly scattered along the northern half of the wallow. Details of the nest structure agree with those given earlier (Rozen, 1967) except as follows: One of the main burrows excavated was 4.5 mm. in diameter; most cells were found at a depth of 50 to 55 cm. (in contrast with the 14 cm. depth at the Portal site, Rozen, 1967); they varied in maximum diameter, 5.25 to 6.25 mm. (five measurements). Heretofore unrecorded information includes the fact that the cells, arranged singly, were found at the bottom of the main burrow and were connected to it by long, filled laterals, in one nest ranging in length from 4.0 cm. to 10.0 cm.



FIG. 2. Nesting area of *Psaenythia bicolor*, 2 miles east of Apache, Arizona.

All larvae uncovered in cells were resting on their dorsa, with their heads closest to the cell closures, as is characteristic of all panurgines. Overwintering as postdefecating forms, the larvae differed from those of other North American panurgines in that the former were able to slowly curl and uncurl at the time they were excavated. In this respect they are similar to the African *Meliturgula braunsi* (Rozen, 1968). Feces were applied to the top rear of the cell as a small patch flush with the cell surface, about 3.5 mm. in diameter and slightly less than 1.0 mm. at maximum thickness. The postdefecating larva was not glued to the meconial mass, as is the case with *Panurginus potentillae* (Crawford) (Rozen, 1967).

Four nests were excavated. The largest contained 12 cells, six with male larvae, two with female larvae, one with a possibly female larva, and three in which the larvae had been eaten or had never developed. Eight larvae were recovered from the second largest nest and several cells had been raided by a predator which had consumed the bee larvae after they defecated. Each of the other two nests contained four cells and one nest also had a number of raided cells. Of the 24 larvae, the sexes of which could be ascertained, 12 were males and 12, females.

Six larvae brought into the laboratory pupated in August, 1969. In one case the duration of the pupal stadium was 12 days.

NEST ASSOCIATES: No parasitic bee larvae were found in any of the nests, nor were bombyliid larvae and mutillid larvae recovered. A large meloid larva, which had perhaps attacked several cells, was exhumed from the cell level of one nest.

