A taxonomic and biological study of the immature stages of some New World Scarabaeinae (Coleoptera: Scarabaeidae) [1]

W. D. EDMONDS

Department of Biological Sciences
California State Polytechnic College
Pomona, California 91768

GONZALO HALFFTER [2]

Departamento de Zoologia,
Escuela Nacional de Ciencias Biológicas, I.P.N.
México 17, D. F.

EDMONS, D. W. & GONZALO, HALFFTER, 1972. A taxonomic and biological study of the immature stages of same New World Scarabaeinae (Coleoptera: Scarabaeidae).[1] *An. Esc nac. Cienc. biol., Méx.*, **19**: 85-122.

Fecha de publicación: Febrero de 1972.

ABSTRACT: This paper describes the larvae and, in some cases, the pupae and biologies of the following, mostly Mexican species of dung beetles: *Liatongus monstrosus* (Bates), *Copris armatus* Har., *C. lugubris* Bohem., *Phanaeus daphnis* Har., *P. mexicanus* Har., *P. palliatus* Sturm, *Canthon humectus humectus* (Say), *Eurysternus magnus* (Lap.) and *Eurysternus* sp. n. The biologies of *Dichotomius carolinus* (L.) and *Glaphyrocanthon viridis leechi* Martinez, Halffter and Halffter are discussed. The larval and pupal descriptions increase our still meager knowledge of immature Scarabaeinae by approximately 50%; special attention is called for the first time to the evidently common presence of vestigial metathoracic spiracles on scarabaeinae larvae. A special section treats the pupation cell and pupal adaptations of Scarabaeinae. Behavioral differences resulting in the construction of brood masses and brood balls are clarified, and the term population cell is formally defined as a structure (usually spheroid) containing a spherical cavity in which pupation occurs. All Scarabaeinae presumably complete development in some type pupation cell constructed by the larva itself (in taxa falling in Group I nidification behavior as defined by Halffter and Matthews, 1966) or by the parents (Groups II, III and IV). Pupal adaptations for development within a confined, spherical cavity include pupal support projections designed to minimize contact with the walls of the pupation cell.

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[1] Work completed in the Departamento de Zoologia, Escuela Nacional de Ciencias Biológicas, I.P.N.

[2] Becario SEDICT-COFFA, I.P.N.

While it has recently received some renewed attention, study of the immature stages of Scarabaeinae remains largely spotty. Ritcher's (1966) treatment of North American species is the most recent comprehensive account of larval taxonomy; there are virtually no comparative works on pupae. What is known about the biology of the subfamily has been reviewed by Halffter and Matthews (1966). Other works on larval development not cited by them include Bornemissza (1969), Goidanich (1961), Goidanich and Malan (1962, 1964) and Malan and Gandini (1966). This paper describes the larvae and, in some cases, the pupae and biologies of the following species: *Liatongus monstrosus* (Bates), *Copris armatus* Har., *C. lugubris* Boheman, *Phanaeus daphnis* Har., *P. mexicanus* Har., *P. palliatus* Sturm, *Canthon humectus humectus* Say, *Eurysternus magnus* (Lap.) and *E.* sp. nov. In addition, notes on the biologies of *Dichotomius carolinus* (L.) and *Glaphyrocanthon viridis leechi* Martinez, Halffter and Halffter are given. A special section treats the pupation cell and pupal adaptations of Scarabaeinae.

The descriptions of genera are based upon the literature and new data. Terminology used there and in the descriptions of larvae is largely that of Ritcher (1966). We here use the term anal lobes for the fleshy prominences of the posterior surface of the last abdominal segment which surround the anus; the subanal lobes are those below the anus. The configuration of the anal lobes appears rather uniform for some supraspecific taxa (e. g., *Copris*). We here mention for the first time the occurrence of a pair of minute, vestigial spiracles on the metathorax of the larva. Heretofore they have evidently been overlooked. Although they are most prominent in the larva of *Liatongus monstrosus*, metathoracic spiracles are present in all larvae described in this paper. Moreover, Ritcher (pers. comm.) has observed vestigial metathoracic spiracles in *Gymnopleurus* and *Licanthe*.

Our designations below of instar are based upon size of the larva in question and the generally accepted supposition that the larval development of Scarabaeinae includes three instars. We have, therefore, assumed that the largest larvae are third instars and, as customary, stressed these specimens in making descriptions. The work of Halffter, López and Halffter (1971), however, suggests that the development of *Phanaeus daphni* includes either 1) a fourth instar or 2) a distinct prepupal stage which terminates the third stadium; the latter seems more probable. The principal observable differences between the third instar "proper" and prepupa, whether or not there might intervene a molt, are in activity and color: from very active to virtual torpor and, simultaneously, from white to deep yellow. Both these changes undoubtedly signal the physiological changes associated with the approach of pupation. No other features yet observed (e. g., facial chaetotaxy) differ between these two larval forms. Another case of presumed intrastadial change in larval form has been observed in *Eurysternus* (see below).

Pupal descriptions a re limited to accounts of the pupal support projections. Although various points of the developing adult do in fact partially support the pupa in the pupation cell (e. g., developing pronotal ridges, etc.), we here restrict the meaning of pupal support projection to include only those supporting lobes, ridges, tubercles, etc., found on the pupa and not retained in the adult stage.

In our discussions of nidification procedure we have found it necessary to distinguish between a brood mass and brood ball. Our use of the term brood mass refers to a quantity of larval provision (usually dung) packed in the end of a burrow in which an egg is laid, other than the packing procedure, the provision is not elaborated by the parent. Such a brood mass is characteristic for those taxa placed in Group I nidification behavior by Halffter and Matthews (1966). A brood ball, on the other hand, is usually an elaborate spheroid fabricated by the parent which, as in *Copris,* may consist entirely of larval provision (usually dung) or, as in *Phanaeus*, a food core enclosed in some type of outer soil cap.

Line drawings were made directly from photographs; all photographs are original. Figures 4-8 were made with a Jeolco, JSM -1, scanning electron microscope kindly placed at our disposal by Dr. A. R. Loeblich of the research facilities of the Standard Oil Company of California. We gratefully acknowledge the technical assistance of Dr. R. S. Daniel and Mr. Ray McAdams in preparation of the electron micrographs.

With the exception of a small amount of field collected material, all immatures described here were obtained by confining field collected adults to terraria, where they were provided with soil and cow dung. The laborious task of maintaining these rearing facilities and collecting material was the patient work of Violeta M. de Halffter and Y. López G., whom we gratefully acknowledge. Some of the field collected material as well as many important biological notes were provided by Biol. Pedro Reyes C., to whom we offer our special thanks. These three persons currently participate in a research program on the biology of Scarabaeinae conducted at the Departamento de Zoología, Escuela Nacional de Ciencias Biológicas, I.P.N. Our special thanks to Eric G. Matthews for his translation of Medveded, 1952.

Study of the immatures of *Eurysternus* was facilitated by a grant to G. Halffter from the Organization for Tropical Studies. (Pilot Research Grant O. T. S. N° 67-31).

PROVISIONAL KEY TO THE NEW WORLD SCARABAEINAE BASED UPON KNOWN THIRD INSTAR LARVAE

The following is an artificial key which will certainly need revision as our knowledge of larval Scarabaeinae increases. It is based upon two principal sources: Ritcher's monograph (1966) and the new data presented below. Since so little is yet known, such a key is admittedly somewhat presumptuous: we intend it to be merely a partial synthesis of our present knowledge and not a definitive identification device. References cited parenthetically below contain descriptions of the lalrval of the genus in question; references to descriptions given later in this paper are indicated by "description(s) below."

