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On Egg Eclosion and Larval Development in Euglossine Bees

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ABSTRACT

This study explores egg eclosion and larval biology of orchid bees (Apidae: Euglossini) in light of existing knowledge from studies dealing with a group of tribes within the Apidae referred to as corbiculate bees. It reports that *Eulaema* (*Apeulaema*) *polychroma* (Mocsáry) has five larval instars, and its first instar exists only briefly in that with the help of a band of spicules along both of its sides its exoskeleton is shed with the remnants of the chorion. Mature larvae of euglossines exhibit two anatomical features that are not characteristic of other corbiculates, namely the elongate, tapering area of the prothorax immediately behind the head and the small size of the cranium. These features are suggested to be accommodations allowing the development of the extremely long labiomaxillary region of the pupa, which in turn accounts for the lengthy mouthparts of the adult. Descriptions of the egg and mature larva of *Euglossa* (*Euglossa*) *hemichlora* Cockerell are appended as well as referenced in the text.

INTRODUCTION

This is another contribution to a series of studies exploring the immature stages of corbiculate bees (i.e., Euglossini, Bombini, Meliponini, and Apini) and how their larvae hatch from eggs. To date a number of papers (Rozen et al., 2017; 2018; submitted) have referred to the Apini and Bombini regarding these matters, and another is in progress pertaining to the Meliponini. An early paper (Rozen, 2016) dealt exclusively with the Euglossini, and, while it described and illustrated euglossine larvae, it was intended to address only last-stage larvae and did not discuss eclosion. Furthermore, it failed to explore what now appears to be two obscure

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Table 1. Mean larval head widths and range (in mm) of *Eulaema* (*Apeulaema*) *polychroma*, demonstrating five larval instars (number of individuals in parentheses).

Instar	1	2	3	4	5
Mean	0.8 (1)	0.975 (1)	1.2 (1)	1.525 (1)	2.1125 (4)
Range					1.95–2.25

apomorphies of mature larvae of the tribe. The current paper addresses these two matters. Also, when this study was nearing completion, David Roubik kindly sent the author larvae and an egg of *Euglossa* (*Euglossa*) *hemichlora* Cockerell, thus permitting their inclusion in the manuscript. Formal descriptions of both are in the appendix. Although Michener (1953) was the first person to describe a euglossine larva, that of *Eufriesea violacea* (Blanchard) (as *Centris* (*Euplusia*) *violacea* (Blanchard)), he illustrated only its head and did not illustrate or describe in length its postcephalic region.

Methods: Immature stages studied herein were initially preserved in Kahle's solution. To be studied, larval specimens were cleared in an aqueous solution of sodium hydroxide and stained with Chlorazol Black E and photographed by use of a Canon Power Shot A2300 camera hand held to one of the eyepieces of a Leitz Wetzlar stereomicroscope or a Carl Zeiss compound microscope. SEM micrographs of the egg of *Euglossa hemichlora* were captured with a Hitachi S5700 in the Microscopy and Imaging Facility of the American Museum of Natural History. All scale bars used in illustrations are 1 mm long.

ECLOSION

The description of the last stage larva of *Eulaema* (*Apeulaema*) *polychroma* (Mocsáry) (Rozen, 2016) was based on three specimens collected in Peru more than 20 years ago and preserved at the American Museum of Natural History. Collected and stored alongside these specimens were a scattering of their younger larvae, egg fragments, pupae, as well as a large number of their nest cells. The larvae are treated now because the first instar reveals how it hatches from the egg and identifies the function of a suspicious "linear band of granules" occurring along both sides of the larva's body mentioned by Garófalo and Rozen (2001: 14) in their study of *Exaerete smaragdina* (Guérin-Méneville).

Table 1 reports the head widths of all larval stages from an inventory of the larval specimens of *Eul. polychroma* preserved in Kahle's solution recovered from the nest. The single first instar when discovered was still partly draped in the egg chorion. When cleared in an aqueous solution of sodium hydroxide, the specimen separated from its chorion and revealed that it contained the entire developing pharate second instar, the head capsule of which was already fully developed within the cranium of the first instar, as was its body within that of the first instar's. After staining with Chlorazol Black E, the tracheae of the second instar were seen to surround those of the first, while, importantly, a distinct band of fine, sharp spicules (i.e., "granules" of Garófalo and Rozen, 2001) was clearly revealed (figs. 1, 2) running along the integument on both sides of the body just above the level of the spiracles starting on the prothorax and extending beyond the spiracles

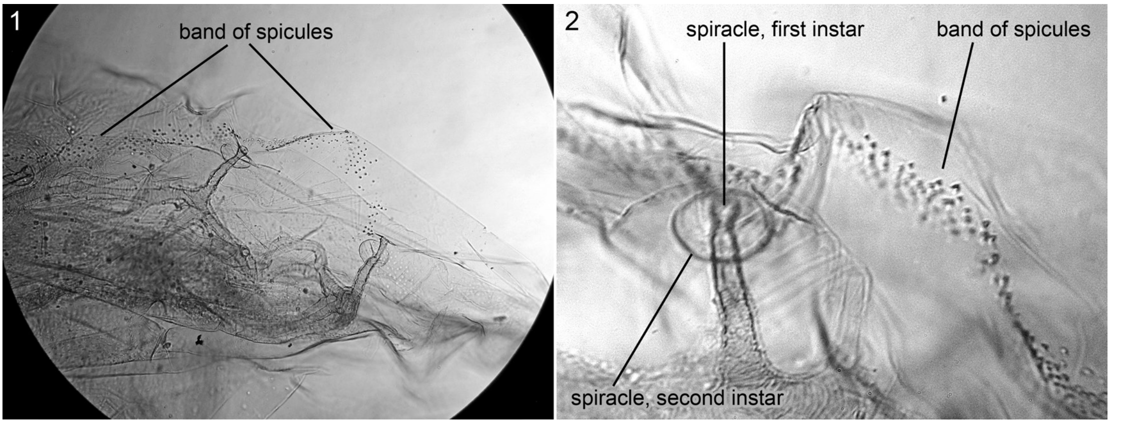


FIGURE 1. Microphotographs of integument of body of cleared first instar of *Eulaema* (*Apeulaema*) *nigrita* (Lepeletier) showing two spiracles, associated trachea, and continuous band of fine spicules extending along one side of body just above spiracular line. Large structure circling each spiracle is large atrium of second instars forming around very small atrium or first instar. FIGURE 2. Close-up of one spiracle.