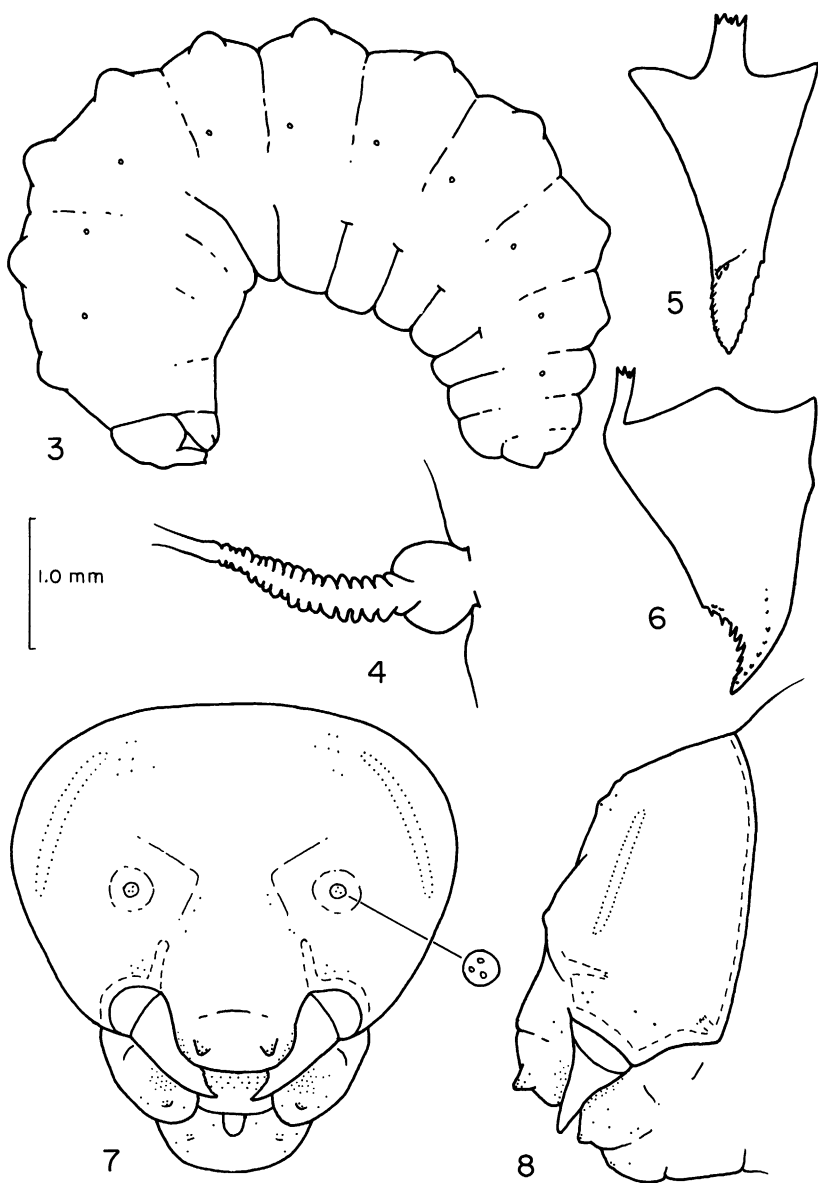
IMMATURE STAGES

MATURE LARVA OF *Hypomacrotera callops callops* Cockerell and Porter

Figures 3-8

This larva is indistinguishable from the larvae belonging to the genera *Calliopsis* and *Nomadopsis* and keys to them in Rozen (1966).

HEAD (FIGS. 5-8): Integument without setae but with widely scattered sensilla; integument unpigmented except for mandibles and for faintly pigmented antennal papillae and palpi; vertex produced only slightly on each side above antenna; antennae arising from moderately low prominences; clypeus normally short; gena not abnormally produced. Tentorium complete, well developed but thin; each posterior pit situated at juncture of hypostomal ridge and posterior thickening of head capsule; posterior thickening of head capsule thin but well defined; hypostomal ridge well developed; pleurostomal ridge well developed; epistomal



FIGS. 3-8. Postdefecating larva of *Hypomacrotera callops callops*. 3. Live larva, lateral view. 4. Spiracle. 5, 6. Right mandible, inner and ventral views. 7, 8. Head, front and lateral views. Scale refers to figure 3.

ridge well developed below anterior tentorial pits, absent mesiad of pits; parietal bands distinct; each antenna a low convexity bearing three sensilla. Labrum bearing two prominent tubercles; epipharynx laterally with moderately large spicules. Mandible (figs. 5, 6) moderately slender, apically simple; upper apical margin bearing moderate-sized teeth; lower apical margin with smaller teeth; cusp moderately produced, bearing several small teeth. Maxilla normal in size, extending slightly beyond labium and with apex not bent mesiad; palpus moderately large but short, not curved downward; integument of maxilla distinctly spiculate on dorsal surface but not on palpus; sclerotized cardo and stipes not evident. Hypopharyngeal groove present. Labium moderately projecting, divided into prementum and postmentum by inconspicuous transverse groove; labial palpus scarcely produced. Salivary opening a U-shaped slit extending to hypopharyngeal groove; integument bounded by slit, smooth.

