The Immature Instars of the Cleptoparasitic Genus *Dioxys* (Hymenoptera: Megachilidae)

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Abstract: The last-stage larva of *Dioxys pomonae pomonae* and *D. productus productus?* are described taxonomically and compared with the previously published account of the larva of *D. cincta* (Jurine). The three other larval instars and the pupa of *D. pomonae pomonae* are also described and the adaptive significance of some of the anatomical features of the larvae are discussed. A preliminary key is presented to distinguish among the genera of parasitic megachilid bees on the basis of the last larval instar.

The purposes of this paper are (1) to describe taxonomically the immature instars of the parasitic bee genus *Dioxys* and (2) to compare the external anatomy of the four larval instars of *Dioxys pomonae pomonae*. At the end, a key is given that may help in the identification of mature larvae of parasitic Megachilidae.

Cleptoparasitism (social parasitism) has evolved in at least three separate cases in the family Megachilidae. *Coelioxys*, usually a parasite of *Megachile* but also associated with *Centris*, *Anthophora*, and probably others, obviously arose from a *Megachile*-like ancestor. *Stelis*, *sensu lato* (including *Euaspis* and *Parevaspis*) and *Dioxys* (and related genera) presumably evolved from separate lineages in the Anthidiini. Most *Stelis*, *sensu lato*, apparently attack megachilids, although some (and perhaps all) species of the subgenus *Odontostelis* attack *Euglossa* (Friese, 1925; Bennett, 1966). The biology and larvae of *Stelis* are sufficiently diverse to raise the question whether this genus is monophyletic (Rozen, 1966). Insofar as known, all members of the *Dioxys* complex parasitize the Megachilinae (Hurd, 1958; Jaycox, 1966), but our lack of knowledge of their immature stages and biology does not permit us to speculate on the origin of parasitism in this group. I hope that data recorded here, as well as biological information presented in the accompanying report (Rozen and Favreau, 1967) will eventually be used for this purpose.

The number of larval instars in bees has been open to question because of the difficulty in rearing these animals. However, Hackwell and Stephen (1966) claim on the basis of carefully accumulated data that the halictid *Nomia melanderi* Cockerell has five instars. These men observed that the egg chorion encased the entire first instar except for most or all of the head capsule and that the first and second instars were similar in size. The first and second instars moved their mandibles back and forth and occasionally consumed liquid and pollen grains. Rozen (1964) stated that the embryo of the anthophorid

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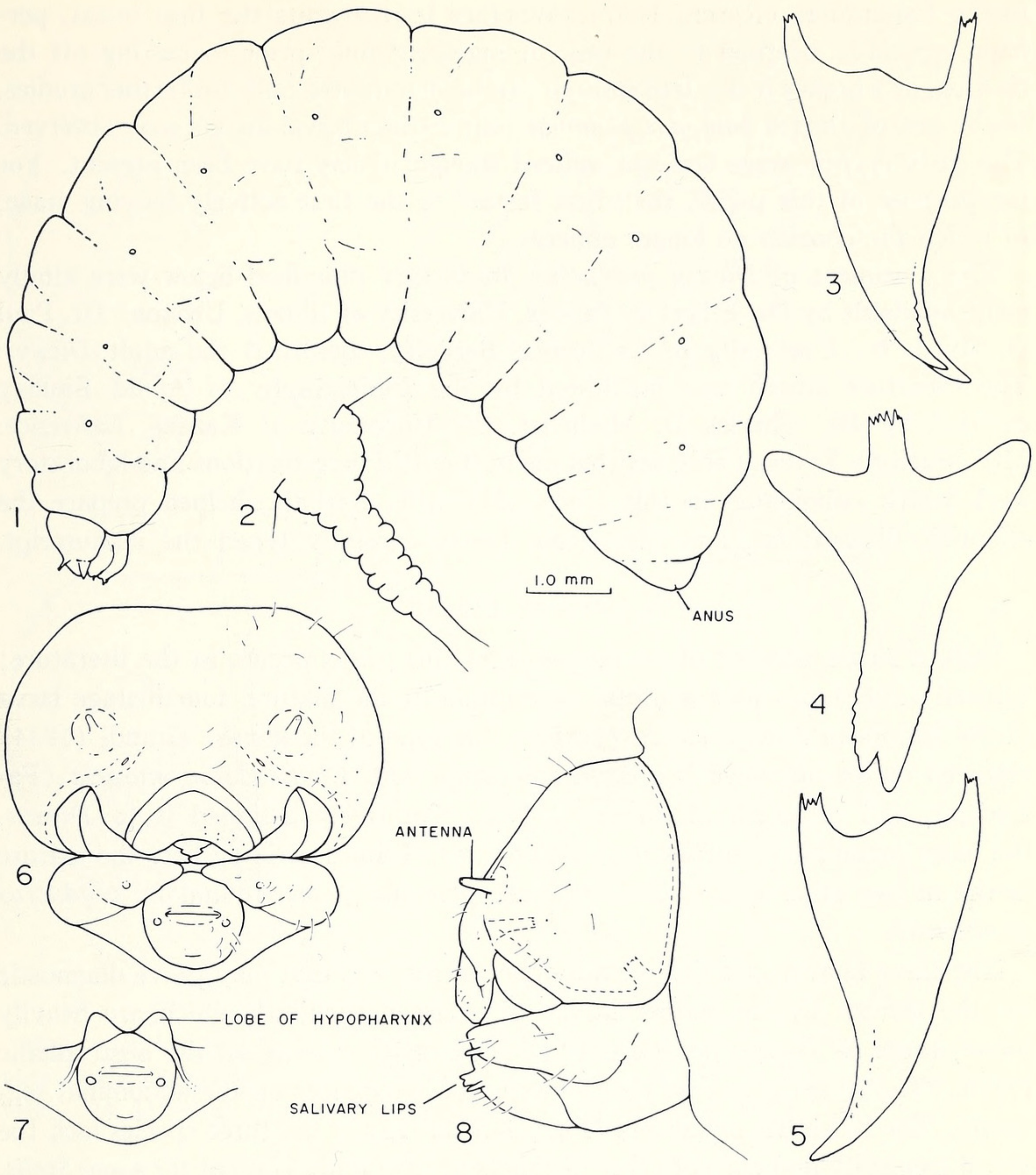