1. Third antennomere dilated distally, bearing a prominent conical sensory organ (Fig. 30); ventral surface of galea with two, prominent sclerotized tubercles each bearing a stout seta (Fig. 34, arrows); frontal suture shaped almost as Greek letter omega (Fig. 29); legs each terminated by tubercle ("claw") surrounded by circlet of short setae, tubercle bearing two long, slender setae (Fig. 33) *EURYSTERNUS Dalman*
(descriptions below)

— Third antennomere not dilated distally, though may bear a conical sensory organ; ventral surface of galea without tubercles; frontal suture diverging its entire length; legs usually not terminated by setose tubercles 2

2. Third abdominal tergum with a prominent, median setose gibbosity ("wart") (Fig. 11, arrow); prothoracic shields, if distinct, without prominent anterior angles 3

— Third abdominal tergum without gibbosity; anterior angles of prothoracic shields usually present 5

3. Scissorial area of left mandible with four distinct teeth; legs clearly three-segmented; labrum only very weakly trilobed distally .... *CANTHOCHILUM* Chapin
(Matthews, 1963.)

— Scissorial area of left mandible with three distinct teeth; legs two-segmented; labrum strongly trilobed distally 4

4. Gibbosity of 3rd abdominal tergum bearing two patches of setae; chaetopariae each of 2—4 setae; third antennal segment with distal conical sensory organ .... *ONTHOPHAGUS* Latreille
(Ritcher, 1966; Medvedev, 1952)

— Gibbosity of 3rd abdominal tergum bearing a single patch of setae; chaetopariae each with 9—10 setae; apex of third antennal segment with flat, oval sensory organ .... *LIATONGUS* Reitter
(Medvedev, 1952; description below)

5. Legs each with a darkly sclerotized, blunt terminal "claw" which bears two elongate, distal setae (Fig. 18); anus flanked below by four lobes (Fig. 17); venter of 10th abdominal segment practically bare, without distinct palidia, but rather few scattered, inconspicuous setae (Fig. 13); apex of 3rd atennomere with subconical sensory organ .... *COPRIS* Müller
(Ritcher, 1966; Medvedev, 1952; descriptions below)

— Legs without "claws"; subanal lobes variable but not like *Copris;* distinct palidia usually present on 10th sternum; antennal organ variable 6

6. Anterior angles of prothoracic shields absent; 10th abdominal sternum with two longitudinal, monostichous palidia *ATEUCHUS* Weber
(Ritcher, 1966)

— Prothoracic shields with distinct anterior angles; palidia, if conspicuous, not monostichous 7

7. Venter of 10th abdominal segment with three distinct polystichous palidia, *viz.*, a large, median, quadrate patch of setae flanked by smaller, irregular

patches (Fig. 12); apex or 3rd antennomere with flat, oval sensory organ .... *PHANAEUS* MacLeay and *COPROPHANAEUS* Ols. (Ritcher, 1966; Edmonds, 1967; descriptions below)

— Palidia, if distinct, not as described above; antennal sensory organ variable 8

8. Venter of 10th abdominal segment appearing bare, pair of very inconspicuous, oval palidia present; apex of 3rd antennomere with subconical sensory organ; uncus of lacinia without basal tooth; each chaetoparia of 10 setae or less .... *CANTHON* Hoffmansegg (Ritcher, 1966; description below)

— Palidia conspicuous, large; antennal organ variable; uncus of lacinia with basal tooth; each chaetoparia with 15 setae or more 9

9. Venter of 10th abdominal segment with two polystichous palidia separated by bare, median area; apex of 3rd antennomore with flat, oval sensory organ .... *DICHOTOMIUS* Hope (= *PINOTUS* Er.) (Ritcher, 1966)

— A single, large, polystichous palidium nearly covering 10th abdominal sternum; apex of 3rd antennomere with subconical sensory organ .... *DELTOCHILUM Scholtz* (Howden and Ritcher, 1952)

LIATONGUS Reiter

This is an Old World tropical genus with three relict species in North America [*californicus* Horn, *rhinocerulus* Bates and *monstrosus* (Bates)]. Although sometimes considered a synonym of *Oniticellus* Serville, this taxon is given genus rank by Janssens (1953), Balthasar (1963) and others. The larva of *L. festivus* (Steven) is described by Medvedev (1952); that of *monstrosus* is described below. Janssens (1953) considered these species problematic, both occupying at best isolated positions within the genus. In Balthasar's classification (1963), *festivus* comprises the subgenus *Paroniticellus* of *Oniticellus*. Unfortunately, the description of the larva of *festivus* is not directly comparable to that given below. However, Medvedev's description indicates two features of *festivus* strikingly different from their counterparts in *monstrosus*, *viz.* prominent anterior angles of the prothoracic shields (his figure 494) and a distal angulate process on the third antennal segment (his figure 493); other illustrated features seem similar to *monstrosus*, particularly the shape of the subanal lobes. According to Ritcher's key (1966, p. 14), *Oniticellus cinctus* F., like *festivus*, has angular prominences on the prothorax. In all likelihood, *monstrosus* will eventually comprise a distinct monotypic genus; its taxonomic isolation is strongly suggested by adult and larval morphology and behavior, all of which seem quite different from their counterparts in other *Liatongus*.

In view of the lack of directly comparable larval descriptions, a description of *Liatongus* is here limited to that of the following species.

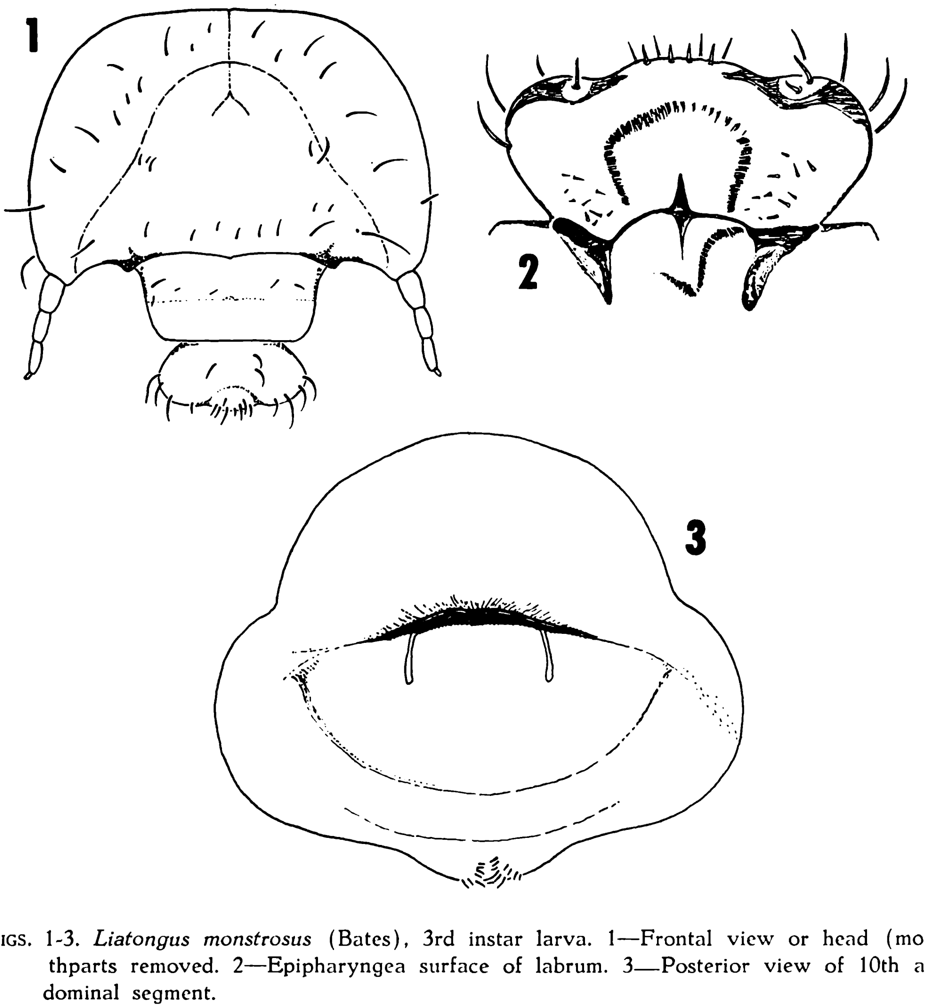
Liatongus monstrosus (Bates)

Material examined: 15 third instar larvae, 1 pupa (female) from nest debris of *Atta mexicana* F. Smith, Ajijic, Jalisco (P. Reyes and G. Halffter, coll.)