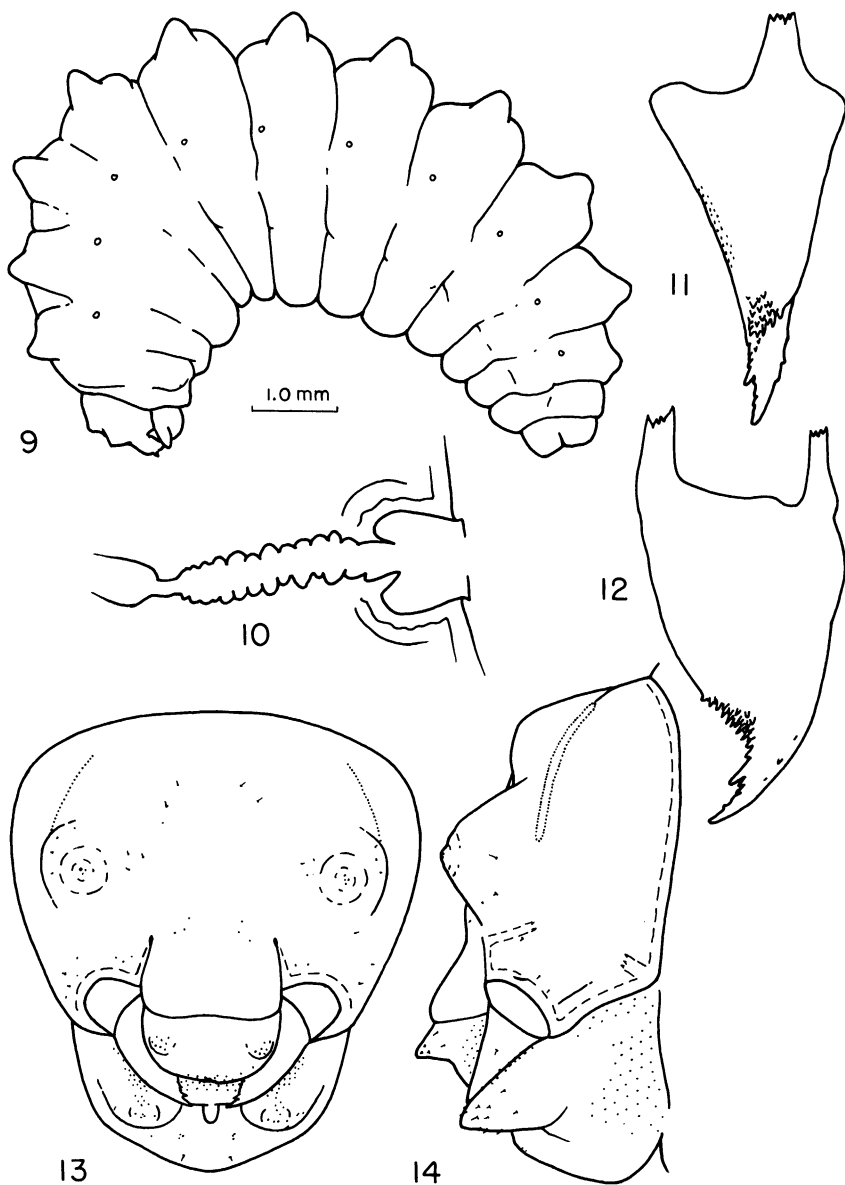
BODY (FIG. 3): Live postdefecating larva pale yellow, with body wall rigid. Integument with some scattered, faintly spiculated areas; ninth and tenth abdominal segments not spiculate ventrally. Paired dorsal tubercles moderately low but distinct on all body segments except most posterior ones; apexes of tubercles nonspiculate but with widely scattered, non-hairlike sensilla; tenth abdominal segment normal, not produced into median dorsal tubercle; pleural regions of abdominal segments not produced at least on postdefecating larva. Spiracles (fig. 4) with atrium projecting above body wall; atrial wall without teeth; peritreme present; primary tracheal opening with collar; subatrium moderately long. Female larva with imaginal cuticular scars of genitalia situated in anterior half of ninth abdominal sternum; these scars separated by about three times diameter of one; scars on preceding sternum similar but more widely spaced; scars not evident on seventh abdominal sternum; imaginal scars of male genitalia not studied.

MATERIAL STUDIED: Three live, postdefecating larvae, Douglas, Cochise County, Arizona, August 31, 1968 (J. G. Rozen and M. Favreau).

MATURE LARVA OF *Psaenythia bicolor* Timberlake

Figures 9-14

Because of the subapical mandibular tooth and lack of spicules on the dorsal tubercles, this larva will key to *Pseudopanurgus* in Rozen (1966). However, the first pair of dorsal thoracic tubercles are not distinctly directed forward, as they are in *Pseudopanurgus*. Because of the close similarity between this larva and the known larvae of *Pseudopanurgus*,