Figs. 1–8. Mature larva of *Dioxys pomonae pomonae* Cockerell. 1. Predefecating larva, lateral view (setae not shown). 2. Spiracle. 3–5. Right mandible, dorsal, inner, and ventral views, respectively. 6. Head, front view. 7. Labium, with mandibles removed, showing hypopharyngeal lobes, front view. 8. Head, lateral view. Scale refers to Fig. 1.

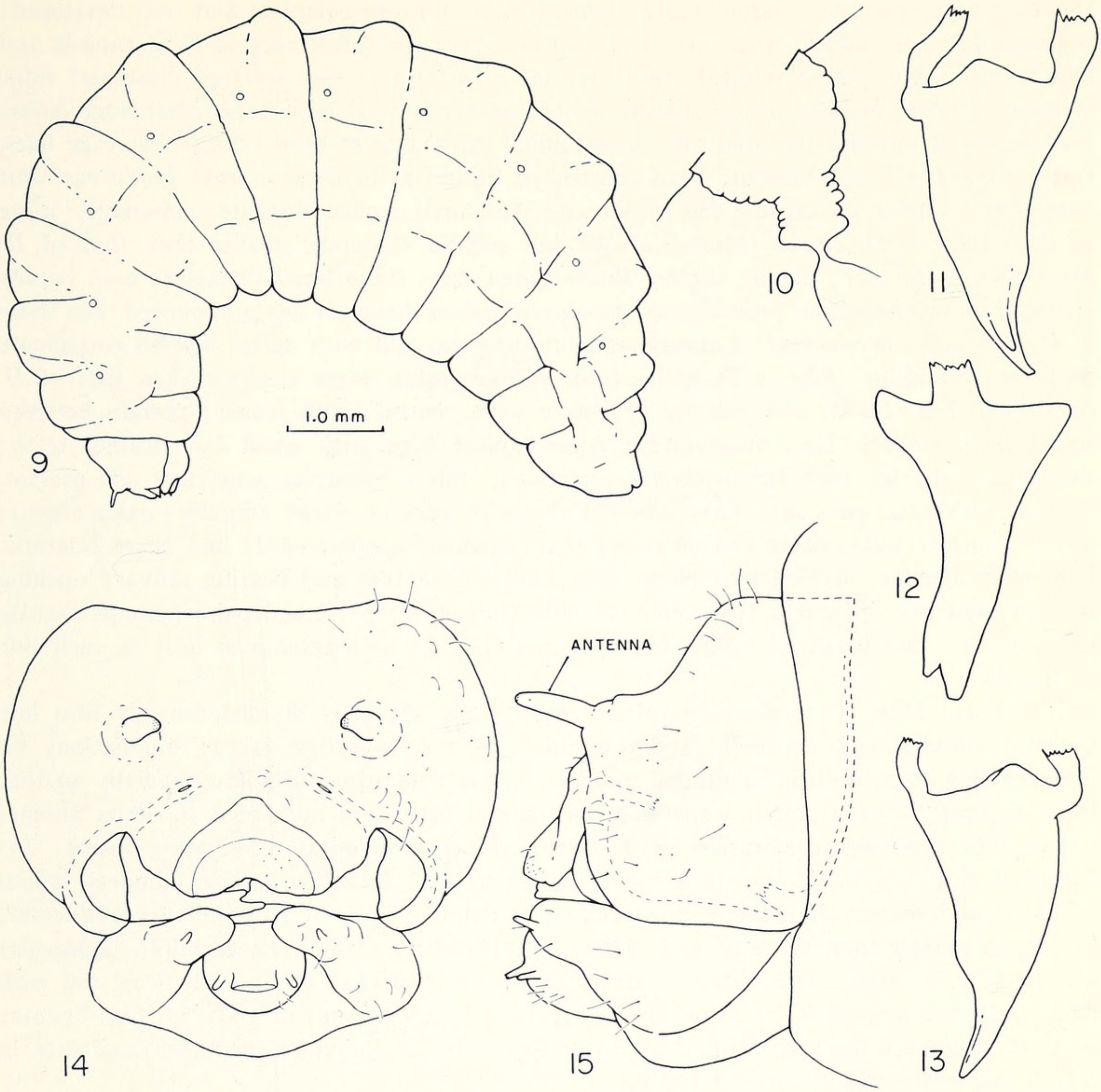
Svastra obliqua obliqua (Say) ingested liquid just before the chorion was cast off; shortly after eclosion a transparent embryonic cuticle was shed. The "first instar" of *Nomia melanderi* and the late "embryo" of *Svastra obliqua obliqua* are probably the same stage. If this is true, then the cryptic early stage may be a widespread phenomenon among bees, as *Nomia* and *Svastra* belong to separate families and as this stage has also apparently been observed in the Panurginae (Rozen, 1967). Whether it represents the first instar, perhaps especially adapted to the task of ingesting fluid prior to casting off the chorion, or whether it is a late embryo can be determined only by further studies. In the case of *Dioxys pomonae pomonae* four distinct larval instars were observed. The early cryptic stage was not noticed though it may have been present. For the purpose of this paper, the "first instar" is the first actively moving stage, to which the chorion no longer adheres.

