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Their Mature Larvae and Pupae  
(Hymenoptera, Anthophoridae, Nomadinae)



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## ABSTRACT

Mature larvae of representatives of four genera of the Ammobatini are taxonomically described—*Pseudodichroa*, *Ammobates*, *Morgania*, and *Oreopasites*. A key is provided for their identification and the tribe is characterized on the basis of the mature larvae. Pupae of representatives of two genera are described—*Oreopasites* and *Morgania*. A preliminary key to the pupae of the subfamily Nomadinae is also presented.

The study was undertaken to illuminate the higher classification and phylogeny of anthophorid bees, to provide means for identifying the tribe Ammobatini and its genera on the basis of immature characters, and to establish a background for a forthcoming evolutionary study of the ammobatine genus *Oreopasites*.

The present paper may be considered a "third generation" investigation on bee larvae. Michener's work on larvae (1953) was the original comprehensive treatment of larval forms but did not describe any of the Ammobatini. Since its publication various workers, with new and more extensive material, readdressed various taxa, and specifically Rozen produced a series of papers treating the larvae of the Anthophoridae. Rozen in 1966 covered the Nomadinae and discussed the only genus of ammobatines (*Oreopasites*) then available. The present paper is yet another refinement, made possible by recent acquisitions of larval specimens of three more genera of the Ammobatini. Pupae of the tribe have gone undescribed until now.

All nomadine bees are parasitic, the larvae feeding in the cells of various solitary bees. Ammobatine bees even as adults are rare in collections. The acquisition of immature specimens for the study, therefore, would have been virtually impossible without the excellent support of the National Science Foundation (grants GB-5407 and GB-32508) which we wish to acknowledge with appreciation. We also thank Ms. Liliane Floge and Mrs. Barbara Rozen who assisted in the illustrations and Ms. Phyllis Browne who typed the manuscript. All specimens are in the collection of the American Museum of Natural History.

## SYSTEMATICS AND PHYLOGENY

The Ammobatini were divided by Popov (1951) into the Ammobatini (*Ammobates*, *Parammobatodes*, and *Oreopasites*) and the Pasitini (including among others, *Morgania* and presumably *Pseudodichroa*). In reviewing *Pseudodichroa*, Rozen (1968) used the older, more conservative classification employed by Michener (1944) and others because there was some evidence that a more detailed study of male genitalia might necessitate a revision of Popov's classification. Recently Baker (1971) has followed Popov's division and correctly pointed out that in the Pasitini the labrum of the adult extends only to the mandible, whereas in the Ammobatini, *sensu stricto*, it extends well beyond the mandibles. However, we note that within the Pasitini there is a difference among the genera with respect to whether the mandibles of adults are directed mesiad so that their points overlap in repose (e.g., *Morgania*) or whether the mandibles are directed somewhat posteriorly so that their apexes cross in repose (e.g., *Pseudodichroa*; see Rozen, 1968, fig. 2). Furthermore, an analysis of larval features does not suggest a grouping of *Morgania* and *Pseudodichroa* on the one hand and *Oreopasites* and *Ammobates* on the other. Indeed a phenetic grouping would seem to place *Oreopasites* and *Morgania* close together, with *Ammobates* somewhat divergent from them and with *Pseudodichroa* apparently farthest away. With respect to phylogeny, such larval features as the anterior placement of the posterior tentorial pits in *Pseudodichroa*, the navicular shape of the predefecating larva of *Pseudodichroa*, the swollen mandibular bases of *Morgania*, and the strong anterior projection of the head features of *Ammobates* are probably derived. However, too few larval characters can be classified as being primitive or specialized to make possible an analysis of the phylogeny of the tribe. We also note the similarity of the pupae of *Morgania* and *Oreopasites*. For all of these reasons we continue to follow the more conservative classification, i.e., placing the Ammobatini, *sensu stricto*, and Pasitini into a single tribe at least for the present, with the hope that a broad comprehensive analysis of all avail-

able characters will lead to a clear understanding of the phylogeny of the group and to an appropriate classification.

### LARVAE

The anatomy of bee larvae and techniques for studying larvae have been discussed by Michener (1953) and more recently by Rozen and McGinley (1974). The posterior margin of the head capsule of the Ammobatini (excepting *Pseudodichroa*) and of *Nomada* possesses two transverse weak internal ridges, one anterior to the other ("apparent posterior thickening" and "posterior thickening," figs. 17, 24). This characteristic is also weakly developed in *Paranomada* but has not been investigated in *Kelita*. We presume the more anterior ridge to be the anatomical posterior margin of the head capsule because the capsule, so defined, would be normal in shape in lateral view for most bee larvae, and because the sclerotization of the capsule ends at the anterior ridge in *Morgania*. If this is the true anatomical boundary of the head, then the sclerotized area behind the posterior thickening in *Ammobates*, *Pseudodichroa*, and *Oreopasites* represents an extension of the functional head capsule. Perhaps it is an ontogenetic holdover of an elongate head capsule of the first instar, an adaptation that could accommodate massive mandibular musculature.

In *Pseudodichroa* (fig. 8) the head exhibits only a single transverse ridge. The placement of the posterior tentorial pit midway along the hypostomal ridge seems to suggest that the true posterior thickening has become obliterated but that the area from the posterior pits to the apparent posterior thickening is still homologous with the extension of the head capsule found in other Ammobatini and in Nomadini.

We note that the mandible of *Pseudodichroa* (figs. 4-6) is peculiar because the abductor apodeme is missing although the adductor apodeme is reasonably well developed. The mandible of *Scapter* (Colletidae), the host of *Pseudodichroa*, has a well-developed adductor apodeme but the abductor apodeme is absent, although the point of attachment of the abductor muscle is evident as a cuticular invagination of the mandibular corium. These differences between *Pseudodichroa*

and *Scapter* seem paradoxical since both feed on the same semiliquid provisions. Loss or reduction of the abductor apodeme is found among certain other colletids with watery nest provisions, e.g., *Colletes* and *Euryglossa*.

Another interesting point concerning *Pseudodichroa* is that both the anterior and posterior points of articulation of the mandible are somewhat separate from the articulating points on the head capsule. This fact plus the missing adductor mandibular apodeme suggests that the mandibular mechanism at least of the last instar may be structurally weak and the mandible may not be required to function very actively during feeding. This deduction would seem to be supported by the very short mandibles, the apexes of which hardly reach the mouth area. On the other hand larval mandibles of almost all the Nomadinae (this apparently is not true of *Paranomada* and *Isepeolus*) have nearly equally short mandibles with adductor apodemes. This situation emphasizes that we know very little about how the short mandibles function, about what role the swollen epipharynx of *Nomada*, *Pseudodichroa*, *Ammobates* and perhaps other Nomadinae play in the ingestion of food, and in general about the feeding mechanisms of these larvae (or any bee larvae).