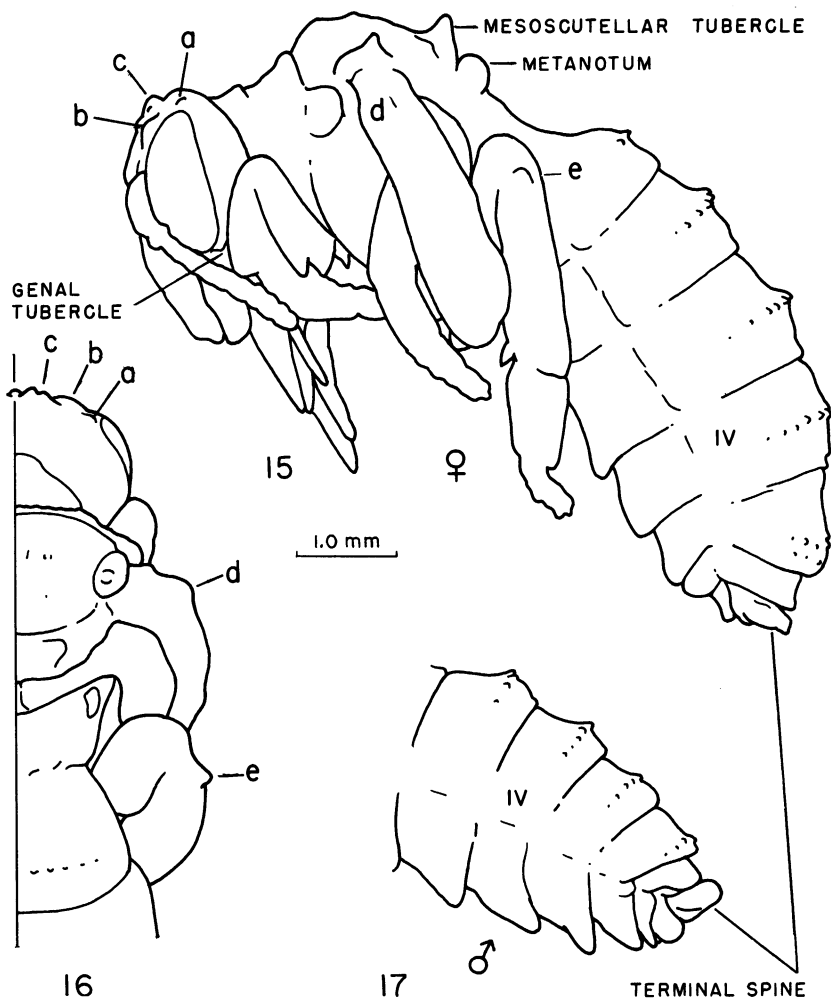
FIGS. 9-14. Postdefecating larva of *Psauenythia bicolor*. 9. Freshly killed larva, lateral view. 10. Spiracle. 11, 12. Right mandible, inner and ventral views. 13, 14. Head, front and lateral views. Scale refers to figure 9.

these two genera may prove to be indistinguishable as postdefecating larvae.

HEAD (FIGS. 11–14): Integument with scattered sensilla, including fine sensory setae; integument unpigmented except for mandibles and for faint pigmentation on antennal papillae; vertex strongly produced on each side above antenna, as in *Pseudopanurgus*; antennae arising from projecting prominences, as in *Pseudopanurgus*; clypeus normally short; gena not abnormally produced. Tentorium complete but thin; each posterior pit situated at juncture of hypostomal ridge and posterior thickening of head capsule; posterior thickening of head capsule well developed; hypostomal ridge well developed; pleurostomal ridge moderately well developed; epistomal ridge below anterior tentorial pit thin but distinct, mesiad of pit absent; each antenna a low convexity bearing three or four sensilla. Labrum bearing two prominent tubercles; epipharynx spiculate. Mandible (figs. 11, 12) slender; upper margin with subapical tooth in addition to smaller teeth both apicad and basad of subapical one; lower apical margin with several small, widely separated teeth; cusp moderately produced and heavily dentate. Maxilla large, as in *Pseudopanurgus*, and projecting well beyond labium; apex perhaps slightly bent mesiad; palpus very large, directed forward; integument spiculate on dorsal surface and on palpus. Hypopharynx spiculate; hypopharyngeal groove distinct. Labium moderately recessed, not distinctly divided into prementum and postmentum; labial palpus not projecting, evident only because of sensilla. Salivary opening a curved slit extending to hypopharyngeal groove; integument bounded by slit, smooth.

BODY (FIG. 9): Live postdefecating larvae pale yellow, with body wall rigid. Integument with some areas spiculate; ninth and tenth abdominal segments nonspiculate ventrally. Paired dorsal tubercles well developed on all body segments except abdominal segments IX and X; anterior tubercles with apices directed only indistinctly cephalad; apices of all tubercles smooth, that is, nonspiculate; tenth abdominal segment, unlike that of most larvae of *Pseudopanurgus* (Rozen, 1966), not produced into median dorsal tubercle; pleural regions of abdominal segments not produced, at least on postdefecating larva. Spiracles (fig. 10) with atrium projecting above body wall; atrial wall without teeth; peritreme present; primary tracheal opening with collar; subatrium moderately long; atrial wall extremely thick, as is body cuticle. Male larva with imaginal discs of genitalia appearing as contiguous white areas on posterior half of ninth abdominal sternum; cuticular scar conspicuous on cleared integument; female larva with imaginal discs appear-

ing on abdominal segments VII, VIII, and IX, as described for *Melitturgula braunsi* (Rozen, 1968); cuticular scars faint but evident.