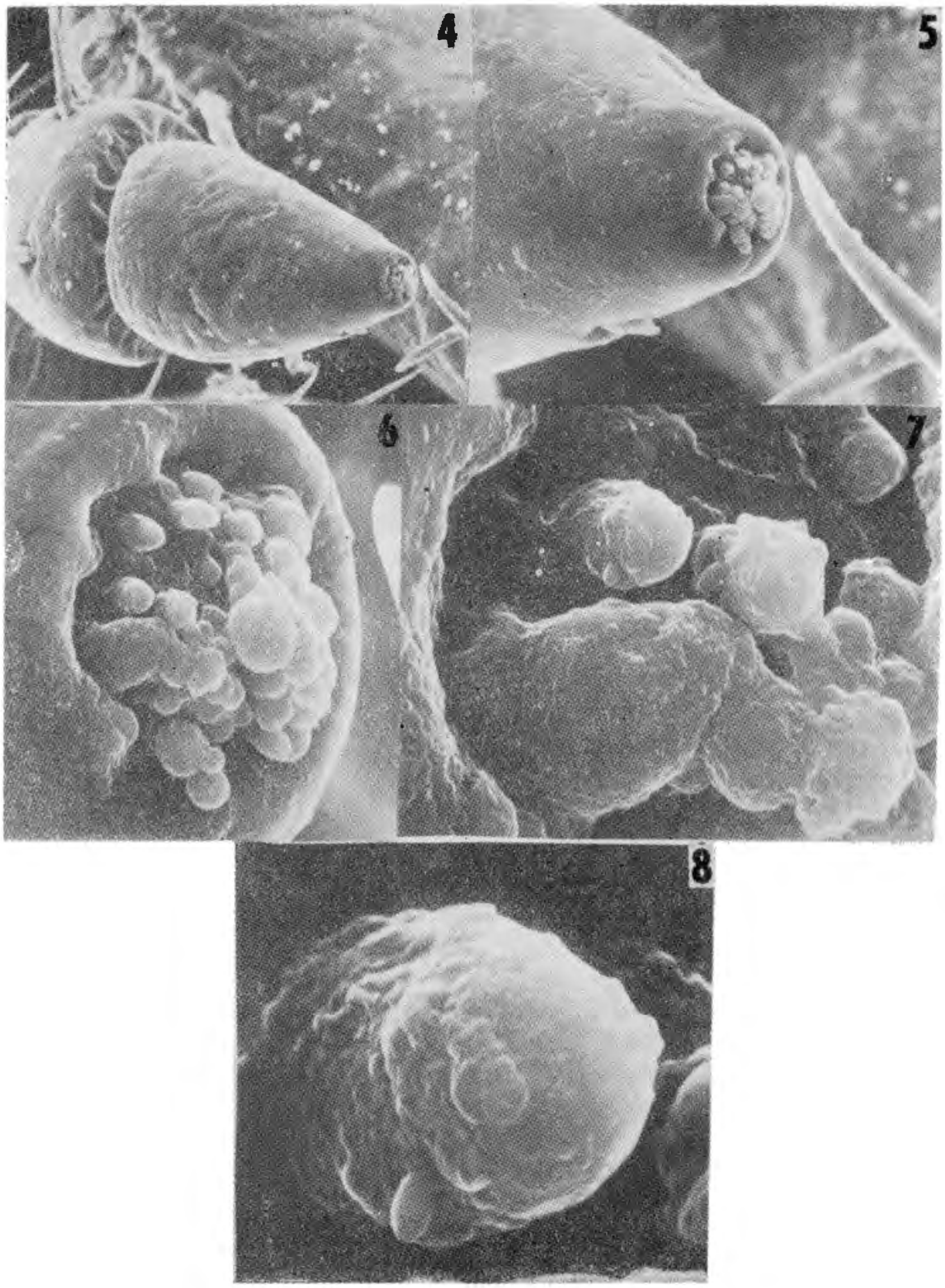
THIRD INSTAR LARVA

General: Body C-shaped, humped dorsally (Fig. 11). Total dorsal length 4.5—5.5 cm.

Head capsule (Gig. 1); Flattened anteriorly rounded laterally, average maximum width 5 mm; epicranial suture extending anteriorly beyond intersection



FIGS. 1-3. *Liatongus monstrosus* (Bates), 3rd instar larva. 1—Frontal view or head (mouthparts removed. 2—Epipharyngea surface of labrum. 3—Posterior view of 10th abdominal segment.



FIGS. 4.8. *Liatongus monstrosus* (Bates), 3rd instar larva. Serial scanning electron micrographs. 4—Apex of maxillary palpus (X150). 5—Apex of 4th palpomere (X450). 6—Tip of 4th palpomere (X1500). 7—Cluster of "sensory nodules" (X4500). 8—Single "sensory nodule" (X15000).

with frontal suture strongly forked; frontal sutures bowed inward. Cranial setae on each side as follows: dorsoepicranials and lateral epicranials together forming loose group of 6—7 setae; 2—3 small posterior frontals; anterior frontals arranged in loose row paralleling fronto-clypeal sulcus; 1 seta in anterior angle of frons; in addition, cranium surface covered with numerous, generally scattered erect setae. *Clypeus* dark basally, with median transverse row of 4—8 setae. *Labrum* symmetrical, trilobed, median lobe with 6 setae, each lateral lobe with 4—5, base with 2—3. Epipharyngeal surface of labrum (Fig. 2); chaetopariae each with 9—11 short, thick setae; pedium appears bare; phobae forming loop, polystichous except left side of anterior phoba; mesophoba estrongly bent, incomplete on right side; tormae united mesally; epitormae narrow, pternotormae wide; haptomerum with 2—3 sensory spots.

Head appendages: *Antennae* 4-segmented, apex of third segment with oval sensory spot, apical segment small with terminal sensory spot. *Mandibles*: left mandible tridentate, right bidentate; dorsomolar setae absent; scrobis of both mandibles reduced to single lateral seta; brustia of left mola with many setae, of right absent; tuft of ventromolar setae on both mandibles. *Maxillae*: Cardo tripartite, stipes with 5—8 very small stridulatory teeth in row; uncus of lacinia with small basal tooth on ental surface; uncus of galea simple; palpus 4-segmented, distal segment with apical sensory area (Figs. 4-8). *Labium*: two irregularly shaped oncyli; glossa buldging, bounded posteriorly by transverse row of setae; palpus 2-segmented, distal segment with apical sensory area.