### Description of the Ammobatini

#### Based on Mature Larvae

*Diagnosis.* Mature larvae of the Ammobatini key readily to couplet 8 in Rozen (1966, pp. 8-10) where *Oreopasites* and *Nomada* appear. Because all ammobatines have a nonspiculate hypopharynx they can be separated from *Nomada* which they tend to resemble. After the publication of Rozen (1966), mature larvae of two other genera of Nomadini, *Kelita* and *Paranomada*, were collected. These demonstrate that the tribe is remarkably diverse (also reflected in the pupa of *Paranomada*) and raise intriguing questions regarding the origin and monophyly of both the tribe and the subfamily. Although these larvae have not been studied in detail they can be clearly distinguished from the Ammobatini because *Kelita* and *Paranomada* possess distinct paired dorsal tubercles on most body segments. Furthermore their hypopharynxes seem to be spiculate as in the hypopharynx of *Nomada*.

*Head.* Integument usually pigmented; scattered nonsetiform sensilla present; epipharynx, hypopharynx, maxillae, and labium all nonspiculate. As seen in frontal view, general outline of head nearly circular (*Pseudodichroa*, fig. 7, and some *Oreopasites*) to distinctly wider than long (*Ammobates*, fig. 16); as for most of Nomadinae, head capsule elongate as seen in lateral view (figs. 8, 17, 24) with frontal area sloping toward produced labroclypeal area; vertex evenly rounded or with pronounced median swelling (*Ammobates*, fig. 17). Tentorium incomplete; anterior arms very short and slender to virtually absent (*Morgania*); posterior arms very short and slender (*Morgania*, *Oreopasites*) or more elongate and threadlike (*Ammobates*, *Pseudodichroa*); dorsal arms absent; anterior pits minute (obscure in *Morgania*) and positioned rather low, near pre-coila; posterior pits minute to small, situated below hypostomal ridge and well anterior to apparent posterior margin of head (pits equidistant from pleurostomal ridge and apparent posterior margin of head in *Pseudodichroa*). All internal ridges of head capsule tending to be weak or absent; as in *Nomada*, head capsule bordered posteriorly by two faint ridges in most cases (see discussion above); hypostomal ridge elongate, tending to be moderately to darkly pigmented; hypostomal ridge slender to moderately well developed anterior to posterior tentorial pits; posteriad of pits, ridge becoming narrower and fading completely before reaching apparent posterior margin of head; pleurostomal ridge moderately developed to poorly developed and indistinct; ridge darkly pigmented to nonpigmented; epistomal ridge virtually absent (*Pseudodichroa*, *Morgania*, *Ammobates*) or weakly developed and reaching level of antennae before completely fading (some *Oreopasites*); coronal cleavage line not visible (*Oreopasites*) or evident as a diffused light line extending anteriorly to clypeal region; parietal bands faint. Antennal papillae low convexities (best developed in *Oreopasites*) each bearing two sensilla; antennal protuberances slightly developed (*Oreopasites*, *Ammobates*, fig. 17) or absent. Labrum moderately (*Oreopasites*, *Pseudodichroa*, fig. 8) to strongly projecting (*Morgania*, fig. 24, *Ammobates*, fig. 17) bearing two narrowly rounded or pointed tubercles of variable size and distance from each other; epi-

pharynx without distinct lobelike swelling above hypopharynx as found in *Nomada* but more (*Pseudodichroa*, fig. 7, *Ammobates* fig. 16) or less (*Oreopasites*, *Morgania*) swollen ventrally. Mandible slender (*Oreopasites*, *Morgania*, figs. 20-22, *Pseudodichroa*, figs. 4-6) or robust (*Ammobates*, figs. 12-14), moderately short, broad at base when viewed adorally and tapering to simple apex; enlarged subapical teeth absent; cuspal area not produced (*Morgania*, *Pseudodichroa*) or produced and poorly defined (*Oreopasites*, *Ammobates*); cuspal teeth absent; dorsal and ventral inner edges well formed and serrate or smooth and nonserrate (*Ammobates*); apical concavity absent or moderately well developed (*Ammobates*). Maxillae recessed, broadly fused with labium; palpi robust basally, short (*Morgania*) to moderately elongate (*Ammobates*). Labium greatly recessed, not divided into prementum and postmentum; palpus minute (*Morgania*) or indicated by single sensillum. Hypopharynx poorly developed or large and well defined (*Ammobates*, fig. 16). Salivary opening small, circular to elliptical in shape; salivary lips absent or present as a low surrounding rim (*Morgania*).

*Body.* Integument of postdefecating forms smooth (*Ammobates*) to wrinkled (*Oreopasites*, *Morgania*), dull (*Oreopasites*) to shiny (*Morgania*); venter faintly to strongly (*Oreopasites*) spiculate; setae absent. Form moderately robust, moderately (*Oreopasites*) to extremely (*Pseudodichroa*, fig. 3) broad in dorsal view, curved anteriorly in postdefecating forms (postdefecating form of *Pseudodichroa* unknown), tapering posteriorly; in postdefecating forms intersegmental lines well defined, shallowly (*Ammobates*) to deeply (*Oreopasites*, *Morgania*) incised; dorsal tubercles absent although dorsum may be produced somewhat dorsolaterally in *Oreopasites* and *Morgania*; swellings below spiracles present and well defined; dorsal intrasegmental lines present and faint (predefecating form of *Pseudodichroa*, fig. 1) to apparently absent; abdominal segment IX not produced ventrally; abdominal segment X central or perhaps dorsal (*Ammobates*, fig. 10) in attachment to segment IX; anus transverse, apical or somewhat dorsal in *Pseudodichroa* (fig. 2); perianal area well defined, elongate-elliptical and smooth (fig. 2). Spiracles (figs. 9, 15, 25) not on elevations (*Ammobates*, *Oreo-*

*pasites* and postdefecating form of *Pseudodichroa*) or on slight elevations, which are lightly sclerotized and pigmented apically (*Morgania*); atrium subglobular to subquadrate (*Morgania*); projecting above body surface, with rim; atrial wall with (*Oreopasites*, *Pseudodichroa*, *Morgania*) or without (*Ammobates*) rows of small denticles; peritreme present, moderately wide to very wide (*Pseudodichroa*); primary tracheal opening with moderately long collar; subatrium annulated, variable in length.