FIGS. 15-17. Pupa of *Psaenythia bicolor*. 15. Female, lateral view. 16. Female, dorsal view of anterior right half. 17. Male, apex of metasoma, lateral view. Scale refers to all figures.

MATERIAL STUDIED: Twenty-four postdefecating larvae, 2 miles east of Apache, Cochise County, Arizona, May 2 and 6, 1969 (J. G. Rozen and M. Favreau).

PUPA OF *Psaenythia bicolor* Timberlake

Figures 15-17

This pupa can be distinguished from those of all other known panurgines (Yager and Rozen, 1966; Rozen, 1968) because of the short terminal spine in both sexes. The pupa of *Melitturga clavicornis* (Latreille) also has a short terminal spine but lacks the vertical tubercles of *Psaenythia bicolor*.

Length, 9.0 to 10.0 mm. Body without setae.

HEAD: Outer apical surface of scape slightly swollen and faintly pigmented; pedicel with small, faintly pigmented tubercle on outer surface and with small nonpigmented tubercle on inner surface. Ventral surface of mandible with small tubercle, which is more pronounced on female (not visible in figures). Vertex with pair of small tubercles immediately above compound eye (a, figs. 15, 16), with pair of moderate-sized, smooth swellings mesiad of upper compound eye (b, fig. 16) and with pair of clusters of low swellings over each lateral ocellus (c, fig. 16); gena with small tubercle.

MESOSOMA: Posterior lobes of pronotum not produced; mesoscutum with several paired obscure swellings; mesoscutellum with pair of large tubercles; metanotum produced on each side; axilla not produced; mesepisternum without tubercle. Tegula with conspicuous tubercle. Anterior part of wing base produced as a low swelling (d, fig. 16). All coxae, each with pointed apical spine; apexes of fore and middle trochanters somewhat produced; hind trochanters not produced; base of fore femur produced; other femora not produced; base of hind tibia with low tubercle on outer surface (e, fig. 16).

METASOMA: Terga I to V (female) (figs. 15, 16) and I to VI (male) (fig. 17) with irregular rows of small tubercles; largest tubercles with small spicule (or perhaps very short seta at apex); sterna without tubercles; terminal spine very short and rounded apically.

MATERIAL STUDIED: Three male pupae, one female pupa, 2 miles east of Apache, Cochise County, Arizona, collected as larvae on May 6, 1969, pupated August 6 to 11, 1969 (J. G. Rozen and M. Favreau).

DISCUSSION AND CONCLUSIONS

The biological information concerning *Hypomacrotera*, although incomplete, is nearly identical to our knowledge of *Calliopsis* and *Nomadopsis* (Rozen, 1967). This similarity comes as no surprise, for the adults of the three genera agree in most respects. *Hypomacrotera*, *Calliopsis*, and *Nomadopsis* share the following biological features: Nesting area horizontal or nearly so; single female per nest; main burrow partly plugged

with soil; nest shallow; cell tilted only slightly to the rear; pollen ball spherical, homogeneously moist, and coated with clear silklike, waterproof coating; egg placed on top of provisions. Like those of all known *Calliopsis* and most *Nomadopsis*, the cells are arranged singly rather than in series. There are no biological characteristics by which *Hypomacrotera* can be distinguished with certainty from these other genera; even the embossing on the cell wall has a counterpart in some *Nomadopsis* cells.

The postdefecating larva of *Hypomacrotera* agrees with the known larvae of *Calliopsis* and *Nomadopsis*. Because some of the immature and biological characters shared by these genera are specialized, I conclude that the three genera have evolved from a common ancestor more recently than any one of them has from other known North American genera.

The agreement between the larva of *Psaenythia bicolor* and the known larvae of *Pseudopanurgus* (Rozen, 1966) is close. They share the following: Strongly produced vertex; pronounced antennal prominences; mandibles slender and with subapical tooth on upper margin; maxillae large; maxillary palpi large and spiculate dorsally; paired dorsal tubercles of body pronounced on most segments. Most of these features are specialized and they indicate therefore that the two genera share a recent common ancestor. The same conclusion was reached from a study of the male genitalia (Rozen, 1951).