Thorax: Prothoracic shields only very weakly indicated, without acute anterior angles; pronotum with two distinct transverse rows of long, erect setae. Mesospiracular plate conspicuous, reniform, only slightly larger than abdominal spiracular plates; metathoracic spiracle present above base of hind leg (Fig. 10, arrow), spiracular plate atrophied (?), represented only by small sclerotic spot adjacent spiracular opening. Legs each 2-segmented, with two slender terminal setae surrounded by circlet of 6—8 short, thick setae (terminal setae often closely appressed, appearing as one).

Abdomen: Third tergum with median hump ("wart"; Fig. 11, arrow) covered by field of closely spaced short, erect setae. Terga 4—9 each with transverse row of conspicuous erect setae anterior to which occur numerous, generally scattered shorter setae. Raster as in figure 9. Anal opening transverse, surrounded by prominent lobes (Fig. 3).

PUPA

The single female pupa examined possessed the following support projections not retained by the adult;

a) small, finger-like projection on middle of mesoscutellum;
b) finger-like projections on each side of terga 3—6;
c) ridges along posterior margins of abdominal terga connected by mid-longitudinal ridge extending length of abdomen.

FIGS. 9-13. 9—*Liatongus monstrosus* (Bates), 3rd instar larva, ventral view of 10th abdominal segment. 10—Same, lateral view of thorax (T_1 = prothorax; arrow indicates metathoracic spiracle). 11—Same, lateral view (arrow indicates gibbosity of 3rd abdominal tergum). 12—*Phanaeus daphnis* Har., 3rd instar larva, ventral view of 10th abdominal segment. 13—*Copris armatus* Har., 3rd instar larva, ventral view of 10th abdominal segment.

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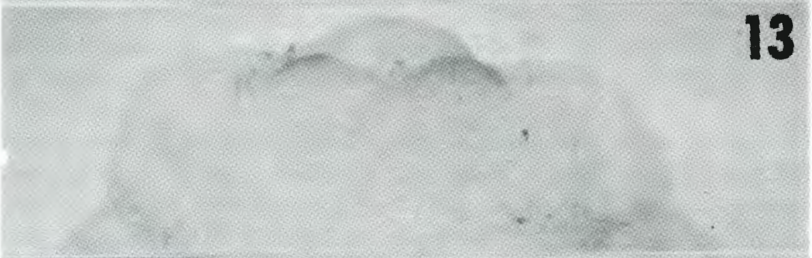

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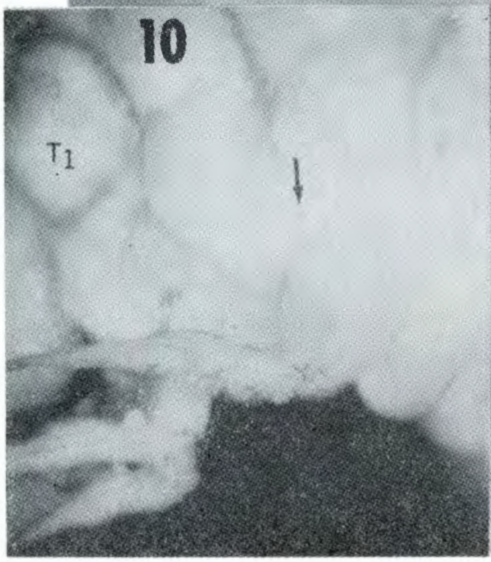

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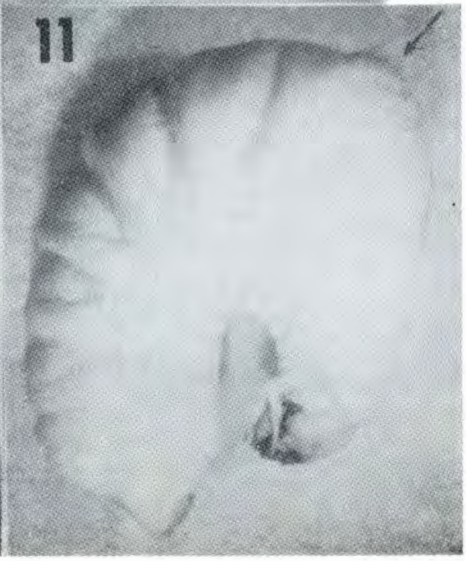
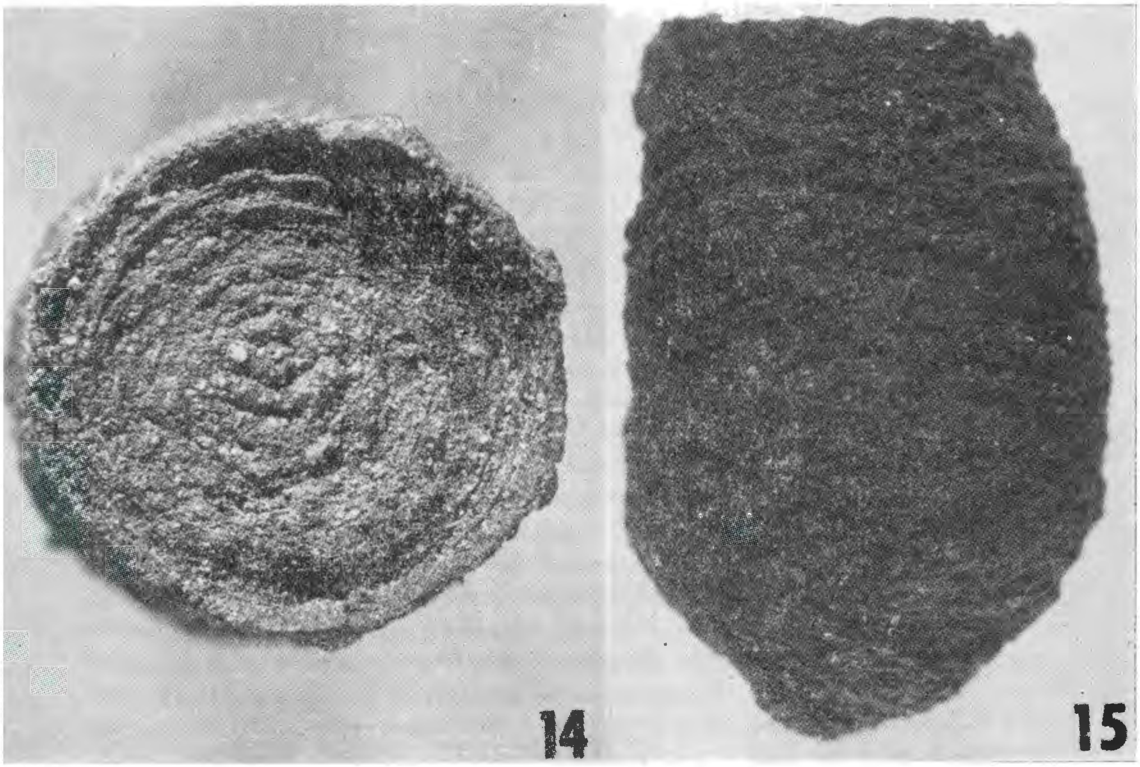


BIOLOGY

Bates (1887: 83, 391) cited this curious species from ant nests in Guadalajara. Only recently has *monstrosus* been "rediscovered" by Mexican workers (J. Hendrichs, G. Halffter and P. Reyes) who, in spite of ten year's careful examination of *Atta* nests in Mexico and Central America, have yet collected in only from the nest debris of *Atta mexicana* F. Smith in Ajijic, Jalisco. Ajijic a small town on the northwestern edge of Lago de Chapala, is situated between the lake and a series of low mountains. The location has disposed the town to a higher prevaling humidity and rainfall than more arid surrounding areas; consequently one notes in the flora of Ajijic decidedly more arboreal elements than is characteristic of the general region (see Rzedowski and Mc Vaugh, 1966: 35-40).