#### KEY TO THE MATURE LARVAE OF THE AMMOBATINI

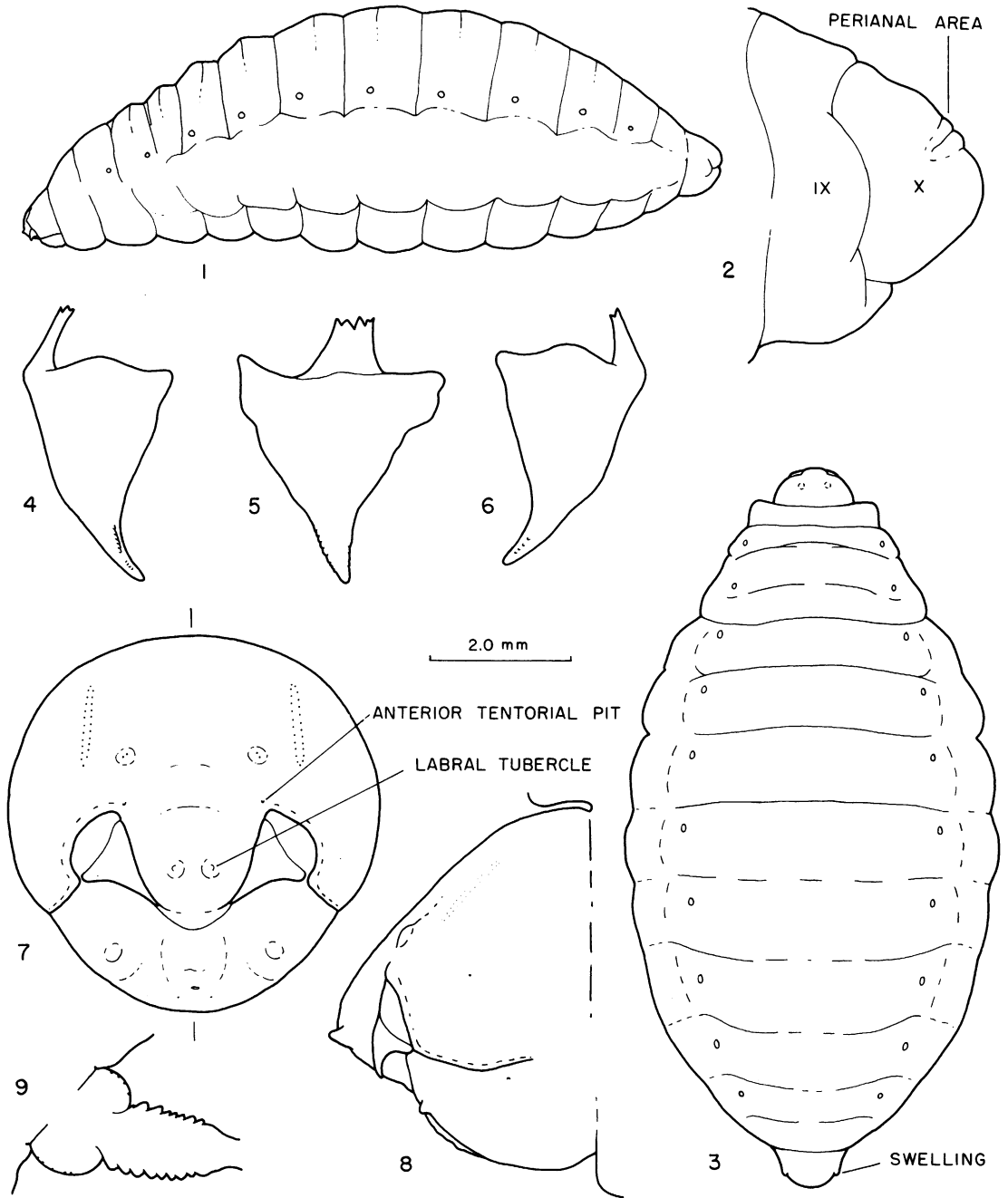
1. Posterior tentorial pit nearly equidistant from pleurostomal ridge and apparent posterior margin of head capsule (fig. 8); labral tubercles separated by about basal diameter of tubercle (fig. 7); adductor apodeme of mandible (fig. 4) absent. . . . . *Pseudodichroa fumipennis*  
Posterior tentorial pit obviously closer to apparent posterior margin of head capsule than to pleurostomal ridge (figs. 17, 24); labral tubercles usually separated by more than basal diameter of tubercle (figs. 16, 23) but, if close set (in undescribed species of *Oreopasites*) tubercles somewhat elongate and pointed; adductor apodeme of mandible (figs. 12, 20) present . . . . . 2
- 2(1). Body outline in dorsal view (fig. 11) with intersegmental lines not incised, hence, outline smooth; hypopharynx well defined and strongly projecting (figs. 16, 17); mandible (figs. 12-14) extremely robust basally with adoral-ventral surface of mandible massively produced and rounded; vertex of head capsule with median, rounded swelling (fig. 17); antennal protuberances small but well defined and conspicuous (fig. 17); maxillary palpi large, larger than labral tubercles (fig. 17). *Ammobates carinatus*  
Body outline in dorsal view (fig. 19) with intersegmental lines moderately to deeply incised; hypopharynx poorly defined and weakly projecting (figs. 23, 24); mandible (figs. 20-22) moderately robust basally with adoral-ventral surface at most only moderately produced and rounded; vertex of head capsule without median, rounded swelling (fig. 24); antennal protuberances only slightly developed (fig. 24); maxillary palpi small, smaller than labral tubercles (fig. 24) . . . . . 3
- 3(2). Body, as seen in dorsal view (fig. 19), conspicuously broad with intersegmental lines deeply incised; spiracular atria (fig. 25) subquadrate, on slightly pigmented and sclerotized elevations; labrum very strongly projecting (fig. 24); cuspal area of mandible not produced (figs. 20, 22); venter of abdomen faintly spiculate . . . . . *Morgania histrio transvaalensis*  
Body, as seen in dorsal view, not conspicuously broad, with intersegmental lines moderately incised; spiracular atria (Rozen, 1954, fig. 2) subglobular, not on distinct elevations; labrum only moderately projecting; cuspal area of mandible moderately produced (Rozen, 1966, figs. 56-58); venter of abdomen strongly spiculate . . . . . *Oreopasites*  
*Pseudodichroa fumipennis* Bischoff  
Figures 1-9

The following description is based on pre-defecating larvae; postdefecating forms are unknown.

*Diagnosis.* The extreme anterior position of the posterior tentorial pits (fig. 8), the narrow separation of labral tubercles (about one basal diameter apart) (fig. 7), and the absence of adductor apodeme of mandible (figs. 4, 6) distinguish *Pseudodichroa fumipennis* from all other known larval ammobatines.

*Head* (figs. 7, 8). As seen in frontal view (fig. 7), head nearly circular; median swelling of vertex absent. Anterior tentorial arms short and slender; posterior arms somewhat elongate and threadlike; anterior pits minute; posterior pits small, situated below hypostomal ridge and unlike all other known larval ammobatines, nearly equidistant from pleurostomal ridge and apparent posterior margin of head (fig. 8); posterior thickening of head capsule obliterated (see discussion above); apparent posterior thickening well defined but weak; entire area anterior to apparent posterior margin of head sclerotized; hypostomal ridge slender and moderately pigmented, only slightly curved dorsally near posterior tentorial pit; pleurostomal ridge poorly developed and indistinct; epistomal ridge virtually absent; coronal cleavage line present as a poorly





FIGS. 1-9. Mature larva of *Pseudodichroa fumipennis*. 1. Entire larva, lateral view. 2. Apex of abdomen, lateral view. 3. Entire larva, dorsal view. 4-6. Right mandible, dorsal, inner and ventral views, respectively. 7. Head, anterior view. 8. Head, lateral view. 9. Spiracle, side view. Scale refers to figures 1, 3.

defined light line extending to clypeal area. Antennal protuberances absent. Labrum moderately projecting (not so strongly projecting as those of *Morgania*, *Ammobates*); labral tubercles moderately large, narrowly rounded and narrowly separated by about one basal diameter of tubercle; epipharynx (fig. 7) strongly swollen. Mandible (figs. 4-6) slender, broad as seen in adoral view and tapering unevenly to apex; cuspal area not produced; dorsal and ventral inner edges serrate with serration more extensive on dorsal edge; apical concavity not developed; unlike all other ammobatines studied, the mandibular adductor apodeme is apparently absent. Maxillary palpi small, short. Labial palpus indicated by single sensillum. Hypopharynx poorly defined, with transverse ridging present, and exceeded by maxillae (fig. 8); hypopharyngeal groove virtually absent. Salivary opening elongate-elliptical; surrounding rim absent.