on abdominal segment 8. The specimen had been killed and preserved in the Kahle's solution shortly before it would have transitioned to the second instar. That is, in hatching, this species casts off the integument of the first instar with the remainder of its chorion, as has been described for *Centris flavofasciata* Friese and many others (see Rozen et al., 2011). Further, the cleared body of the specimen showed no pollen within the intestinal track proving that the first instar of this species does not feed on pollen-laden provisions.

Obscure Apomorphies

Many but not all studies of mature last larval instars of the Euglossini reveal an interesting feature that appears intermittently in publications: it is the peculiar hooked shape of the instar in lateral view with a pronounced, strongly curved anterior body in contrast to a straighter posterior part, accompanied by an elongation and narrowing of the body between the head capsule and first thoracic segment. All of this is further accentuated by the very small size of the head relative to body size as demonstrated by figures shown below and referenced in table 2. These features for *Euglossa* (*Glossuropoda*) *intersecta* Latreille were well illustrated by Zucchi et al. (1969a: fig. 3), and his diagram is reproduced here (fig. 3) because it not only shows these features but also depicts the pharate-developing pupa. The external features are also seen here for *Euglossa* (*Euglossa*) *hemichlora* Cockerell (fig. 16) and additionally were identified by Rozen (2016: for *Eug.* (*Euglossa*) *cordata* (L) (fig. 6), *Eufriesea surinamensis* (L.) (fig. 7), *Eufriesea mussitans* (Fabricius) (fig. 8), and *Eulaema polychroma* (fig. 9). In contrast to table 2, table 3 lists diagrams of last larval instars to lack such an elongation of the front part of the body. Reproduced here are *Eufriesa surinamensis* (L.) (fig. 10), *Exaerete smaragdina* (fig. 11), and *Eulaema* (*Apeulaema*) *nigrita* Lepeletier (fig. 12). While at first it appears that there are two body types for mature larvae of the Euglossini, these dissimilar body types are actually age differences created by the development of the pupa within the last larval instar. João M.F. de Camargo

Table 2. Original references to diagrams of last larval instars of euglossine with elongate, necklike extension of prothorax.

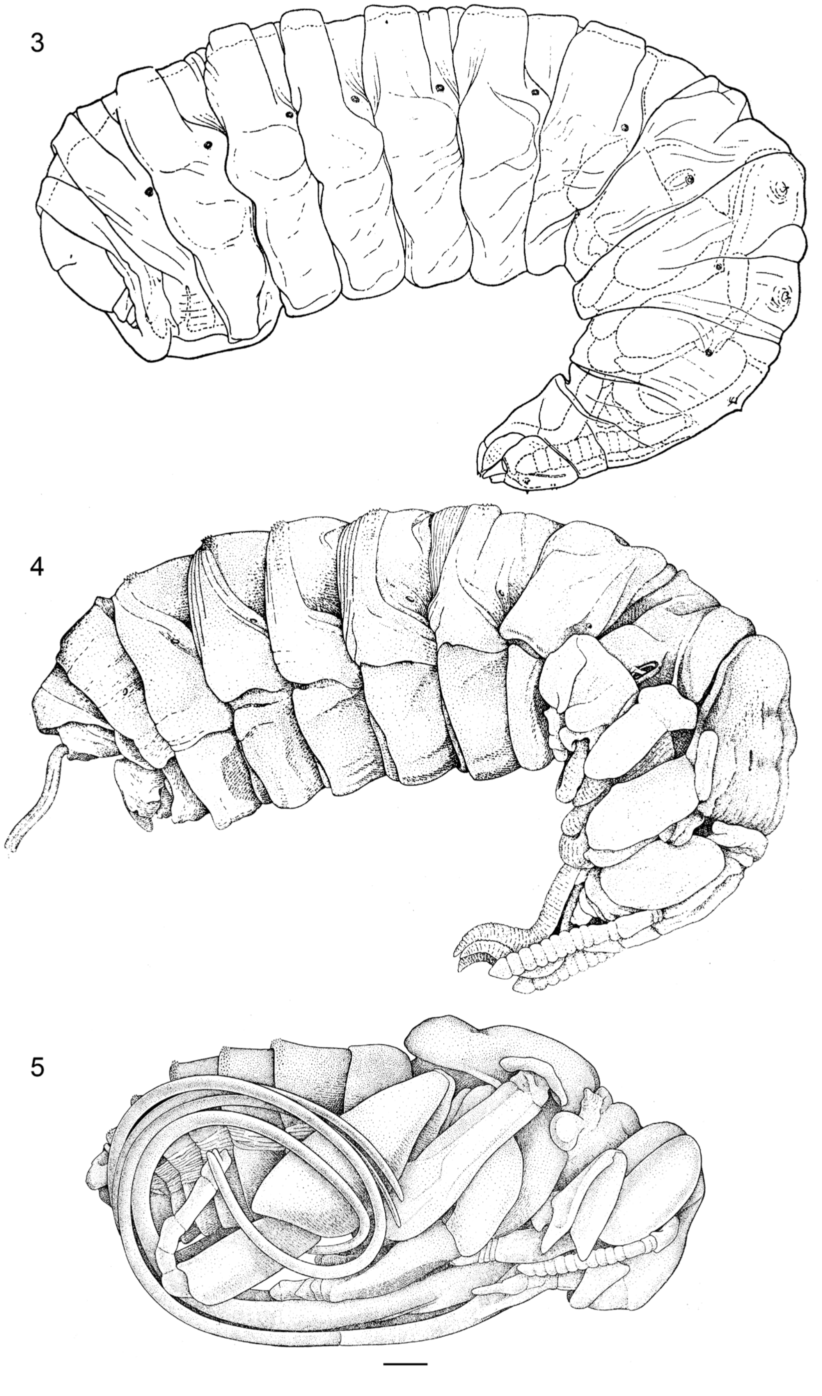
Species	Reference: diagram(s)
Eufriesa surinamensis (L.)	Rozen, 2016: figs. 1, 8
Euglossa (*Glossura*) *imperalis* Cockerell	Roberts and Dodson, 1967: figs. 7, 8
Euglossa (*Glossura*) *intersecta* Latreille	Zucchi et al., 1969a: fig. 3
Euglossa (*E.*) *cordata* (L.)	Rozen, 2016: fig. 17
Euglossa (*E.*) *hemichlora* Cockerell	herein: fig. 18
Eulaema (*Apeulaema*) *polychroma* (Mocsáry)	Rozen, 2016: fig. 27