Although nest of *A. mexicana* are very abundant in Ajijic, *monstrosus* is by far most abundant in nests found in the small, but dense groves of fruit trees ("huertas") common to the area where dense shade and regular watering maintain high humidities. Although *A. mexicana* ranges widely in Mexico, nests situated in areas similar to Ajijic (e. g., Tizapan, on the southern shore of Cha-



FIGS. 14-15. *Liatongus monstrosus* (Bates), pupation cell. 14.—Dorsal view. 15.—Lateral view.

pala) have yet to yield *monstrosus*, which appears to be associated with the microclimatic peculiarities of Ajijic.

The debris deposits of *Atta* are mixtures of the consistency of wet sawdust containing primarily stems, bits of dry leaves and ant corpses. They build up around the perimeter of the nest complex, particularly in areas where some type of declivity permits easy expulsion of waste material to one side (next to a large rock, stone fence or hillock, in a dry ditch, etc.). The deposits can reach a depth of a meter or more and, inwardly, are progressively more humid, descomposed, compressed and warmer (as much as 9°C warmer than ground surface). The interior of the debris mass supports a rich fauna with many endemic species (see Halffter and Matthews, 1966: 51-56, Scarabaeinae; Reyes-Castillo, 1970: 190-196, Passalidae).

Halffter and Matthews (1966) have suggested that the larvae live freely in the debris o *Atta* nests. However, intensive field studies by Halffter and Reyes in Ajijic have produced the following data:

1) Numerous adults have been collected from June to September, characteristically wet months in central Mexico; they have not been found in drier months (February to May). Adults have been collected only from debris deposits from a depth of 5 cm and below, even though fresh or dry cow dung might be nearby.
2) In September two short tunnels (10 and 14 cm long) were found in the lower extremity of a debris mass. A pair of *monstrosus* occupied one while a single female occupied the other.
3) The anterior tibiae and upper head surface of adults collected in June show almost no signs of wear (as might be caused by digging); wear is quite distinct on specimens collected in September. Moreover, at both times tibial and cephalic wear is more marked in females than in males.
4) Careful examination of debris deposits in February produced no adults. However, in the interface between soil and debris many pupation capsules were collected, each a vertical, tubular structure with a rounded base and very flat, circular cap (length 25—31 mm, maximum width 18—24 mm) (Figs. 14-15). Externally the walls appear to consist of precise earthen rings; the cap consists of well defined, concentric rings with a definite center. The inner surfaces of the walls is covered by a fine, smooth layer of what appears to be larval excrement. Wall thickness varies from 3.5 mm at the bottom to 1—1.5 mm at the sides; the thickness of the cap is usually about 1 mm. The composition of the capsule, which is quite hard, appears to be a mixture of soil debris cemented together by larval excrement.
5) All capsules collected in February contained third instar (large) larvae. Many were carried to the laboratory and allowed to continue development within the capsule. Pupae appeared from mid-May until July; the first adult emerged near the end of May while others emerged as late as the beginning of August. Adults escape from the capsule by breaking through the circular cap; they seldom lived as long as a month in captivity.

The foregoing data, when compared to that known about the nidification behavior of other Scarabaeinae, suggests the following, as yet somewhat hypothetical description of the life cycle of *L. monstrosus*: As is common for central Mexican Scarabaeinae, adults appear at the beginning of the rainy season (May-June) and live until the onset of a drier season (September-October). Although present evidence suggests that they are confined to the debris deposits, it would not be suprising to later find that they do disperse (perhaps in response to very precise environmental cues). We can only guess that adults (and larvae) feed on the debris itself, which is undoubtedly quite rich organically. Although they live within the debris mass, tibial and cephalic wear indicates that the adults dig tunnels in unerlying soil for feeding and/or nidification. In a manner similar to other known Scarabaeinae (Group I of Halffter and Matthews, 1966), we assume that the female lays an egg in a debris-filled tunnel, within which the larva develops during drier seasons (October-May). It is possible that the early larval instars live freely within the debris mass (as do many cetonine larvae), but the probability seems rather remote. Probably sometime during the third stadium, the larva constructs a pupation cell, which takes the shape of the larval feeding gallery. Fabrication of a pupation chamber by the larva in Scarabaeinae is discussed below.

Although we have not directly observed it, larval construction of the pupation cell is strongly suggested by the following:

1) The succesively ringed structure of the walls and top of the pupation cell are easily pictured as the result of layer-wise deposition of fecal matter by the larva as described for *Onthophagus* by Goidanich and Malan, 1964 (see below "The Pupation Cells and Pupae of Scarabaeinae"); 2) The tubular form of the cell suggests its having been made using the blind end of a tunnel as a "mold"; moreover, the incorporation of particles of soil within the outer layer of the cell walls alludes contact with the soil (walls of a tunnel) during its construction.

COPRIS Müller

This is a cosmopolitan (except Australia) genus with most species occurring in the tropics of the Old World. Known larvae agree well with the generic features given below and seem to form a quite cohesive group. The description of the larva of *C. lunaris* (L.) by Medvedev (1952), while not directly comparable with those below nor with those of Ritcher (1966), nevertheless is unmistakeably quite similar to other known *Copris* larvae. Of particular note are the non-united tormae of *Copris armatus* (Fig. 19); although they are generally united in the Scarabaeinae (Ritcher, 1966: 13), they are also separated in *Scarabaeus* (Paulian, 1945: his figure 31A).

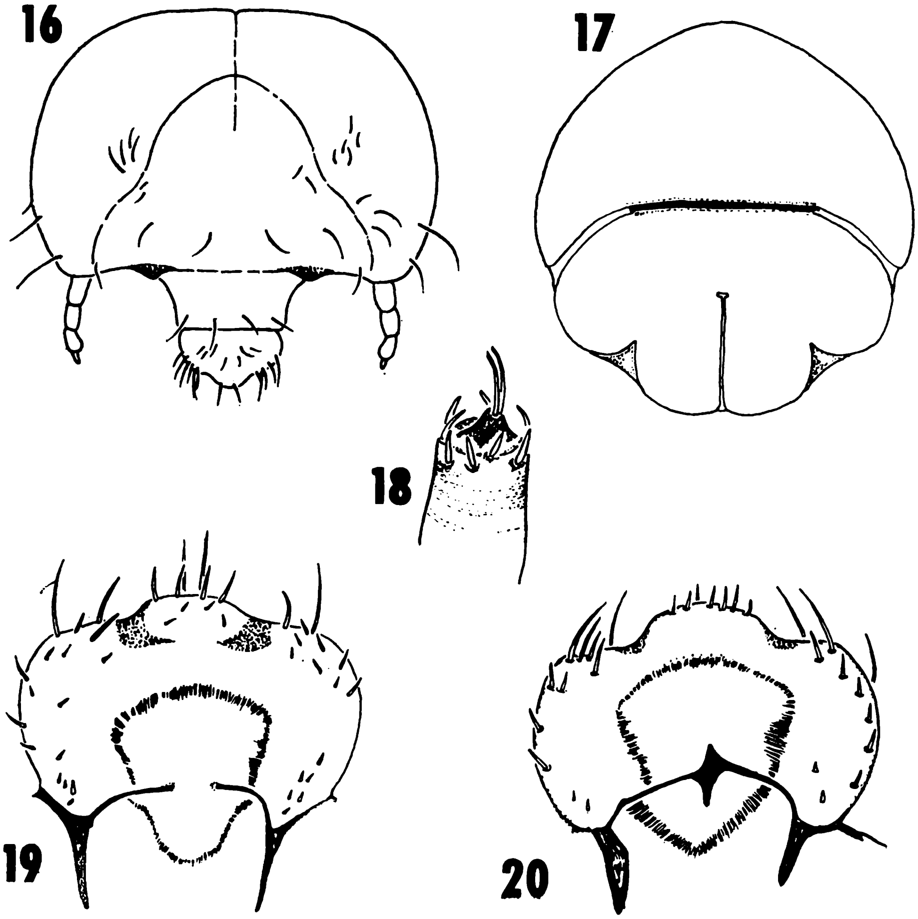
Description of copris based upon larvae: 1) surface of head capsule faintly reticulate laterally; 2) epicranial suture not distinctly forked distally; 3) chaetopariae each with less than 8 setae; 4) stipes with a row of less than 10 stridulatory teeth; 5) uncus of lacinia with a basal tooth; 6) apex of third antennomere with a conical sensory organ; 7) prothoracic shields with prominent anterior angles; 8) legs each with a terminal, darkly sclerotized tubercle ("claw"), itself bearing apically one or two long setae (Fig. 18); 9) venter of tenth abdominal segment lightly sclerotized, appearing practically bare, with but a few, generally scattered, inconspicuous setae (Fig. 13); 10) anal opening transverse, bounded below by four large fleshy lobes as in figure 17.