*Body* (figs. 1-3). Integument smooth, not shiny; venter faintly spiculate. Form conspicuously broad as seen in dorsal or ventral view (fig. 3), uncurved and gently tapering anteriorly, sharply tapering posteriorly; form navicular in shape on live larva (Rozen and Michener, 1968); intersegmental lines not deeply incised; paired dorsal tubercles absent although anterior segments produced somewhat dorsolaterally; dorsal intrasegmental lines present but very faint; unlike other known larval ammobatines, abdominal segment X may have conspicuous lateral swellings (fig. 3) immediately anterior to perianal area; abdominal segment X centrally attached to segment IX; unlike other ammobatines, anterior diameter of segment X much less than that of segment IX; anus apical or perhaps slightly dorsal. Spiracles varying in size; first two pair moderately large, last small, all others large; spiracles tending to be directed dorsally because of broad body, not on elevations; atrium (fig. 9) subglobular; atrial wall with numerous rows of small denticles; peritreme very wide; subatrium broad but short, length less than two atrial lengths. Imaginal discs of genitalia not visible.

*Material Studied.* Two predefecating larvae, Kommetjie, Cape Province, Republic of South Africa, November 8, 1966, from cell of *Scapter crassula* (J. G. Rozen). Adults determined by Rozen.

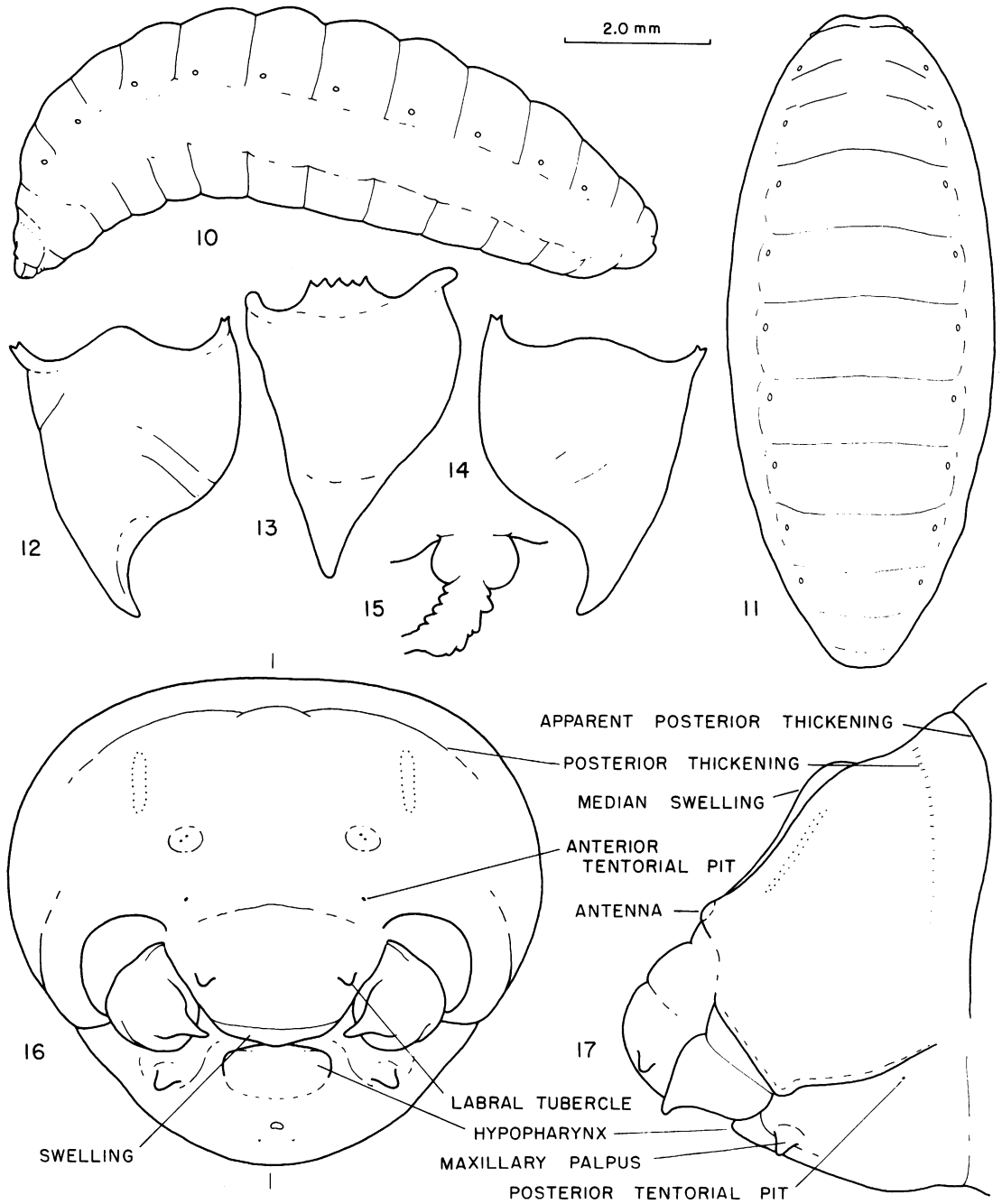
The biology of this species was described by Rozen and Michener (1968).

*Ammobates carinatus* Morawitz

Figures 10-17

*Diagnosis.* This species can be distinguished from other known larval ammobatines because of the smooth lateral outline of its body as seen in dorsal view (fig. 11), the well-defined and strongly projecting hypopharynx (fig. 16), the massively produced adoral-ventral surface of mandible (figs. 12, 14), the very wide separation of labral tubercles (over four basal diameters apart) (fig. 16), the large maxillary palpi (figs. 16, 17), the presence of small antennal protuberances and the median swelling of the vertex (fig. 17).

*Head* (figs. 16, 17). As seen in frontal view (fig. 16), head distinctly wider than long, similar in overall shape to that of *Morgania*; vertex produced medially as a rounded swelling. Anterior tentorial arms short and slender, better developed than those of *Morgania*; posterior arms somewhat elongate and threadlike; anterior pits minute but conspicuous; posterior pits small, situated well below hypostomal ridge (lower than those of *Morgania*) and anterior to apparent posterior margin of head; posterior thickening of head capsule nearly obliterated; apparent posterior thickening weak but quite evident; area between thickenings sclerotized; hypostomal ridge moderately well developed and darkly pigmented although fading and incomplete just posterior to pleurostomal ridge, curved dorsally posterior to posterior tentorial pit; pleurostomal ridge poorly developed and indistinct; epistomal ridge virtually absent; coronal cleavage line present as a diffused light line extending anteriorly to clypeal region. Antennal protuberances small but well defined. Labrum very strongly projecting; labral tubercles small, narrowly rounded and widely separated, about four basal diameters of tubercle apart, epipharynx distinctly swollen. Mandible (figs. 12-14) robust; unlike other ammobatines treated here, adoral-ventral surface massively produced and rounded so that mandible appears broader in dorsal and ventral views than in adoral view; tapering unevenly to apex as seen in adoral view; cuspal area produced but poorly defined; dorsal and ventral inner edges apparently without



FIGS. 10-17. Mature larva of *Ammobates carinatus*. 10, 11. Entire larva, lateral and dorsal views, respectively. 12-14. Right mandible, dorsal, inner and ventral views, respectively. 15. Spiracle, side view. 16. Head, frontal view. 17. Head, lateral view.