The specimens of *Dioxys productus productus?* described below were kindly made available by Dr. Elbert R. Jaycox, University of Illinois, Urbana. Dr. Paul D. Hurd, Jr., University of California, Berkeley, identified the adult *Dioxys*. The literature search was facilitated by the Bibliography of Apoid Biology directed by Dr. Charles D. Michener, the University of Kansas, Lawrence. Mrs. Marjorie Favreau ably assisted me in the field investigations and laboratory work which culminated in this study. My wife, Barbara, helped prepare the scientific illustrations, and Mrs. Rose Ismay carefully typed the manuscript.

MATURE LARVAE

Only a single account of an immature of this genus occurs in the literature; Micheli (1936) provided a useful description of the mature, fourth-stage larva of the European *Dioxys cincta* (Jurine), the type of the genus. Grandi (1934) reported on an unknown bee larva associated with *Chalicodoma muraria* (Fabricius), and although Michener (1953a) tentatively assigned it to *Dioxys*, the hairy mandible identifies it as a *Coelioxys*. I am describing here the mature larvae of two other species of *Dioxys*, *D. pomonae pomonae* and *D. productus productus?*.

The three known species have a number of features that may prove diagnostic for the genus. Unlike mature larvae of other megachilids, which are heavily pilose, those of *Dioxys* possess only widely scattered setae on the postcephalic region. The setae, sparse on the thorax, are even sparser on the abdominal segments. The bidentate mandibles (Figs. 3–5, 11–13) of the three species lack the apical concavity and cusp of other members of the family (except for some *Stelis*, Rozen, 1966) and differ from those of other Anthidiini (except some *Stelis*, *ibid.*, and *Trachusa*, Michener, 1953a) in that there are no small teeth on the margin between the apical teeth; of the three forms, only *D. pomonae pomonae* (Figs. 3–5) has such teeth on the upper and lower mandibular edges. The antennae of *D. cincta* apparently are not abnormally large for a megachilid but those of *D. pomonae pomonae* (Fig. 8) are distinctly greater in size than those of members of other genera. The antennae of *D. productus productus?* (Fig. 15), however, are the largest of any bee larva that I have seen. Antennal size therefore is helpful, both for species separation and, in some cases, for identification of the genus.



Figs. 9–15. Mature larva of *Dioxys productus productus* (Cresson)? 9. Larva, lateral view (setae not shown). 10. Spiracle. 11–13. Right mandible, dorsal, inner, and ventral views. 14, 15. Head, frontal and lateral views. Scale refers to Fig. 1.

In other respects, the fourth instar of *Dioxys* seems to possess the features of other members of the family. Whether the distinctive characters mentioned above warrant placing the genus in a separate tribe as contemplated by Michener (1944) after studying the adults, is open to question. In general the larvae of megachilids appear so similar that it is difficult to imagine that larval features will be of much assistance in arranging the higher classification of the family.