Table 3. Original references to diagrams of last larval instars of euglossine apparently lacking elongate, necklike extension of prothorax.

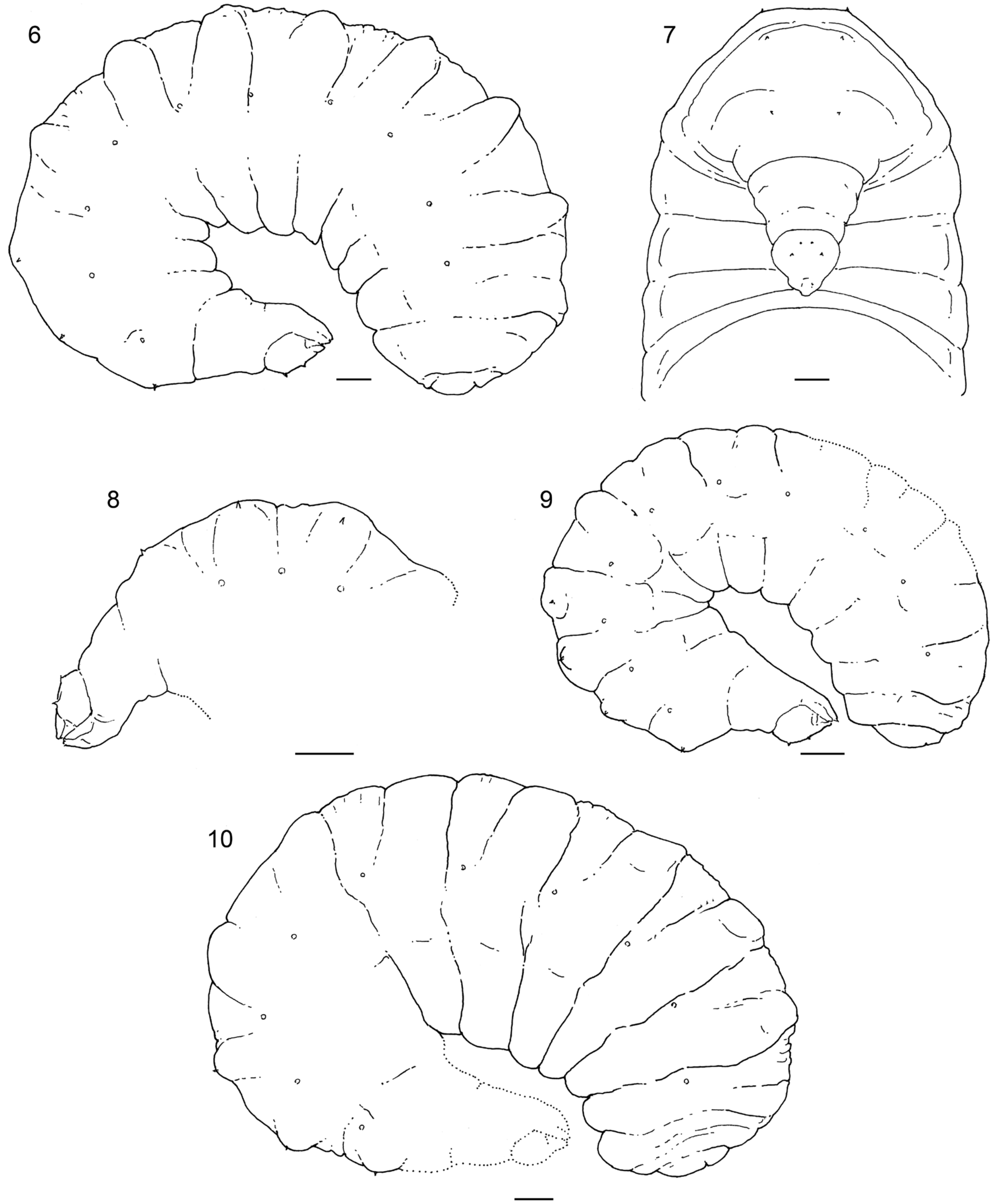
Species	Reference: diagram(s)
Eufriesa surinamensis (L.)	Rozen, 2016: figs. 6, 7
Euglossa (*E.*) *hemichlora* Cockerell	herein: fig. 21
Exaerete smaragdina (Guérin-Méneville)	Garófalo and Rozen, 2001: fig. 29
Eulaema (*Apeulaema*) *nigrita* (Lepeletier)	Zucchi et al., 1969b: fig. 8