Scale refers to figures 10, 11.

teeth or serrations; apical concavity moderately well developed and adoral in position. Maxillary palpi moderately large and elongate. Labial palpus indicated by single sensillum. Hypopharynx well defined and strongly projecting, greatly exceeding maxillae and labium; hypopharyngeal groove weakly defined. Salivary opening nearly circular; surrounding rim absent or perhaps only poorly developed.

*Body* (figs. 10, 11). Integument smooth, only moderately shiny, venter faintly spiculate. Form moderately broad in dorsal view (fig. 11); intersegmental lines at most only shallowly incised; these lines not incised laterally, hence, lateral outline of body smooth as seen in dorsal view; paired dorsal tubercles absent; lateral swellings below spiracles well defined although not so well developed and conspicuous as those of *Morgania*; dorsal intrasegmental lines apparently absent; abdominal segment X slightly dorsal in attachment to segment IX; anus apical. Spiracles (fig. 15) uniform in size, not an elevation; atrium subglobular; atrial wall without denticles; peritreme moderately wide; subatrium moderately long. Imaginal disc of male genitalia transverse oval, with cuticular scar, situated medially near posterior margin of sternum IX; discs of female unknown.

*Material Studied.* One postdefecating larva, 10 km. south of Skhirate, near Rabat, Morocco, April 29, 1968 (J. G. Rozen), from cell of small *Eucera*. Adult determined by Rozen.

*Morgania histrio transvaalensis* Bischoff

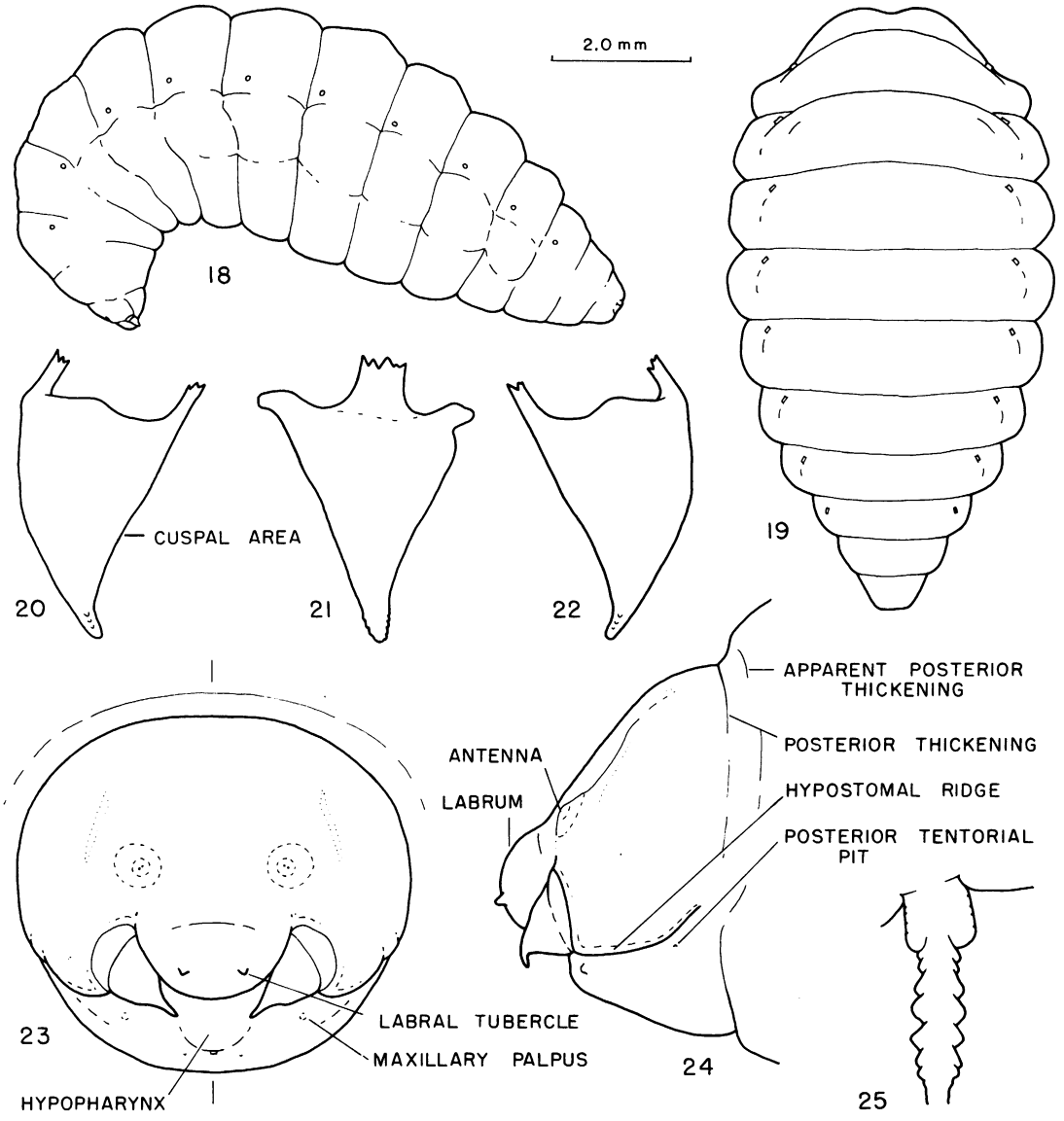
Figures 18-25

*Diagnosis.* The combination of deeply incised intersegmental lines of the body as seen in dorsal view (fig. 19), wide separation of labral tubercles (about two basal diameters of tubercle apart) (fig. 23), and subquadrate spiracular atria (fig. 25) on pigmented and slightly sclerotized spiracular elevations distinguishes this species from other known larval ammobatines.

*Head* (figs. 23, 24). As seen in frontal view (fig. 23), head distinctly wider than long; median swelling of vertex absent. Anterior tentorial arms virtually absent; posterior arms very short and slender; anterior pits obscure; posterior pits small, situated well below hypostomal ridge and

considerably anterior to apparent posterior margin of head; posterior thickening of head capsule virtually absent being indicated by faint line; apparent posterior thickening present but indefinite; area between thickenings not so sclerotized as head capsule; hypostomal ridge moderately well developed (thinner than that of *Oreopasites*) and darkly pigmented, bending dorsally (fig. 24) just anterior to posterior tentorial pit; pleurostomal ridge poorly developed and indistinct; epistomal ridge virtually absent; coronal cleavage line present as a diffused light line extending anteriorly to clypeal region. Antennal protuberances absent. Labrum strongly projecting; labral tubercles small, narrowly rounded, well separated by about two basal diameters of tubercle; epipharynx only slightly swollen. Mandible (figs. 20-22) slender, broad basally as seen in adoral view and evenly tapering to apex; cuspal area not produced, possibly indicated by very slight and gradual adoral swelling; dorsal and ventral inner edges well formed and serrate; apical concavity not developed. Maxillary palpi small, short. Labial palpus indicated by single sensillum. Hypopharynx poorly defined but exceeding maxillae and labium; hypopharyngeal groove virtually absent. Salivary opening nearly circular and surrounded by low, projecting rim.