Dioxys pomonae pomonae Cockerell
Figures 1–8

Head: (Figs. 6–8) Integument with numerous scattered long setae and without spicules; antennae, labrum, pleurostomal ridges, hypostomal ridges, mandibles, cardines, stipites, palpi, and base of prementum conspicuously pigmented. Tentorium complete and well developed; posterior pits conspicuous and normal in position; posterior thickening of head capsule and hypostomal ridge well developed; pleurostomal ridge and lateral arms of epistomal ridge moderately developed but not so sharply defined as hypostomal ridge; epistomal ridge fading just mesiad of anterior tentorial pits; longitudinal thickening of head capsule, cleavage lines, and parietal bands not evident; head constricted behind as in *D. productus productus?* but dorsolateral angles of capsule less produced. Antennal papilla elongate, apparently more so than that of *D. cincta* (Micheli, 1936) but papilla distinctly smaller than that of *D. productus productus?*; papilla slightly shorter than three times basal diameter; each papilla arising from inconspicuous prominence; these prominences distinctly less pronounced than those of *D. productus productus?*. Labrum without tubercles and with apical margin emarginate medially. Mandible (Figs. 3–5) without conspicuous setae, more elongate than that of *D. cincta* (Micheli, 1936), and apically bidentate with ventral tooth longer; margin between apical teeth smooth (i.e., nonserrate); dorsal apical edge with small but distinct teeth; ventral apical edge with inconspicuous serrations; apical concavity and cusp not present. Maxilla with basal part somewhat enlarged and with apex produced adorally; galea absent; palpus elongate but shorter and narrower than antennal papilla; cardo and stipes sclerotic. Labrum projecting, divided into prementum and postmentum and bearing salivary opening at apex; salivary opening a transverse slit with projecting lips; labial palpi perhaps slightly more slender than maxillary palpi; hypopharynx (Fig. 7) with prominent lobe on each side of maxilla.

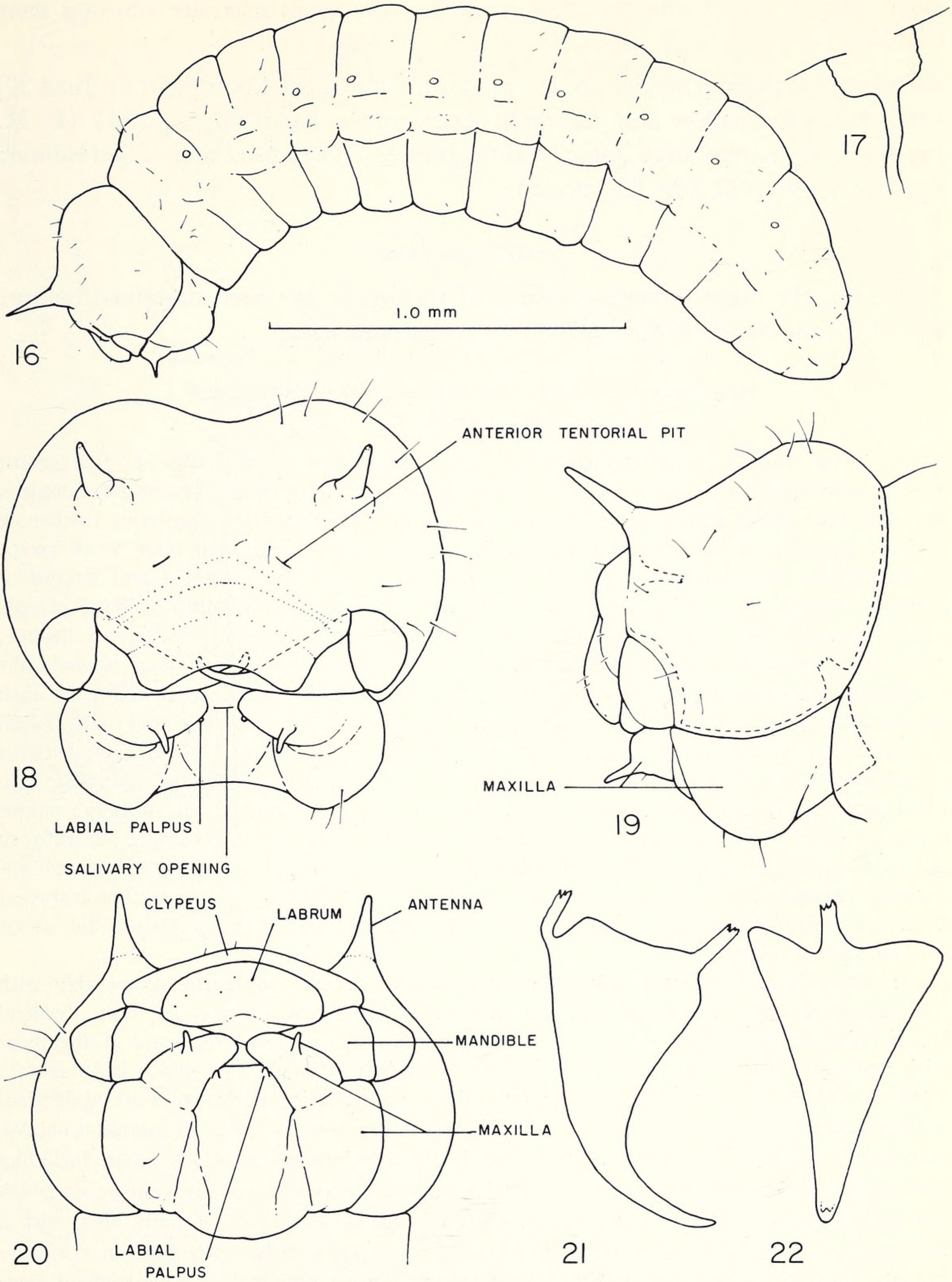
BODY: Form (Fig. 1) moderately robust; most body segments divided dorsally into low cephalic annulet and elevated caudal annulet on postdefecating larva; annulations on predefecating form indistinct; caudal annulets on postdefecating form low medially so that larva appears to have paired transverse dorsolateral tubercles; middorsal tubercles absent; lateral tubercles (below spiracles) well developed (at least on postdefecating form). Integument soft; scattered setae (not shown in illustration) found on caudal annulets, lateral tubercles, and venter; these setae approximately as dense as those of *D. productus productus?*, but much sparser than those of host *Osmia nigrobarbata* and other megachilids. Spiracular atrium (Fig. 2) large, with ridges; atrium projecting somewhat above body wall and with rim; peritreme present but narrow so that opening appears large; primary tracheal opening without distinct collar; subatrium normally long. Tenth abdominal segment moderate in length and with anus situated dorsally.