probably realized this when he depicted (in Zucchi et al., 1969a: fig. 3) the pharate pupa within the hooked-shaped larval body. The head of the pupa is seen developing in the larva's prothorax. His subsequent illustration (fig. 10, reproduced here as fig. 4) shows a so-called prepupa presumably removed from the larva's exoskeleton and clearly supports the conclusions that the prolongation of the region between the larval head and prothoracic segment is an accommodation that allows for the development of the elongate proboscis of adult Euglossini, a feature characteristic of the tribe (Michener, 2007). While the last larval instar feeds and spins its cocoon, its thorax often accommodates the developing proboscis by retracting the cranium into the prothorax, and the full length of the prothorax is not typically revealed, as diagramed in Rozen (2016: figs. 6, 7) and reproduced herein as figures 12 and 13 for *Eufriesea surinamensis*. However, near the end of the period of defecation/cocoon production, development of pupal features within the larva commences. In doing so, the elongate, folded and coiled labiomaxillary mouthparts and antennal apices form in the larval head and extend posteriorly to the front of the pupal cranium, which is closely attached to the anterior surface of the pupa's mesosoma, as shown in figure 3 and to some extent in figure 4.

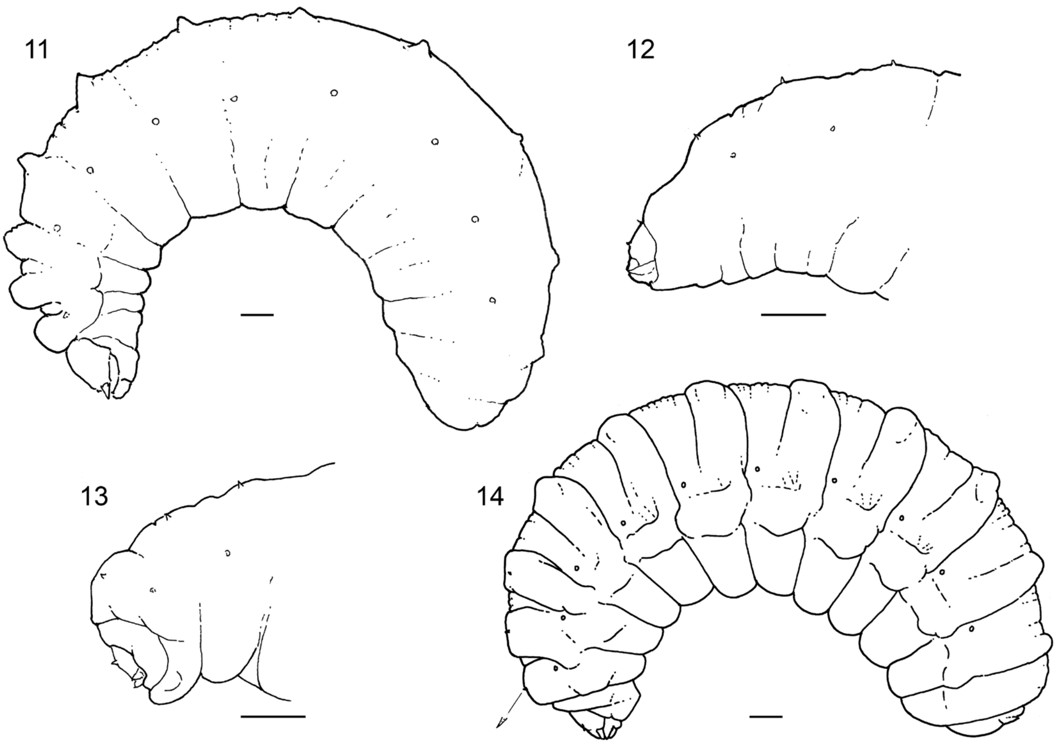
Although the beginning of developmental of this "prepupal" period cannot be externally pinpointed, its identification can be detected in the gradual change in the external form of the larva created by the gradual internal development of its adult apomorphy, namely the elongate labiomaxillary region, enabled by a necklike extension of the larval prothorax immediately posterior to the larval head. Thus, this larval apomorphy is a developmental precursor to the adult's extremely elongate labiomaxillary appendages.



FIGURES 3–5. Illustrations of sequence of immature stages of *Euglossa* (*Glossura*) *intersecta* Latreille reproduced from Zucchi et al. (1969b: figs. 3, 10, and 9, respectively), all to approximately same scale. **3.** Postdefecating larva showing internal position of developing pharate pupa (dashed lines). **4.** Prepupa. **5.** Pupa, showing elongate mouthparts that form under the head and mesosoma of the prepupa.



FIGURES 6–10. Euglossine taxa exhibiting elongate, necklike prothoracic segment and small cranium in Rozen (2016) for: **6, 7.** *Eufriesea surinamensis*, **8.** *Eufriesea mussitans,* **9.** *E.* (*Euglossa*) *cordata*, **10.** *Eulaema* (*Apeulaema*) *polychroma*.



FIGURES 11–14. Euglossine taxa not exhibiting elongate, necklike prothoracic segment. **11.** *Eulaema* (*Apeulaema*) *nigrita* modified from Zucchi et al. (1969a: fig. 8) and **12, 13.** *Eufriesea surinamensis* from Rozen (2016: figs. 6, 7) (both of which were identified as predefecating). **14.** *Exaerete smaragdina*, identified as postdefecating in Garófalo and Rozen (2001: fig. 28), presumably was in an early stage that had not yet started to develop pupal tissue internally.

Not to be overlooked, there also exists a subtler larval feature involved with the exaggeration of the elongate labiomaxillary features of adult euglossines: the extremely small head size of the mature larva. It seems likely that with most developing late-stage bee larvae, the head appendages of the pupa start developing within the head capsule of the larva. However, because those of euglossines become so elongate, space for the developing pupal head as well as most of the appendages is provided by the elongation of the larva's necklike extension of the prothorax. As a consequence, only the tips of the head appendage remain in the mature larva's head capsule just before ecdysis. This is shown in Zucchi et al. (1969a) and herein (fig. 3); the elongate, necklike prothorax provides space for developing head appendages, and thereby permits head size reduction in the last larval instar of the Euglossini.