*Body* (figs. 18, 19). Integument smooth or distinctly crinkled, venter faintly spiculate. Form extremely broad in dorsal or ventral aspect, sharply curved anteriorly; intersegmental lines deeply incised; intersegmental lines deeply incised laterally so that lateral outline appears strongly ridged when viewed dorsally (fig. 19); paired dorsal tubercles absent although most body segments produced somewhat dorso-laterally; dorsal intrasegmental lines indicated on most body segments as faint lateral lines, not extending dorsally, hence, segments not divided into cephalic and caudal annulets; segment X centrally attached to segment IX; anus apical. Spiracles (fig. 25) uniform in size, on slight elevations which are moderately pigmented and sclerotized apically; atrium subquadrate; atrial wall with numerous rows of small denticles; peritreme moderately wide; subatrium moderately long with approximately eight wide annulations. Imaginal disc of male genitalia situated medially immediately in front of ventral intersegmental



FIGS. 18-25. Mature larva of *Morgania histrio transvaalensis*. 18, 19. Entire larva, lateral and dorsal views, respectively. 20-22. Right mandible, dorsal, inner and ventral views, respectively. 23. Head, frontal view. 24. Head, lateral view. 25. Spiracle, side view. Scale refers to figures 18, 19.

line separating abdominal segments IX and X; cuticular scar transverse linear, slightly more pigmented than surrounding integument, and almost on intersegmental line; characteristics of female unknown.

*Material Studied.* Two postdefecating larvae, 3 miles west of Grahamstown, Cape Province, South Africa, November 28, 1966, from cells of *Tetralonia* (J. G. Rozen). Adults determined by Rozen.

The biology of this species was discussed by Rozen (1969).

#### OREOPASITES COCKERELL

The following account is based on larvae of several undescribed species as well as of specimens nominally assigned to *Oreopasites vanduzeei* Cockerell, a name that apparently encompasses a species complex.

*Diagnosis.* The moderately wide body, as seen in dorsal view, distinguishes the mature larvae of *Oreopasites* from those of *Morgania histrio transvaalensis* and *Pseudodichroa fumipennis*. The moderately well-incised intersegmental lines of the abdomen, the poorly developed hypopharynx and the small maxillary palpi further distinguish larval *Oreopasites* from *Ammobates carinatus*. Unlike other known larval ammobatines, *Oreopasites* usually has moderately large, pointed labral tubercles, although some forms of *O. vanduzeei* do have small labral tubercles.

*Head* (Rozen, 1954, figs. 5, 6). As seen in frontal view, head nearly circular; vertex without produced, rounded swelling. Anterior and posterior tentorial arms very short and slender; anterior and posterior pits minute; posterior pit below hypostomal ridge and anterior to apparent posterior margin of head; posterior thickening of head capsule virtually absent, indicated by faint line; apparent posterior thickening present but indefinite; area between thickenings sclerotized; hypostomal ridge moderately developed and darkly pigmented anterior to posterior pits (somewhat more slender and lightly pigmented in one species); posteriad of pits, ridge becomes very thin or virtually absent, curving dorsally, or only faintly so; pleurostomal ridge moderately developed and darkly pigmented to indistinct and lightly pigmented; epistomal ridge virtually absent or weakly developed and extending dorsally to level of antennae; coronal cleavage line not visible. Antennal protuberances absent. Labrum moderately projecting; labral tubercles moderately large (small in some forms of *O. vanduzeei*) and pointed, narrowly separated to separated by at least two basal diameters of tubercle; epipharynx only slightly swollen. Mandible (Rozen, 1966, figs. 56-58) slender, broad basally as seen in adoral view and tapering somewhat

unevenly to apex; dorsal and ventral inner edges serrate (serrations possibly absent in one species); apical concavity not developed. Maxillary palpi moderately small, tending to be slightly elongate but still much less developed than those of *Ammobates*. Labial palpus indicated by single sensillum. Hypopharynx poorly developed although exceeding maxillae and labium; hypopharyngeal groove weakly indicated. Salivary opening elongate-oval, not surrounded by low rim.

*Body* (Rozen, 1954, fig. 1). Integument of postdefecating forms finely wrinkled, dull to moderately shiny; venter strongly spiculate. Form moderately broad in dorsal view; intersegmental lines moderately well incised, hence lateral outline of body, as seen in dorsal view, ridged (not so pronounced as in *Morgania*); paired dorsal tubercles absent although most body segments produced dorsolaterally; dorsal intrasegmental lines not evident; abdominal segment X central in attachment to segment IX; anus apical. Spiracles (Rozen, 1954, fig. 2) uniform in size, not on distinct elevations; atrium subglobular; atrial wall with rows of small denticles; peritreme moderately wide; subatrium moderately long to long. Female with paired imaginal discs on segments VII, VIII, and IX (best visible on predefecating forms); discs on segment IX near midpoint of segment and approximately one disc diameter apart; discs on segments VII and VIII in posterior half of segment with those on segment VIII about three disc diameters apart and those of segment VII approximately five disc diameters apart; male sexual characters not observed.

*Material Studied.* *Oreopasites vanduzeei*, 11 postdefecating larvae, Skeleton Canyon, Arizona, September 3, 1966, from nests of *Nomadopsis puellae* (J. Bath, F. Andrews, L. LaPré). *Oreopasites vanduzeei*, one postdefecating and one predefecating larva, Tuolumne, Tuolumne County, California, 1973, from a nest of *Nomadopsis anthidia anthidia* (Fowler) (J. G. Rozen). *Oreopasites* sp., one postdefecating larva, Fort Robinson, Dawes County, Nebraska, August 10, 1972, from cell of *Nomadopsis helianthi* (J. G. Rozen and R. J. McGinley). *Oreopasites* species, one postdefecating and two predefecating larvae, 13 miles southwest of Apache, Arizona, September

1, 1971, from cells of *Perdita* (J. G. Rozen and M. Favreau).

PUPAE

Although mature larvae of bees have been subjected to considerable evolutionary and systematic study recently, pupae are poorly known. Of the Nomadinae, only the pupae of *Holcopasites* (as *Neopasites*, Michener, 1954) and *Isepeolus* (Michener, 1957) have been briefly described and compared with other bee pupae. Now, however, the pupae of a number of genera of nomadines are preserved in the collections held by the American Museum of Natural History, making possible the following remarks and key. They include *Isepeolus* (one species), *Protepeolus* (one species), *Oreopasites* (two species), *Morgania* (one species), *Nomada* (two species), *Paranomada* (one species), *Epeolus* (one species), and *Neolarra* (one species). In addition, a poorly preserved specimen of *Odyneropsis* and a very poor specimen of *Holcopasites* are also on hand.