MATERIAL STUDIED: One postdefecating larva, 3 miles north of Apache, Cochise County, Arizona, April 30 through May 4, 1966; larva preserved October 14, 1966; from nest of *Osmia nigrobarbata* Cockerell (J. G. Rozen and M. Favreau); two predefecating mature larvae, same data except preserved at time of collection.

Dioxys productus productus (Cresson)?
Figures 9–15

These larvae were discussed by Jaycox (1966).

HEAD: (Figs. 14, 15) As described for *D. pomonae pomonae* except for following: Dorsolateral angles of head produced, apparently as in *D. cincta* (Micheli, 1936), and more so than in *D. pomonae pomonae*. Antennal papilla enormously elongate, being a little over three times longer than basal diameter; each papilla arising from restricted but pronounced prominence. Mandible (Figs. 11–13) like that of *D. pomonae pomonae* except dorsal and ventral apical edges without teeth or serrations.



FIGS. 16–22. First instar of *Dioxys pomonae pomonae* Cockerell. 16. Larva, lateral view. 17. Spiracle. 18–20. Head, frontal, lateral, and ventral views, respectively. 21, 22. Right mandible, dorsal and inner views. Scale refers to Fig. 16.

BODY: (Fig. 9) As described for *D. pomonae pomonae* except spiracular subatrium short (Fig. 10).

MATERIAL STUDIED: One mature larva, Smithfield, Cache County, Utah, June 30, 1962, from *Anthidium* nest in small plastic tube; fixed July 2, 1962 (E. R. Jaycox); one mature larva, same locality, June 31, 1961; from nest of *Anthidium*; fixed July 19, 1962 (E. R. Jaycox).

OTHER INSTARS

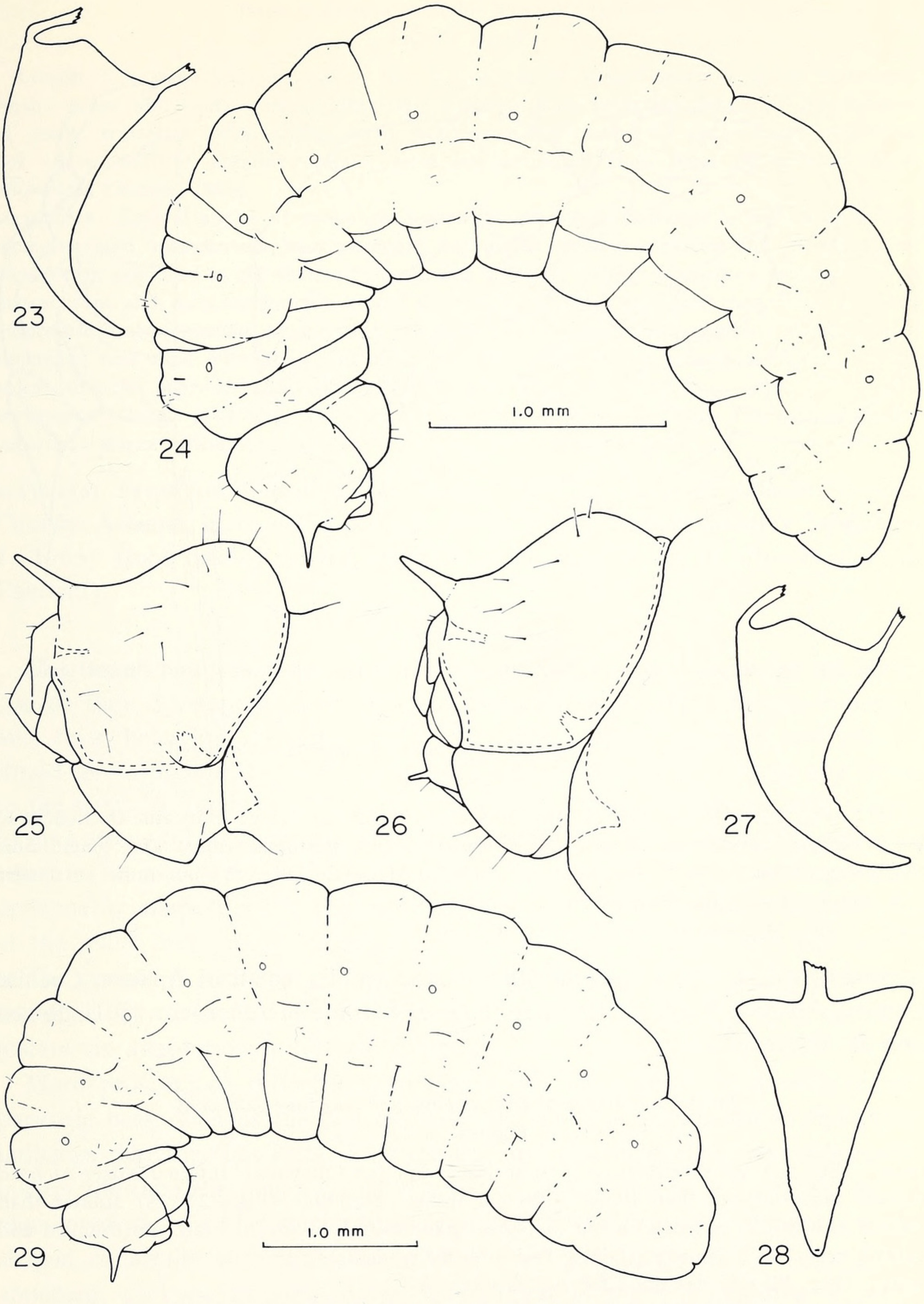
None of the other immature instars of this genus has been described before; all of the following belong to *Dioxys pomonae pomonae*.