Copris armatus Har.

Material examined: 2 third instar larvae, 1 female pupa; Salazar, state of Mexico, G. Halffter, coll.

Third instar larva

General: Body C-shaped, humped dorsally; total dorsal length 3.9 and 4.8 cm.



Figs. 16-20. Larval structures of *Copris*. 16—*C. armatus* Har., frontal view of head (mouthparts removed). 17—Same, posterior view of 10th abdominal segment. 18—Same, tip of leg. 19—Same, epipharyngeal surface of labrum. 20—*C. lugubris* Boheman, epipharyngeal surface of labrum.

Head capsule (Fig. 16): Flattened anteriorly, rounded laterally; maximum width 4.7 and 5.0 mm; epicranial suture extending anteriorly beyond intersection with frontal suture, not conspicuously forked; frontal sutures bowed in ward; cranium faintly reticulate laterally. Cranial setae on each side as follows: dorsoepicranial apparently absent: lateral epicranials small, in cluster of 4—5; 2—3 posterior frontals; 4 large anterior frontals; 1 seta in each anterior angle of frons. *Clypeus* uniformly sclerotized, 4 large setae along ventral margin. *Labrum* symmetrical, trilobed; median lobe with 2 setae, each lateral lobe with 6, base with two clusters of 3—4 setae each. Epipharyngeal surface of labrum (Fig. 19); chaetopariae with 4—6 setae; pedium appears bare; phobae forming symmetrical loop; mesophoba polystichous, symmetrical; tormae *not* united mesally, epitormae consequently absent; pternotormae straight, slightly convergent: haptomerum with 3— sensory spots.

Head appendages: *Antennae* 4-segmented; third segment with conical sensory spot; apical segment small, with terminal sensory area. *Mandibles*: left tridentate, right bidentate; brustiae apparently absent or very inconspicuous; dorsomolar setae arranged in fimbria; tuft of ventromolar setae on each; single lateral molar seta. *Maxillae*: Cardo tripartite; each stipes with 6—8 stridulatory teeth; uncus of lacinia with large, rectangular, prominent basal tooth on ental surface; uncus of galea dentiform; palpus 4-segmented, distal segment small with apical sensory area. *Labium*: oncyli 2; glossa with posterior transverse row of recumbent setae; palpus 2-segmented, apical segment with distal sensory area.

Thorax: Prothoracic shields well sclerotized, each with prominent acute anterior angle. Mesothoracic spiracular plate larger than abdominal plates. Legs each 2-segmented, terminated by sclerotized conical process ("claw") bearing two slender setae; "claw" surrounded by circlet of 8 short, spine-like setae (Fig. 18).

Abdomen: Third tergum without "wart". Tergal setae inconspicuous terga 4—9 each with polystichous tranverse row of small setae paralleling posterior margin. Raster (Fig. 13) comprising inconspicuous setae; 10th sternum weakly sclerotized medially. Anal opening transverse, surrounded by prominent lobes (Fig. 17).

PUPA

The single female pupa examined possesses the following support projections.
a) very small tubercle on mesoscutellum;
b) slender, acute processes at sides of terga 3—6;
c) prominent ridges along posterior margins of abdominal terga 2—6 connected by a longitudinal ridge extending the length of the abdomen.

BIOLOGY

The initial nidification behavior of *C. armatus* is described by Halffter and Matthews (1966). Male and female together dig a tunnel at the end of which

Figs. 21-23. *Copris armatus* Har., brood ball. 21—Lateral view of exterior. 22—Saggital section; cavity occupied by early instar. 23—Same; cavity occupied by late instar (arrow indicates fibrous plug).

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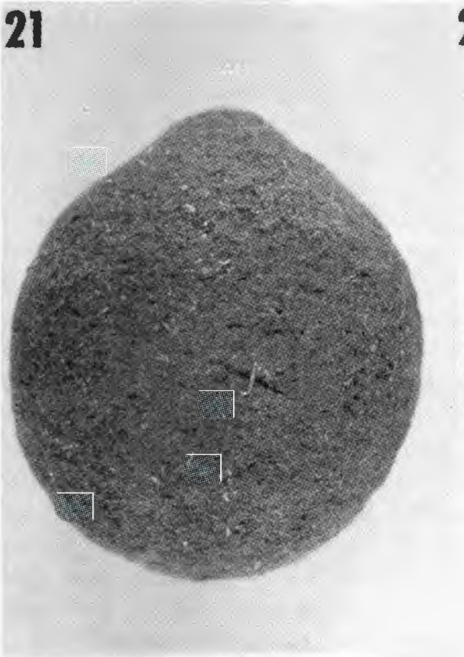

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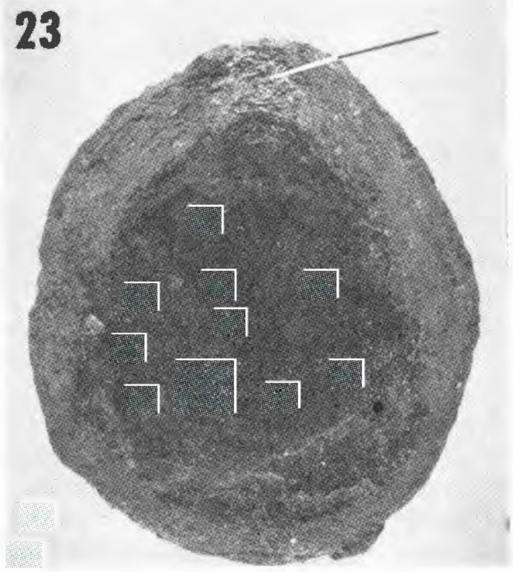

is excavated a fist-sized chamber. The chamber is packed with dung which is later compacted to form a dung mass ("cake") (Fig. 24). From the cake the female constructs pear-shaped brood balls, each one containing an egg (Fig. 25). Heretofore, the remainder of the cycle has been assumed to continue as in European *Copris* and in *Synapsis;* new data from field and laboratory studies support this assumption.