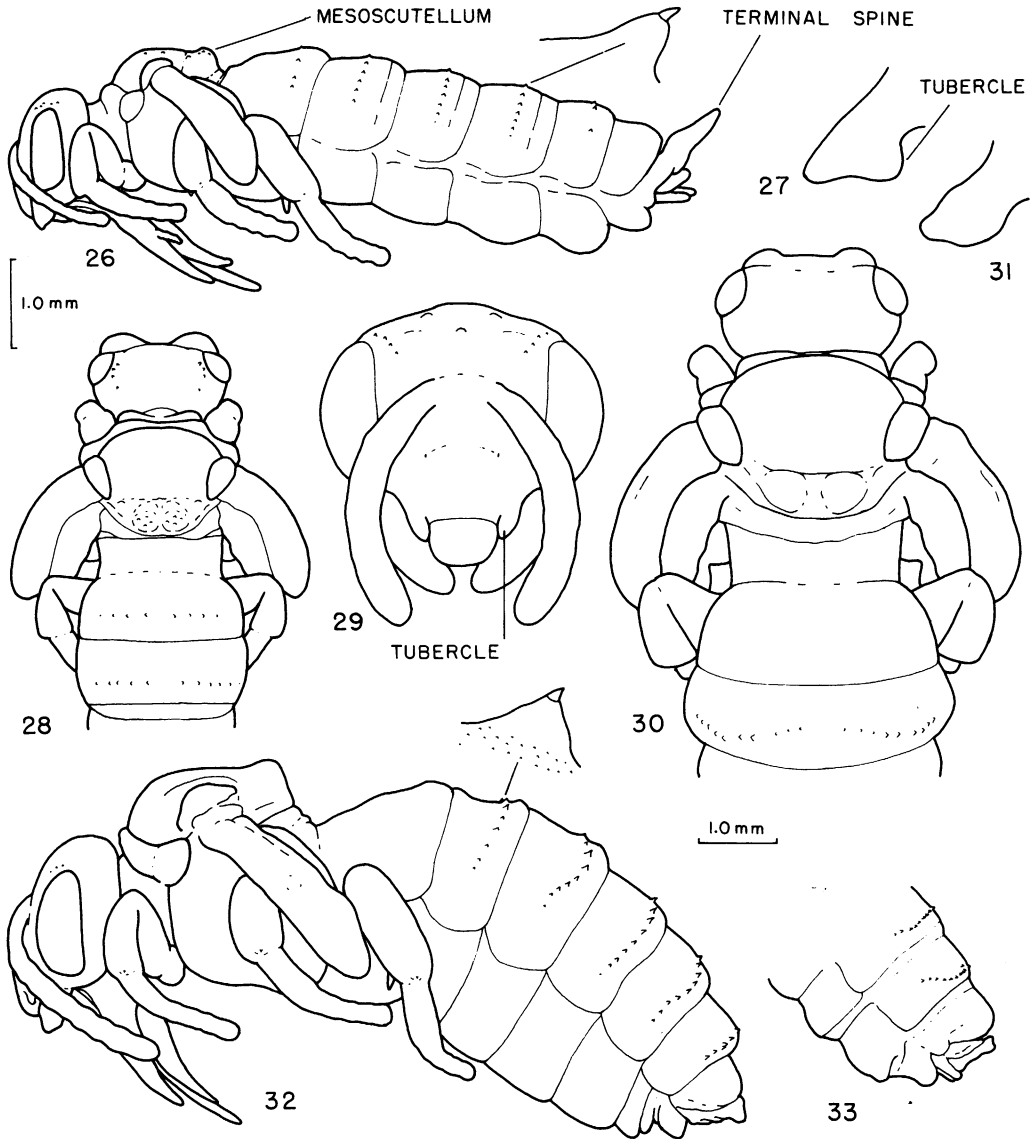
The pupae of these genera are diverse so that characterization of the subfamily is not possible, at least at this time; no single feature or set of features can be presented to distinguish the Nomadinae from other anthophorids or apoids. All have rows of small tubercles on the apical margins of most metasomal terga (e.g., figs. 26, 28, 30, 32) as is characteristic of most bee pupae. These tubercles are usually sharp-pointed, bearing sclerotized tips that at least in some instances represent setae. These setae are normally short and spinelike but in some instances are quite long. Similar spined tubercles are found on the vertex, scutum, scutellum, and outer surfaces of the tibiae of many but not all nomadines, a situation that is not widespread among other bees. Furthermore, pupae of many of the nomadine genera have large rounded paired tubercles arising from the mesoscutellum, but large tubercles tend to be absent from other parts of the body, perhaps an indication that the adults tend to have short setae. Hence tubercles are usually absent from coxae, trochanters, femora, pronota, and scuta and only *Paranomada* has a tubercle projecting from each tegula. The poorly preserved specimen of *Holcopasites* lacks tubercles on the basal segments of the leg although

Michener, 1954, indicated that tubercles were present on his specimen.

PRELIMINARY KEY TO PUPAE OF SOME NOMADINE GENERA

- 1. Apical lateral angle of clypeus with downward directed tubercle (fig. 29). Ammobatini . . . . . 2
- Apical lateral angle of clypeus without tubercle . . . . . 3
- 2(1). Terminal metasomal spine moderately long (fig. 26); mesoscutellum with spined tubercles (figs. 26, 28) . . . . . *Oreopasites*
- Terminal metasomal tubercle very small and short (figs. 32, 33); mesoscutellum without tubercles . . . . . *Morgania*
- 3(1). Axillae distinctly produced; if indistinctly produced (*Protepeolus*), then mesoscutum with pair of large, strongly elevated rounded tubercles. . . . . 5
- Axillae inconspicuous, not produced; mesoscutum without tubercles or with numerous, small, sharp-pointed tubercles. Nomadini . . . . . 4
- 4(3). Tegula with strongly projecting tubercle . . . . . *Paranomada*
- Tegula without tubercle. . . . . *Nomada*
- 5(3). Most metasomal sterna each bearing apical row of distinct tubercles which may or may not bear setae. Epeolini. . . . . 6
- Metasomal sterna without distinct tubercles . . . . . 7
- 6(5). Vertex, scutum, and scutellum with numerous small sharp-pointed spined tubercles. . . . . *Epeolus*
- Vertex, scutum, and scutellum without tubercles. . . . . *Odyneropsis*
- 7(5). Mesoscutum without rounded tubercles. Neolarrini . . . . . *Neolarra*
- Mesoscutum with large rounded paired tubercles. Protopeolini. . . . . 8
- 8(7). Mesoscutum with single pair of rounded tubercles; mesoscutellum and axillae only faintly produced . . . . . *Protepeolus*
- Mesoscutum with two pairs of rounded tubercles; mesoscutellum with pair of large, elevated tubercles; axillae strongly produced. . . . . *Isepeolus*

A pair of tubercles at the apicolateral angles of the clypeus (fig. 29) distinguishes the pupae of *Morgania* and *Oreopasites* from those of the other Nomadinae keyed above. These structures allow for the development of specialized hair



FIGS. 26-28. Pupa of *Oreopasites vanduzeei*. 26. Female pupa, lateral view. 27. Left mandible, lateral view. 28. Anterior part of pupa, dorsal view.

FIGS. 29-33. Pupa of *Morgania histrio transvaalensis*. 29. Head, frontal view. 30. Anterior part of pupa, dorsal view. 31. Left mandible, lateral view. 32. Male pupa, lateral view. 33. Apex of metasoma of female pupa, lateral view.