First-Stage Larva of *Dioxys pomonae pomonae* Cockerell
Figures 16–22

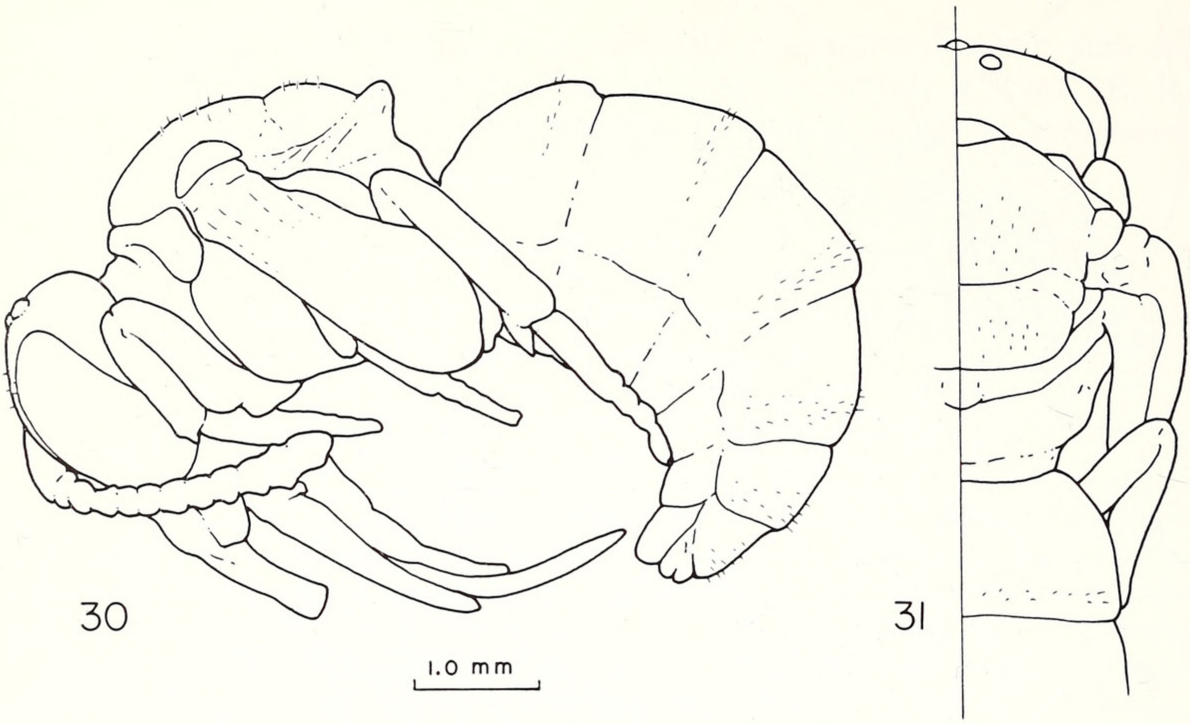
HEAD: (Figs. 18–20) Head hypognathous, not prognathous as in *Coelioxys*. Integument slightly pigmented and, unlike that of host, with scattered long setae. Tentorium complete, including thin dorsal arms; posterior tentorial pits normal in position; posterior thickening of head capsule and hypostomal ridge slender but evident; pleurostomal ridge weak except at mandibular articulations; epistomal ridge scarcely evident, both mesiad and laterad of anterior tentorial pits; these pits well developed; longitudinal thickening of head capsule faint; cleavage lines and parietal bands not evident; head somewhat constricted behind; genal area, unlike that of *Coelioxys*, not produced anteroventrally into long tubercle-like projection. Antennal papilla greatly elongate, length about four times basal diameter; each papilla arising from conspicuous prominence. Labrum without tubercles and with apical margin emarginate medially and with sensilla. Mandible (Figs. 21, 22) elongate, without conspicuous setae, and with apex simple, tapering, curved, and pigmented. Maxilla with basal part greatly enlarged and sclerotized (Fig. 19); apical part directed adorally; palpus elongate; galea absent. Labium, unlike that of other bee larvae, not extending ventrally so far as maxillae; labium recessed, not divided into prementum and postmentum, and apparently somewhat sclerotized though not so strongly sclerotized as that of first instar of *Coelioxys*; salivary opening a small transverse slit; palpi shorter than maxillary palpi, about as long as basal diameter.