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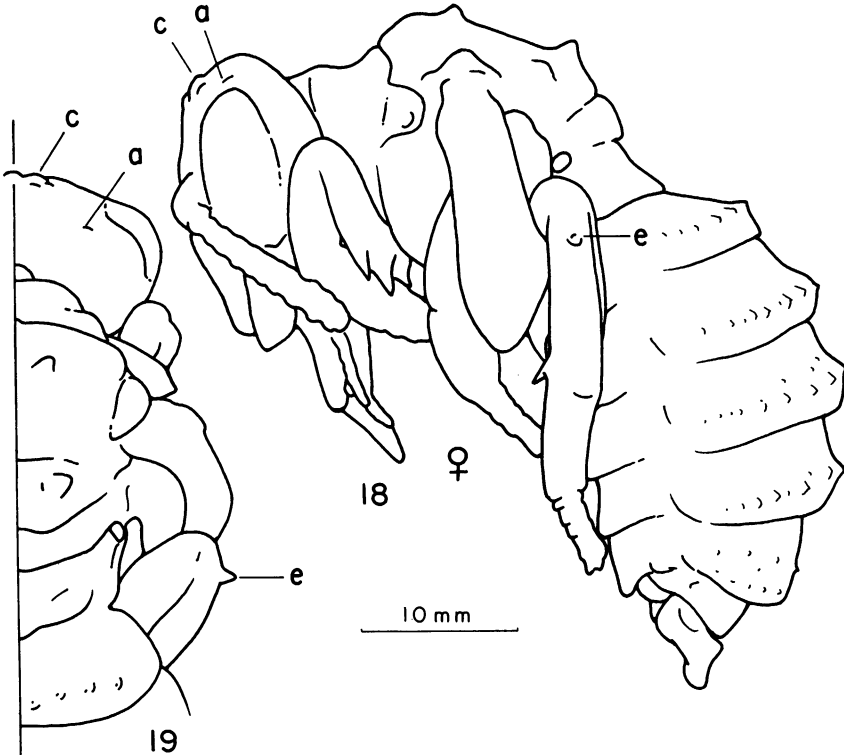
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ADDENDUM

PUPA OF *Hypomacrotera callops callops* Cockerell and Porter

Figures 18, 19

This pupa, which emerged when the manuscript was in galley proof, has been compared with all available pupae of panurgine bees (i.e.,



FIGS. 18, 19. Female pupa of *Hypomacrotera callops callops*. 18. Lateral view. 19. Dorsal view of anterior right half. Scale refers to both figures.

those described by Yager and Rozen, 1966; Rozen, 1968; and those of a number of species of *Panurgus* and *Panurginus*, as well as those of *Psaenythia bicolor* treated in the present paper). It agrees in most respects with the pupae of *Nomadopsis* and *Calliopsis*. The low vertical tubercles of *H. callops callops* are also present in some *Nomadopsis* (although they were overlooked by Yager and Rozen, 1966). It can be distinguished from pupae of panurgine genera other than *Nomadopsis* and *Calliopsis* on the

basis of the following combination of features: distinct scutellar tubercles present, tubercle at the base of the hind tibia normally short, and terminal spine moderately produced.

Length, 5.0 mm. Body without setae.

HEAD: Outer apical surface of scape and pedicel faintly pigmented but apparently not swollen and without tubercles; inner surface of pedicel slightly swollen but not pigmented. Ventral surface of mandible with small tubercle (not visible in figures). Vertex with some of the tubercles (a, c, figs. 18, 19) found in *Psaenythia bicolor* but tubercles less pronounced; gena with small tubercle.

MESOSOMA: Lateral angles of pronotum not produced; posterior lobes produced; mesoscutum with pair of pronounced paramedian tubercles; mesoscutellum with pair of tubercles larger than scutellar tubercles; axilla slightly produced; metanotum with indistinct median swelling; mesepisternum without tubercle. Tegula produced. Anterior part of wing base produced as low swelling. Each coxa with pronounced apical spine; apex of fore and middle trochanters produced as distinct spine; apex of hind trochanter produced; base of fore femur produced as sharp spine; base of midfemur somewhat produced; base of hind femur not produced; base of hind tibia with tubercle (e, figs. 18, 19) on outer surface.

METASOMA: Terga I to IV with irregular rows of small tubercles; tergum V with small tubercles over most of dorsal surface; largest tubercles with small apical spicules (or perhaps very short setae); sterna without tubercles; terminal spine moderately developed, with apex rounded.

MATERIAL STUDIED: One female pupa, Douglas, Cochise County, Arizona, collected as larva August 31, 1968, pupated February 11, 1970 (J. G. Rozen and M. Favreau).