DISCUSSION

Rozen et al. (2017) pointed out that melittologists use the term "prepupa" (plural, "prepupae") for two very different phenomena: (1) the diapausing, quiescent last larval instar that hibernates/aestivates usually for much of a year before transforming to a pupa and emerging shortly there-after as an adult in the next period of adult activity the following year (although the length of the inactive period can extend for years in the case of some species), and (2) an early pupal substage as the pharate pupa gradually develops within the larval exoskeleton immediately before ecdysis at which time the larval cuticle is cast off (Salmah et al., 1996). Because of their long lifespan, diapausing prepupal larvae are likely to be found and collected, and their stable anatomy is likely to be documented. Development of the pupa does not take place during this diapausing stage. However, at the end of the diapausing period an obvious quick development of pupal features must occur, followed immediately by pupation. This transformation process is the same developmental step as the "prepupal stage" sensu Salmah et al., 1996.

Toward the end of the current study when the author tried to compare Euglossini with Bombini (*Bombus*), he became aware of the similarities in their development. The postdefecating larvae of a number of species of *Bombus* were seen with pupal heads developing in the prothoracic segment while much of each developing antenna was coiled, filling the parietal on its side of the cranium. This was clearly discernable in an extensive collection of *B.* (*Fervidobombus*) *steindachneri* Handlirsch bearing the following data: Mexico: Tepoztlan, VIII.3.90 (G. Chavarría). The pupal head was appressed to the rim of the larval cranium, and the extension (neck) separating the cranium from the prothorax was short. Not surprisingly the larval cranium of this species is not extensively reduced in size. Similar observations were noted for *Bombus* (*Pyrobombus*) *bimaculatus* Cresson from New Jersey: Bergen Co.: Closter, V.18.1968 (J.G. Rozen), and *Bombus* (*Thoracobombus*) *pensylvanicus* (DeGeer), Kansas: Douglas Co.: Lawrence, VIII.20.1950 (C.D. Michener). This information suggests that the difference between the known euglossine larval head anatomy and that of bombine larvae is primarily involved with the disparity between the lengths of their labiomaxillary appendages.

In the next study treating corbiculate bees, this author will point out that among the Meliponini, mature larvae of certain species also have extremely small heads compared with body size. However, this anatomical feature is not correlated with a narrow, elongate necklike feature of the larva. How does this larva function differently from that of a euglossine? Many studies dealing with immature bees have focused on distinguishing the immature of one taxon from another; see papers by Michener, 1953; Lucas de Oliveira, 1960, 1965, 1968, 1970; and the current author. Such investigations obviously are necessary, but they are only the first step in understanding how an organism functions, as will be explained when that study is completed.

ACKNOWLEDGMENTS

Although attempts were made to obtain permission to reproduce figures 3–5 from the journal Boletim da Universidade Federal do Panamá, Zoologia, that journal no longer exists. The paper was titled "Notas Bionômicas sôbre *Euglossa* (*Glossura*) *intersecta* Latreille 1838 e descrição de suas larvas e pupa (Euglossini, Apidae)." It was authored by R. Zucchi, B. Luca de Oliveira, and J.M.F. de Camargo. It should be recognized that their beautifully crafted figures 3, 8, and 10 (herein referred to as 3, 5, and 4, respectively) clearly indicate that the authors were the first to understand the developmental processes of euglossine bees that are discussed here.

David Roubik, Smithsonian Tropical Research Institute, is thanked most sincerely for all specimens *Euglossa* (*Euglossa*) *hemichlora* Cockerell treated herein, permitting the first description of the egg and mature larva of this species.

Museum Specialist Corey Shepard Smith operated the scanning electron microscope to take the SEM micrographs presented herein and proofread the completed manuscript. Museum Specialist Stephen Thurston arranged and labelled all illustrative materials for the manuscript.

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APPENDIX

Descriptions of Egg and Last Larval Instar of *Euglossa* (*Euglossa*) *hemichlora* Cockerell

Egg

Figures 15–17

The following description is incomplete because much of both ends of the elongate egg were badly torn from poor preservation.

Description: Length 3.3 mm; maximum diameter 0.74 mm. Color nearly white. Shape (fig. 17) elongate, distinctly curved; both ends hemispherical and nearly identical; long tubular surfaces between them nearly parallel with one end only slightly slimmer than other end. Surface smooth but not shiny when viewed with stereomicroscope; position of micropyle not evident with stereomicroscope. When viewed with SEM, both ends so damaged that micropyle missing resulting in a questionable determination of egg orientation (see following Discussion); chorion of much of long surface of egg exhibiting faint but distinct hexagonal patterning (fig. 15) suggestive of a thin, fragile chorion.