Scales refer to figures 26, 28, and 30, 32, 33, respectively.

tufts in adult males. Although tufts are absent or greatly reduced in females, the tubercles are present on female pupae as well. Because the tufts

are characteristic of all the Ammobatini, the corresponding tubercles are probably present on all ammobatine pupae.



*Oreopasites vanduzeei* Cockerell

Figures 26-28

*Oreopasites vanduzeei* is the only named species for which pupae are known. However, a pupa of an undescribed species is also on hand; some distinct features of it are parenthetically included in the following description.

**Diagnosis.** The pupae of *Oreopasites* and *Morgania histrio transvaalensis* can be distinguished on the basis of differences in the number and distribution of spined tubercles and in the length of the terminal metasomal tubercles.

**Head.** Integument microscopically spiculate; setae absent. Scape and frons without tubercle; vertex just mesiad of compound eye with very small, spined tubercles (in undescribed species these tubercles large and conspicuous); genal tubercles absent; each apicolateral angle of clypeus with downward-directed and narrowly rounded tubercle (as in fig. 29); mandible (fig. 27) with large tubercle on ventral surface; dorsal surface evenly curved, without tubercles or swellings.

**Mesosoma.** Integument microscopically spiculate; setae absent. Lateral angles of pronotum broadly rounded; posterior lobe of pronotum indistinctly produced; mesepisternum without tubercles; mesoscutum with very small spined tubercles (in undescribed species these tubercles and their setae larger and conspicuous); axilla rounded, slightly produced; scutellum with low, broadly rounded tubercles (not so strongly produced as those of *Morgania*), bearing small, spined tubercles (these tubercles quite pronounced in undescribed species); metanotum without tubercles but with rather distinct, transverse lateral swellings; propodeum without protuberances. Tegula without tubercles; wing without tubercle or swelling. Coxa, trochanter, and femur all without tubercles; foretibia without tubercles (undescribed species with approximately four small spined tubercles on outer surface); apex of midtibia with several indistinct spined tubercles (undescribed species with a number of spined tubercles on outer surface); hind tibia with several minute, indistinct spined tubercles on outer surface (undescribed species with numerous distinct spined tubercles).

**Metasoma.** Integument microscopically spiculate; setae absent. Tergum I with indistinct row of small spined tubercles; terga II-V (and presum-

ably II-VI in males) with distinct row of moderately large, spined tubercles, tubercles on tergum V few in number; tergum VI without tubercles (in undescribed species of *Oreopasites* tubercles on tergum I virtually absent; large strongly projecting spined tubercles present in distinct rows on terga II-V of females and II-VI of males; female with a few small tubercles present on tergum VI); sternal tubercles absent; terminal tubercle moderately elongate, rounded apically.

**Material Studied.** One female, Skeleton Canyon, Arizona, September 3, 1966, from cell of *Nomadopsis puellae* (J. Bath, F. Andrews, L. LaPré).

*Morgania histrio transvaalensis* Bischoff

Figures 29-33

**Diagnosis.** See diagnosis of *Oreopasites vanduzeei*.

**Head.** As discussed for *Oreopasites vanduzeei* except for the following: vertex just mesiad of compound eye with minute spine-tipped tubercles that are much smaller than those of *Oreopasites vanduzeei*; mandible (fig. 31) with low, broad swelling on ventral surface and on dorsal surface.

**Mesosoma.** As discussed for *Oreopasites vanduzeei* except for the following: Mesoscutum without tubercles; axilla not produced; scutellum with pair of large rounded, moderately well-produced tubercles (perhaps larger in females); these tubercles without small spined tubercles as found in *Oreopasites* but with small indistinct swellings that may be homologous. Wing without distinct tubercle although forewing bearing low, medial swelling. Forecoxae, unlike those of *Oreopasites*, with low, rounded tubercles; outer apical surfaces of each tibia with one (or sometimes more) spined swellings.

**Metasoma.** Integument microscopically spiculate; setae absent. Tergum I of male without tubercles, of female with several small tubercles; terga II-V (female) and II-VI (male) with distinct rows of moderately large, spined tubercles; tergum VI of female with few tubercles; tergum VII of male without tubercles; sternal tubercles absent; terminal tubercle very short and rounded but distinct, in both sexes.

**Material Studied.** One male, one female, 3

miles west of Grahamstown, Cape Province, South Africa, November 28, 1966, from cells of *Tetralonia minuta* (J. G. Rozen).

#### LITERATURE CITED

- Baker, D. B.  
1971. A new *Pasitomachthes* from Rhodesia (Hymenoptera, Apoidea). *Novos Taxa Ent.*, no. 98, pp. 1-8, figs. 1-6.
- Michener, Charles D.  
1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). *Bull. Amer. Mus. Nat. Hist.*, vol. 82, art. 6, pp. 151-326, figs. 1-246, diagrams 1-13.  
1953. Comparative morphological and systematic studies of bee larvae with a key to the families of hymenopterous larvae. *Univ. Kansas Sci. Bull.*, vol. 35, pt. 2, no. 8, pp. 987-1102, figs. 1-287, table 1.  
1954. Observations on the pupae of bees (Hymenoptera: Apoidea). *Pan-Pacific Ent.*, vol. 30, pp. 63-70, fig. 1, table 1.  
1957. Notes on the biology of a parasitic bee, *Isepeolus viperinus* (Hymenoptera, Anthophorinae). *Ent. News*, vol. 68, no. 6, pp. 141-146, figs. 1-5.
- Popov, V. V.  
1951. The parasitic bees of the genus *Ammobates* Latr. (Hymenoptera, Anthophoridae). *Trudy Zool. Inst.*, vol. 9, pp. 895-949, figs. 1-19, tables 1, 2.
- Rozen, Jerome G., Jr.  
1954. Morphological description of the larva of *Oreopasites vanduzeei* Cockerell (Hymenoptera: Anthophoridae). *Pan-Pacific Ent.*, vol. 30, pp. 203-207, figs. 1-6.  
1966. The larvae of the Anthophoridae (Hymenoptera, Apoidea). Part 2. The Nomadinae. *Amer. Mus. Novitates*, no. 2244, pp. 1-38, figs. 1-83.  
1968. Review of the South African cuckoo-bee genus *Pseudodichroa* (Hymenoptera, Apoidea). *Ibid.*, no. 2347, pp. 1-10, figs. 1-10.  
1969. Biological notes on the bee *Tetralonia minuta* and its cleptoparasite, *Morgania histrio transvaalensis* (Hymenoptera: Anthophoridae). *Proc. Ent. Soc. Washington*, vol. 71, no. 1, pp. 102-107, figs. 1-5.
- Rozen, Jerome G., Jr., and Ronald J. McGinley  
1974. Phylogeny and systematics of Melitidae based on the mature larvae (Insecta, Hymenoptera, Apoidea). *Amer. Mus. Novitates*.
- Rozen, Jerome G., Jr., and Charles D. Michener  
1968. The biology of *Scapter* and its cuckoo bee *Pseudodichroa* (Hymenoptera: Colletidae and Anthophoridae). *Amer. Mus. Novitates*, no. 2335, pp. 1-13, figs. 1-12, tables 1, 2.