BODY: Form (Fig. 16) moderately slender and straight; some body segments possibly with intrasegmental lines; middorsal tubercles absent; distinct lateral tubercles (i.e., "ventral lateral tubercles" of *Odontostelis*, Rozen, 1966) conspicuous on most segments. Integument with scattered setae (in contrast with integument of first instar of host which lacks setae); setae on anterior part of body longer than those on posterior part; on most abdominal segments setae situated on posterior part of segment dorsally, at apices of lateral tubercles, and widely scattered on venter; integument finely spiculate in numerous areas, including most of the tenth abdominal segment. Spiracles moderately large except for second pair which are distinctly smaller than others; atrium (Fig. 17) not projecting above body wall, with a peritreme, and slightly wider than deep; atrial wall apparently with indistinct ridges; primary tracheal opening apparently without collar. Tenth abdominal segment without large lobes or other modifications; anus slightly dorsal in position.

MATERIAL STUDIED: One first-stage larva, 3 miles north of Apache, Cochise County, Arizona, April 30, 1966; from nest of *Osmia nigrobarbata* (J. G. Rozen and M. Favreau).



Figs. 23–29. *Dioxys pomonae pomonae* Cockerell. 23. Right mandible of second instar, dorsal view. 24. Second instar, lateral view. 25. Head of second instar, lateral view. 26. Head of third instar, lateral view. 27, 28. Right mandible of third instar, dorsal and inner views. 29. Third instar, lateral view. Scales refer to Figs. 24 and 29, respectively.



Figs. 30, 31. Pupa of *Dioxys pomonae pomonae* Cockerell, lateral and dorsal views.

Second-Stage Larva of *Dioxys pomonae pomonae* Cockerell
Figures 23–25

HEAD: (Fig. 25) As described for first instar except for following: Posterior thickening of head capsule, hypostomal ridges, pleurostomal ridges, epistomal ridge, and longitudinal thickening of head capsule slightly more evident. Mandible (Fig. 23) not quite so slender and slightly shorter in relation to size of head.
BODY: (Fig. 24) As described for first instar.

MATERIAL STUDIED: One second-stage larva, 3 miles north of Apache, Cochise County, Arizona, April 30, 1966; from nest of *Osmia nigrobarbata* (J. G. Rozen and M. Favreau).

Third-Stage Larva of *Dioxys pomonae pomonae* Cockerell
Figures 26–29

HEAD: (Fig. 26) As described for first instar except for following: Internal ridges of head capsule more distinct than those of second instar. Mandible (Figs. 27, 28) stouter than that of either first or second instar and shorter in relation to size of head. Both dorsal and ventral subapical inner edges faintly and indistinctly dentate.
BODY: (Fig. 29) As described for first instar.

MATERIAL STUDIED: One third-stage larva, 3 miles north of Apache, Cochise County, Arizona, May 4, 1966; from nest of *Osmia nigrobarbata* (J. G. Rozen and M. Favreau).

Pupa of *Dioxys pomonae pomonae* Cockerell
Figures 30–31

Length, 6.75 mm; body curved so that tip of tongue almost touching tip of metasoma.
HEAD: Scape and frons without tubercles; vertex without tubercles except for low mounds of ocelli; scattered small, unpigmented setae occurring mesiad of upper inner orbits but not above level of anterior ocellus; setae less abundant than those on head of *Stelis bilineolata* (Rozen, 1966).
MESOSOMA: Lateral angles of pronotum somewhat produced; posterior lobes not produced; mesepisternum, mesoscutum, mesoscutellum, and axillae without tubercles and not produced; metanotum produced as distinct median rounded tubercle; slightly pigmented setae present on mesoscutum and mesoscutellum but not on axillae; these setae fewer than those of *Stelis bilineolata* and somewhat longer than those of head; tegula not produced; wing without tubercles; fore tibia with apical tubercle; mid and hind tibia each with somewhat smaller apical tubercle; other leg segments without distinct tubercles.
METASOMA: Terga I–VI with apical bands of short, unpigmented setae rising from minute tubercles; sterna without tubercles or setae; terminal spine absent.

MATERIAL STUDIED: One live female pupa, 3 miles north of Apache, Cochise County, Arizona, larva collected May, 1966, pupated approximately September 1, 1966; from cell of *Osmia nigrobarbata* Cockerell (J. G. Rozen and M. Favreau).