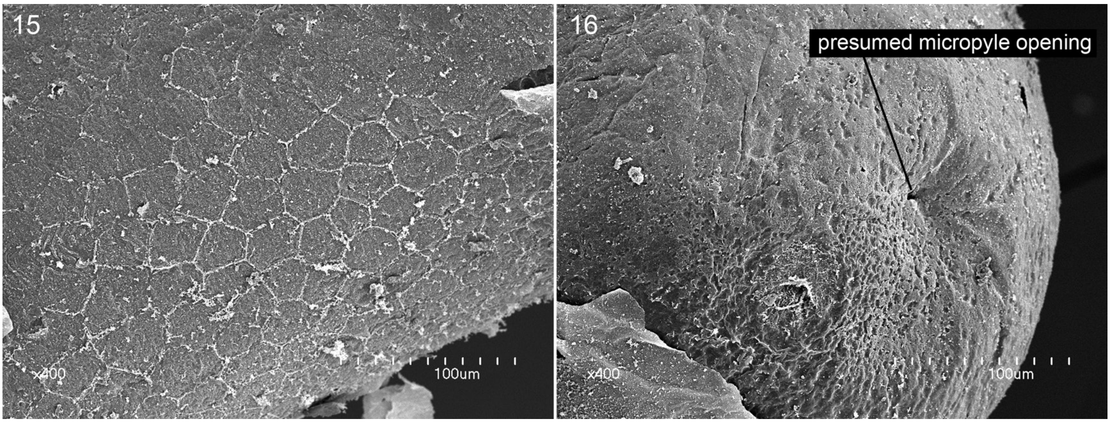
Discussion: The chorion of this specimen was so torn that its micropyle could not be identified. However, when the damaged chorion at the slightly smaller end of the egg was removed, a single small opening surrounded by a faint depression in the yolk was revealed (fig. 16). Because it strongly resembled the micropyle opening through the vitelline membrane into the yolk of *Bombus griseocollis* (DeGeer) (Rozen et al., 2018: fig. 10), the more symmetrical (in lateral view, fig. 17) end of the egg of *Eug. hemichlora* is provisionally considered the anterior one.

Material Examined: One egg, Panamá: Colón Prov.: 4 km SE Sabanitas, Roubik Reserve, March 2018 (D. Roubik).

Last Larval Instar

Figures 18–28

Although the larval collection of *Eug. hemichlora* consisted of 10 last larval instars, only one was a postdefecating form and three or four were judged to be mature predefecating forms. Because of the wide range in body size of all specimens, their identification as last larval instars came as a surprise, when width of head capsule on all specimens was found to range between



FIGURES 15, 16. SEM micrographs of egg of *Euglossa* (*Euglossa*) *hemichlora*. **15.** Surface of chorion from side showing faint hexagonal patterning. **16.** Presumed front end of egg revealing presumed opening through the vitelline membrane.

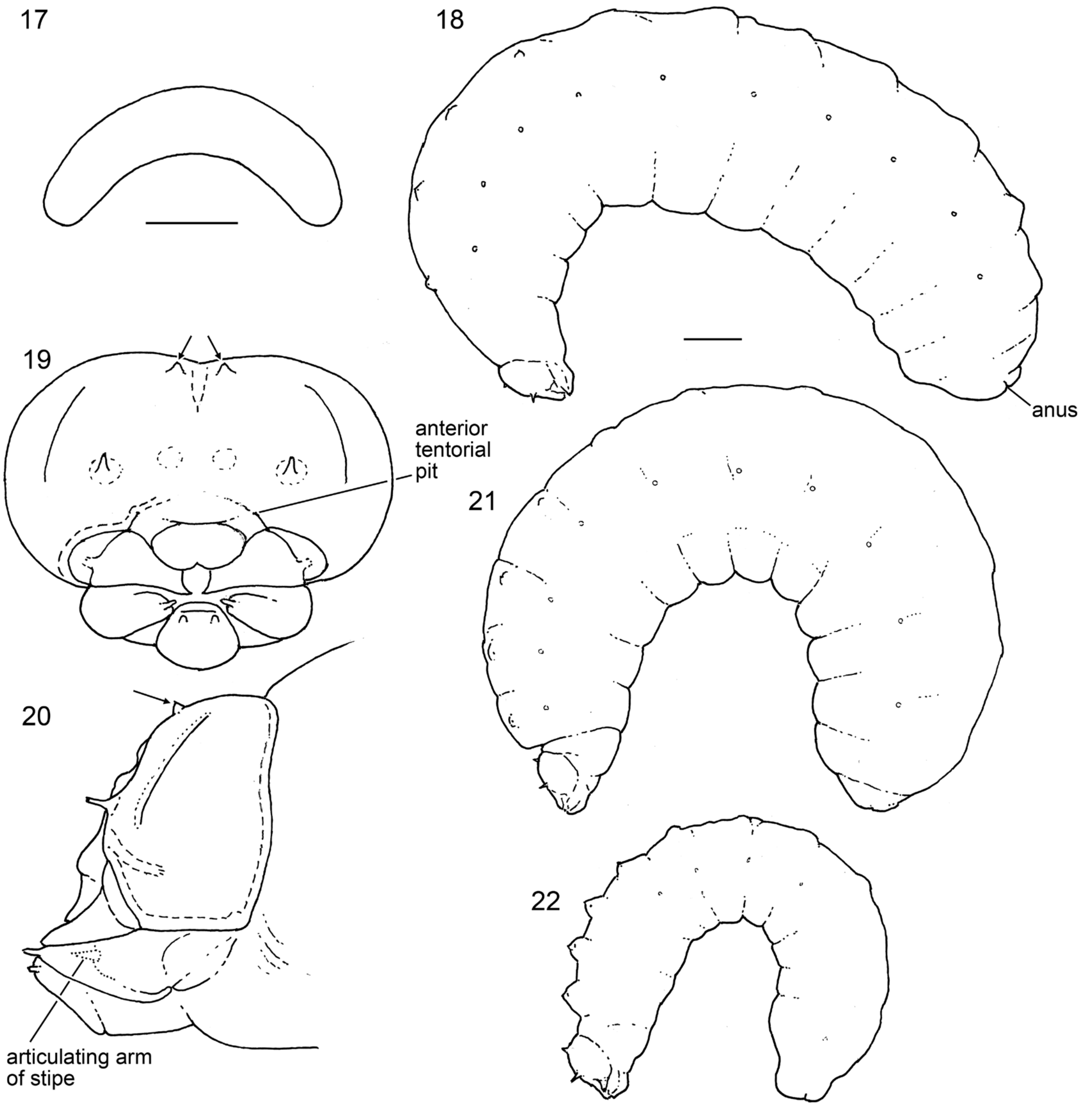
1.4 to 1.625 mm with an average of 1.515 mm. The cranium width of the single postdefecating larva and one predefecating larva was 1.625 mm. To illustrate the change in body size that takes place within the last larval stadium, compare figure 18, a mature predefecating last larval instar, with that of figure 22, an early stage predefecating last larval instar. To preserve the single postdefecating specimen as much as possible, only one spiracle with attached integument was excised from the specimen, cleared, and stained. After the head of a mature predefecating form was removed from the body, both parts were cleared and stained. Consequently, the following description includes details of both forms, as indicated.