In January two nests were excavated from beneath dried cow dung in a pasture near Salazar (State of Mexico); a female remained in only one. The brood chamber of each was well preserved although galleries communicating with the surface had collapsed (or been filled in). One chamber contained four, the other five brood balls; each ball was pear shaped, with the narrower end up, and between 29 and 31 mm high and 26—27 mm wide (Figs. 21-23). The walls of the brood balls consisted of three layers with a combined thickness of 2—3.5 mm: a fine, very smooth outer layer of soil-dung mixture, a middle layer of compacted cow dung and a fine, inner layer of larval excrement. As in some other Scarabaeine brood balls, there is a dorsal plug constructed of fibrous elements contained in the dung; this plug evidently permits gas exchange. (As will be noted by comparing figures 22 and 23, the plug is much more conspicuous in the brood ball largely hollowed out by the developing larva [Fig. 23, arrow]. We do not yet know if the plug is constructed by the female [and perhaps later modified by the larva] or made by the larva itself.) Each brood ball contained a large, third instar larva.

In the laboratory brood balls kept without attendant female and those cared for by a female produced adults in mid-May. The female was frequently observed astride the brood balls, continually re-working them with the front legs and making slight changes in their position. These manuevers may inhibit fungal growth.

Copris lugubris Boheman

Material examined: One third instar larva and four pupae, progeny of adults collected by G. Halffter in Dos Amates (Catemaco), Veracruz (February).

THIRD INSTAR LARVA

Description of the larva is here limited to the following features which differ from their counterparts in *C. armatus* (see above): Total length, 2.6 cm; maximum width of head capsule, 2.5 mm; 2 or 3 lateral epicranial setae; loose cluster of 5 or 6 anterior frontal setae on each side; chaetopariae each with 2 setae (Fig. 20); tormae united medially, slightly asymetrical (Fig. 20); stipes with 4 or 5 stridulatory teeth.

PUPA

Support projections as described for *C. armatus* (see above).

FIGS. 24-25. *Copris armatus* Har. 24—Excavation of nest chamber containing female astride dung "cake" from which brood balls fabricated. 25—Dorsal view of brood ball cluster.


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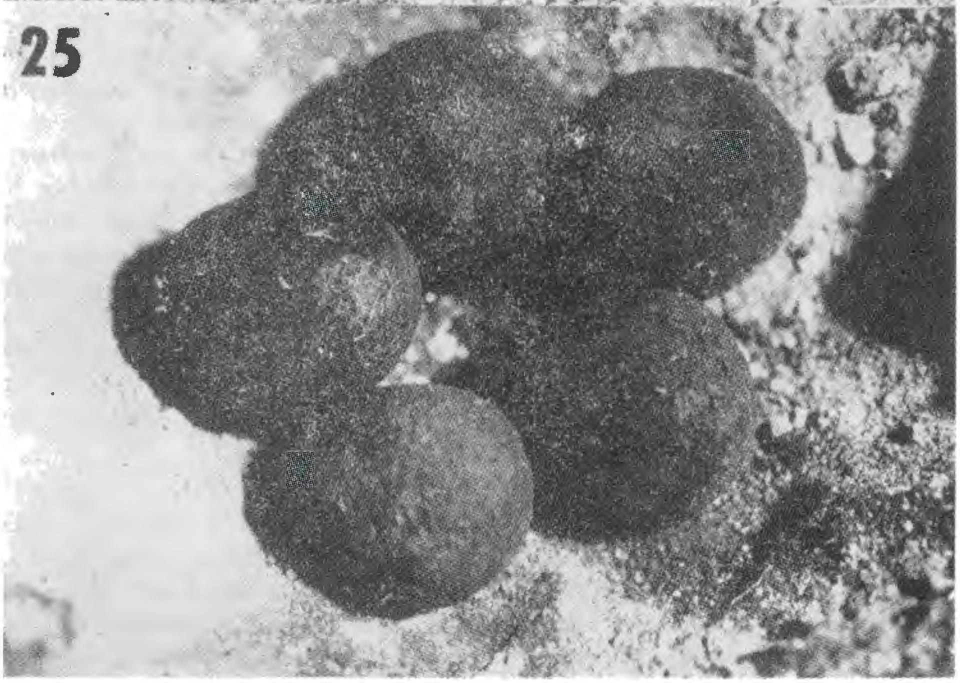
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Biology

A description of the nidification of *lugubris* is given by Halffter and Matthews (1966), to which we add the following observations. In February a pair of specimens from Catemaco (Veracruz) were placed in a terrarium and provided with cow dung. Excavation of the terrarium in May produced a single brood chamber containing the female and four brood balls; the male had died. The female left fresh cow dung untouched and probably did not leave the brood chamber to feed. A third instar larva was recovered from one ball on May 11; the other balls remained with the female. Two brood balls opened at the end of May contained pupae; an adult male emerged from the fourth on June 18. The brood balls were elliptical, averaging 31 mm high, 23 mm wide and capped with fibrous plugs; the walls were 4 to 5 mm thick and, like those of *armatus*, three-layered. To emerge, the adult cuts a circular opening in the top of the brood ball.

A second nest, containing two brood balls and a female, was opened in April; each ball contained a pupa. In both nests, the female remained with the brood until the emergence of adults.

DICHOTOMIUS Hope

We have examined the larva and pupa of *Dichotomius carolinus* (L.), the most widely distributed member of this large genus. The larva was described by Ritcher (1945, 1966), as *Pinotus*. We have examined the following material: four 3rd instar larvae, the progeny of adults collected in Tepoztlán, Morelos (June), and recovered from terraria in August, as well as two field collected larvae from the same locality collected in May, and three third instar larvae from Cuernavaca in September. Two pupae were collected in May in Tepoztlán. The larvae agree well with Ritcher's description based upon U. S. material, to which we add the following: mandibular scrobis of 3 setae; small metathoracic spiracle and degenerate spiracular plate above base of hind leg. The pupae, which has heretofore not been discussed, bears the following support projections: 1) a small, finger-like lobe in the middle of the posterior margin of the metanotum; 2) prominent, raised ridges along the posterior margin of abdominal terga 3—7; 3) prominent finger-like projections at each side of abdominal terga 3—6. There are no pronotal projections.

Biology

The nidification of *carolinus* is detailed by Halffter and Matthews (1966). The blind end of a tunnel is packed with a dung mass in which the female lays an egg; this brood mass is followed by another, from which it is separated by an earthern partition. The following data, from new field studies in Morelos and laboratory rearing, supplement Halffter and Matthew's discussion.

1) The female can make and provision the nest alone although she may be aided initially by a male.
2) Brood masses are always constructed in pairs; the first (deepest) mass is

bell shaped, the second more cylindrical. Both masses consist of carefully packed excrement from which large foreing objects have been removed. The earthen partition separating the masses is not disturbed during larval development and pupation. Brood masses measure 2.4—3.5 cm wide and 4.5—5 cm long and occur between 30 and 40 cm deep in soil with high clay content.

3) All development occurs within the brood mass, which, toward the end of larval development, takes on a pyriform shape. The fully developed larva occupies chamber enclosed by a 3—8 mm thick layer of dried dung; the inner surface of the chamber is plastered with larval excrement.

4) Within the remains of the chamber created in the original brood mass, pupae are found in more-or-less spherical cells, about 30 mm in diameter. These pupation cells are formed by concentric layers consisting of what appears to be a mixture of uneaten dung and larval feces and a thin, outer layer of soil; the 2—3 mm thick walls are very hard and plastered on the inside with a fine layer of larval excrement. As in *Liatongus monstrosus*, we assume that the pupation cell is fabricated by the larva.