DISCUSSION

The larvae of most nonparasitic bees superficially seem to change merely in size as they develop. Indeed, the four instars exist in the same environment, and their behavior, concerned primarily with feeding, is quite uniform. It would be surprising, therefore, if marked differences occurred from one instar to the next. A number of workers have noticed, however, changes with respect to the various tubercles on the postcephalic region in some groups. The tubercles seem to be associated with the feeding habits of the larva; the changes are presumably adaptations to the modifications in the shape, consistency, and size of the pollen mass as it is being consumed. Conspicuous changes also appear in the larvae of cocoon-spinning bees; such features as long palpi, projecting labiomaxillary region, and protruding salivary lips, that appear in the later instars are adaptations to cocoon spinning.

More pronounced differences among instars have been noted with certain parasitic bees, such as the Nomadinae. The mode of parasitism in this group indicates that the first instar kills the egg or larva of the host and subsequent instars consume the pollen-nectar mixture. The first instar is equipped with a pigmented, more or less prognathous head capsule and greatly elongate, sickle-shaped mandibles with which it destroys the host's offspring. The tip of the abdomen, at least in some cases, is modified into a pygopod-like structure enabling the larva to move about in search of its prey. Not only is the host's egg or larva eliminated but also sibling larvae, for a female nomadine often lays more than one egg in a cell. The second and subsequent instars are much more "normal," lacking most of the specialized modifications of the first stage. This pattern of parasitism seems to be the most common in the Apoidea and has arisen *de novo* a number of times.

Another mode of parasitism occurs in the subgenus *Odontostelis* (Bennett, 1966) and apparently in *Sphecodes*; the adult cuckoo bee removes the host egg or young larva before depositing her own egg, and the first instar hatches as a "normal" type.

In *Dioxys* still another pattern of parasitism seems to be represented: the host's offspring may be killed by the first, second or third instar of the cuckoo bee. Not only the first instar but also the second and third possess large sickle-shaped mandibles, and at least the first and second instars display an aggressive behavior when touched with forceps (Rozen and Favreau, 1967). None of the instars has an obvious pygopod-like structure for pushing itself around the cell or on the pollen mass. These facts suggest that the larva, because of a slow mobility, may pass through several stages before it encounters and eliminates the host larva. Also, the egg of *Dioxys* is apparently inserted through the cell wall, probably after the cell is closed. Hence parasitism of a cell may take place over a considerable period of time. The first three instars of *Dioxys* are equipped to kill eggs of other *Dioxys* when and if they are introduced into an already parasitized cell. The ability of the intermediate instar to eliminate host and siblings may also be found in *Coelioxys* (Michener, 1953b) and in those *Stelis* which have apically simple mandibles in the last larval stage (Rozen, 1966).

The changes that occur from one larval instar to the next in *Dioxys pomonae pomonae* involve the change in body size and form (Figs. 1, 16, 24, 29); the width of the head capsule of the four instars is as follows: first, 0.65 mm (one datum); second, 0.875 mm (one datum); third, 0.95 mm (one datum); fourth, 1.10–1.13 mm (three data). The antennae become relatively smaller with each instar though they are still large even in the fourth instar. The mandibles become shorter in relation to head size and the denticles on the upper and lower subapical edges first appear in the third stage. However, the dorsal apical tooth is a feature solely of the last instar as are the projecting enlarged labium, the division of the labium into a prementum and a postmentum, the protruding salivary lips, and the annulations of the spiracular subatria. The basal part of the maxilla is greatly enlarged in the first instar, a condition that holds for the second and third stages and persists to some extent in the last larval instar. The internal ridges of the head, including the stipites and the cardines, appear to become successively more pronounced with each instar.

In other respects the larval instars of *D. pomonae pomonae* are remarkably similar. Even the setae which become shorter in relation to the body size, from instar to instar, maintain the same general distribution on the body through all instars. Indeed, the overall constancy of the external anatomical features is a more surprising result of the study than are the changes that take place in the development of the larva.

Key to Some Genera of Cleptoparasitic Megachilidae, Based on the Mature Larvae

Although this key is based only on the few species that I have examined, it may be of some value in separating the genera of megachilid cuckoo bees. Mature megachilid larvae, as a group, can be recognized because of the setae found on the postcephalic region; only the anthophorid genus *Allodape* and its relatives also bear conspicuous setae.

1. Mandible with more than four conspicuous setae on outer surface (Michener, 1953a, Figs. 160–161); gena, at least usually, produced into downward-pointing tubercle immediately behind posterior mandibular articulation (Michener, 1953b, Fig. 26) .... *Coelioxys* (two species)
   Mandible with at most one or two inconspicuous setae (Figs. 3, 5, 11, 13); gena without tubercle (Figs. 8, 15) 2
2. Body setae widely scattered and few; dorsal body setae restricted to caudal annulets on middle segments; vertex depressed medially; basal part of maxilla somewhat enlarged (Figs. 8, 15) .... *Dioxys* (two species)
   Body setae abundant; dorsal body setae numerous on both the caudal and cephalic annulets of middle segments; vertex not abnormally depressed medially; basal part of maxilla normal in size (Rozen, 1966, Figs. 5, 10) .... *Stelis* (three species)

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