The mature larva of this species keys to genus in Rozen (2016), although pigmentation of the paired dorsal tubercles on abdominal segment is often faint compared with that of the paired dorsal thoracic tubercles.

Diagnosis: After completing this description, post- and predefecating larvae of *Eug. hemichlora* were compared with the predefecating larva of *Eug. cordata* (L.), described and illustrated in Rozen (2016: figs. 17–19); no critical difference could be detected, although the diameter of the atrial rim of *Eug. hemichlora* appears about 1/5 smaller than that of *Eug. cordata*.

Description: **Head** (figs. 19, 20): Integument with scattered fine setae. Apices of mandibles and paired paramedian tubercles of vertex darkly pigmented; hypostomal ridge, articulation areas of mandibles, and sclerotized areas of mouthparts at most faintly pigmented.

Head size very small relative to body. Cranium in frontal view (fig. 19) more than 1.5× wider than height; clypeus, labrum, and labial apex moderately broad in frontal view (as in *Eug. cordata*, Rozen, 2016: figs. 17–19); labral apex faintly bilobed. Coronal ridge extending forward beyond paired paramedian tubercles of vertex before abruptly ending; postoccipital ridge well developed; as seen from above, this ridge extending nearly directly across cranium, not curving forward at median line; hypostomal ridge well developed; dorsal ramus not evident; epistomal ridge present both laterad of (below) anterior tentorial pits and between pits, but between pits was difficult to detect because it did not stain well; frons bearing paramedian pair of depressions short distance above level of antenna; tentorium at least of predefecating

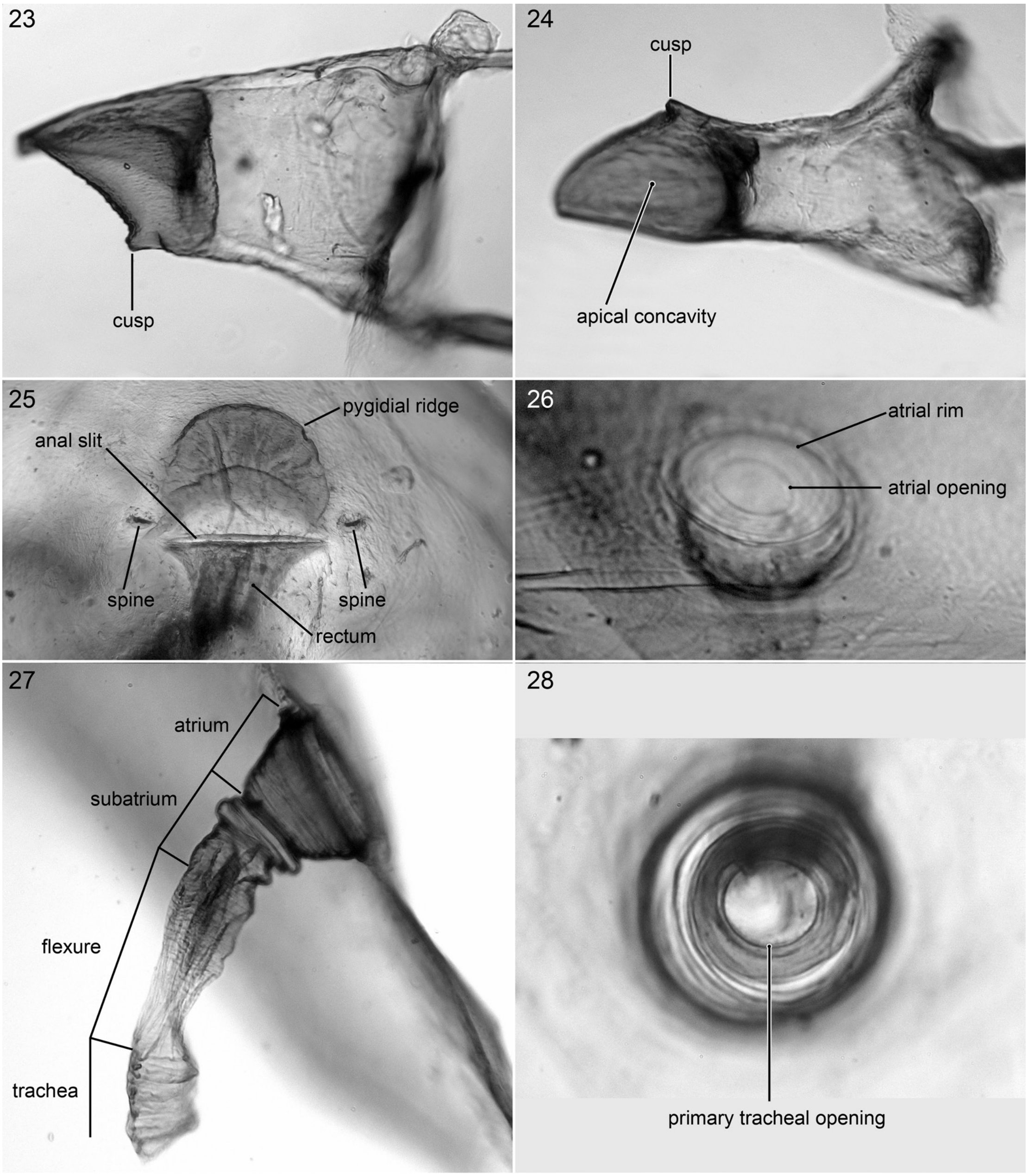


FIGURES 17–22. Diagrams of immature stages of *Euglossa* (*Euglossa*) *hemichlora*: figs. 18, 21, 22 to same scale. **17.** Egg, presumed front end left. **18.** Postdefecating larva, lateral view, anterior end left. **19, 20.** Head of same, frontal and lateral views, respectively. **21.** Late stage predefecating last larval instar, anterior end left. **22.** Early stage of predefecating last larval instar, anterior end left.

form robust including dorsal arms. Vertex bearing paired, pigmented, well developed, apically pointed tubercles (arrows, figs. 19, 20). Parietal bands evident. As seen in lateral view (fig. 20) antennal prominence scarcely evident and cranium above prominence evenly curved; antennal papilla elongate, conical, tapering, projecting more than twice basal diameter.

Mandible robust in dorsal (fig. 23) and ventral views; mandible tapering somewhat apically, but as seen in inner view (fig. 24) extreme apex with dorsal edge curving and intersecting at right angle with nearly straight lower edge (fig. 24); mandible bearing large, well-formed, darkly pigmented apical concavity adorally directed, with smooth inner surface except at inner base; curved dorsal edge of apical concavity with projecting cusp at base as seen in dorsal view (fig. 23); outer surface of mandible with two small seta-bearing tubercles near base. Labiomaxillary region elongate as seen in lateral view, so that apex extending forward but narrowing, and maximum thickness below hypostomal ridge in lateral view (fig. 20) less than 1/2 height distance from hypostomal ridge to top of vertex; cardo and stipital rod sclerotized but not extensively pigmented; articulating arm of stipes faintly pigmented as seen on cleared specimen; maxilla narrowing apically, its surface well supplied with rather short setae; maxillary palpus and galea positioned at maxillary apex, with galea adoral to palpus; maxillary palpus slender, elongate, more than three times longer than basal diameter; galea elongate with long apical setae. Labium elongate, clearly divided into pre- and postmentum, with surface of both faintly sclerotized and with, shape of prementum bulging beyond postmentum; labial palpus slender, elongate, length at least two times basal diameter. Salivary lips projecting, rather narrowly transverse but as wide as distance between outer bases of palpi. Hypopharynx apically bilobed with indistinctly spiculate or roughened surface.

Body (figs. 18, 21): Body form of postdefecating larva robust with head fully exposed; front part of body (head and thorax) acutely angled from the axis of abdominal segments 2–10; thorax narrow, elongate in lateral and dorsal views due to extremely elongate prothorax. Body form of mature predefecating larva slightly more robust than that of postdefecating, with body curvature tending to be evenly C-shaped viewed laterally rather than with long axis of thorax acutely angled from axis of abdominal segments 2–10. Head tending to be partly withdrawn into thorax, resulting in lack of elongate necklike region. In both pre- and postdefecating forms dorsum of the three thoracic segments and first abdominal segment each bearing pair of sublateral moundlike swellings on the caudal annulets; each mound supporting distinct tubercle with more or less pigmented, sclerotized, single apical spine (spines of immature last larval instar lacking pigmentation). On cleared specimens stained with Chlorazol Black E, integument of mound substantially darker, thus forming transverse oval, dark integumental surface under each tubercle, with those of prothorax so large that they meet at median line and those of following body segments becoming decreasingly smaller so that staining on dorsum of second abdominal segment merely a faint stain on each side of median line, lacking tubercle altogether. On both pre- and postdefecating larvae, body vestiture consisting in many areas of regular pattern of minute spicules (so small as to be seen only with compound microscope) intermixed with far sparser, very fine setae; spicules appearing more abundant on dorsal and lateral surfaces then on ventral surfaces. Abdominal segment 10 (fig. 25) attached to approxi-



FIGURES 23–28. Microphotographs of mature larvae of *Euglossa* (*Euglossa*) *hemichlora*. **23, 24.** Right mandible, dorsal and inner views, respectively**. 25.** Anal area of cleared and stained predefecating larva with darkly stained integument above transverse anal slit above which is the pygidial ridge; dark area below slit is rectum seen through integument. Note short pigmented spines laterad of anal slit. **26.** Spiracle of cleared predefecating larva seen from exterior, demonstrating width of peritreme relative to atrial opening. **27**. Side view of spiracle of predefecating larva with its anatomical parts identified. **28.** External view of spiracle of predefecating larva focused on unadorned primary tracheal opening; gray-toned ring immediately outside of opening caused by subatrium beneath transparent atrium.

mate middle of segment 9; transverse slitlike anus positioned dorsally on abdominal segment 10, with short pigmented spine (fig. 25) at both ends of anal slit and with low median semicircular unpigmented pygidial ridge (fig. 25) extending dorsally from spines; enclosed integument above slit colorless on postdefecating larva but staining deeply on predefecating larva (fig. 25).

Spiracles (figs. 26–28) very small relative to size of entire larva, faintly pigmented, subequal in diameter; peritreme broad, so that diameter of atrial opening not much longer than radius of peritreme; atrium somewhat wider than deep, with distinct rim projecting slightly beyond body wall; atrial wall faintly concentrically ringed; primary tracheal opening circular, without ornamentation; first chamber of subatrium, forming short collar into atrium; first chamber of subatrium shorter than atrium but forming conspicuous ring when viewed externally, other subatrial chambers far less distinct, leading to long collapsible flexure which in turn connecting to tracheal system. Sex-specific characters unknown.

Material studied: One postdefecating larva, 3+ mature predefecating last larval instars: Panamá: Colón Prov.: 4 km SE Sabanitas, Roubik Preserve, March 2018 (D. Roubik).

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