The larval development and pupation cell of *D. carolinus* appears very similar to that described for *Chironitis* by Goidanich (1961).

PHANAEUS MacLeay

This genus is restricted to the New World, principally to the tropical regions of Mexico and South America. Known larvae closely resemble each other as well as those of *Coprophanaeus*, a related South American genus. Ritcher (1966) describes the larva of *P. vindex*; Edmonds (1967) has done so for two *Coprophanaeus*. The following description applies to both genera.

Description of Phanaeus (and Coprophanaeus) based upon larvae: 1) head capsule not distinctly reticulate laterally; 2) epicranial suture not obviously forked distally; 3) chaetopariae each with more than 10 setae; 4) stipes with a row of 5—15 stridulatory teeth: 5) uncus of lacinia with a basal tooth;[3] 6) apex of 3rd antennomere with flat, oval sensory organ; 7) prothoracic shields with prominent anterior angles; 8) legs without "claws", each with usually two terminal setae; 9) venter of 10th abdominal segment with three distinct polystichous palidia, *viz.* a large median, quadrate patch flanked on each side by a smaller, irregular patch; 10) subanal lobes variable; but usually as in figure 27.

Phanaeus daphnis Harold

Material examined: 37 3rd instar larvae, 3 pupae, progeny of adults collected in Tepoztlán, Morelos (June). G. Halffter, coll.

THIRD INSTAR LARVA

General: Total length along dorsal surface: 30—40 mm.

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[3] Edmonds (1967) erroneously states that *Coprophanaeus jasius* lacks this tooth.

Head capsule (Fig. 26); Maximum width 3.5—4 mm; epicranial suture extending beyond frontal suture, not distinctly forked distally; frontal suture bent medially on each side. Cranial setae on each side as follows: dorsal and lateral epicranials forming group of 4—5 setae, posterior frontals inconspicuous; anterior frontals in very loose row, 2 or 3 of which conspicuous; 1 seta in anterior angle of frons. *Clypeus* with 1 or 2 conspicuous exterior setae en each side. *Labrum* symmetrical, trilobed, 4—5 setae on each lateral lobe, 4—5 setae on margin of middle lobe. Epipharyngeal surface of labrum (as in Fig. 28): phobae forming more or less symmetrical loop, right phoba least distinct; chaetopariae each with 14 or 15 setae; mesophoba weakly developed; tormae united, epitormae reduced; 6 macrosensilla on haptomerum.

Head appendagess Antennae four-segmented, basal two segments very weakly (lightly) sclerotized; apex of third segment with flat, oval sensory organ. *Mandibles*: right bidentate, left tridentate; setation of both as follows: conspicuous row of dorsomolar setae; scrobis reduced to single lateral seta; ventromolar se-

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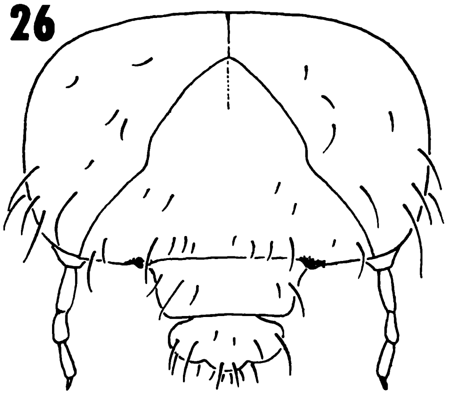

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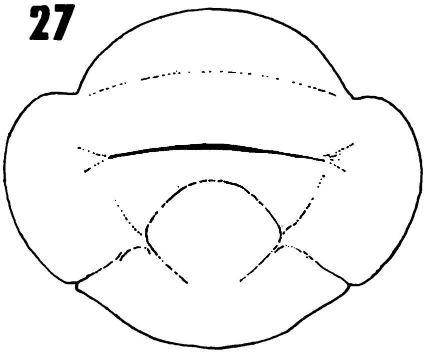

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FIGS. 26-28. Larval structure of *Phanaeus*. 26—*P. daphnis* Har., frontal view of head (mouthparts removed). 27—Same, posterior view of 10th abdominal segment. 28—*P. mexicanus* Har., epipharyngeal surface of labrum.

tal tuft present; brustia inconspicuous. *Maxillae*: stipes with 6—9 stridulatory teeth; uncus of lacinia with basal tooth; uncus of galea dentiform; palpus four-segmented, basal two segments weakly sclerotized. *Labium*: two irregularly shaped oncyli, right one much larger than left; glossae bounded posteriorly by transverse row of setae; palpus two-segmented, distal segment with apical sensory spot.

Thorax: Prothoracic shields weakly sclerotized, anterior angles distinct. Legs two segmented, each with two long, terminal setae surrounded by circle of shorter, stouter setae. Very small metathoracic spiracle above base of hind leg.

Abdomen: Third tergum without gibbosity; terga 3—9 with inconspicuous transverse rows of short setae. Venter of 10th segment as in figure 12. Anal lobes as in figure 27. Each tergal annulet of abdominal segments 1—3 with transverse usually monostichous, row of setac; terga 4—9 each with single, monostichous transverse row.

PUPA

The pupa, very similar to that of *Coprophanaeus jasius* (Oliv.) (Edmonds, 1967), bears the following support projections.

a) a pair of laterally inclined, elongate tubercles in the middle of the pronotum;
b) small papilla on the postero-median angle of the mesoscutellum;
c) a finger-like, recumbent lobe on the postero-median angle of the metascutellum;
d) each of terga 2—6 with a raisde, transverse ridge extending the width of the respective tergum;
e) a finger-like process at each side of terga 3—6.

Male and female pupae are virtually identical with respect to support projections in all except one respect; the pronotal processes (a) of the male were decidelly more elongate, extending beyond the cephalic process which rest upon the pronotum. These projections evidently preclude contact between the male cephalic process and the wall of the pupal chamber.

BIOLOGY

The biology of *daphnis* is discussed in detail by Halffter, López and Halffter (1973).

Phanaeus mexicanus Harold

Phanaeus palliatus Sturm

We have examine the following material collected by G. Halffter: *P. mexicanus*: one 2nd instar larva, Tenancingo, Mexico (27 March); three 3rd instar larvae and 2 pupae, Tepoztlán, Morelos (13 May); *P. palliatus*: three 2nd instar, two 3rd instar larvae, 2 pupae, progeny of adults collected 21, June, Ocoyoacac, Mexico (larvae recovered 23, November).

Although the larvae of these species differ in minor, inconsistent ways from that of *daphnis*, we have yet discovered no reliable way to distinguish them from each other or from *daphnis* even though the adults of the three species are quite distinct. Moreover, the pupal support projections of these species are as described for *daphnis.* The biology of *mexicanus* and *palliatus* is discussed by Halffter, López and Halffter (1973).

EURYSTERNUS Dalman

This genus is restricted to the New World tropics and, although usually placed near or within the tribe *Scarabaeini*[4] its affinities are still very obscure. We have examined material of two species, but since the genus is in dire need of revision, our identification of them here is somewhat tenuous.

Description of Eurysternus based upon larvae: 1) head capsule not distinctly reticulate laterally; 2) epicranial suture at most only very weakly forked distally; frontal suture almost omega-shaepd (Fig. 29); 3) chaetopariae each with less than 6 setae (Fig. 32); 4) stipes each with less than 8 stridulatory teeth; 4a.) ventral surface of galae each with two prominent, sclerotized tubercles, each bearing laterally a stout seta (Fig. 34, arrows); 5 uncus of lacinia without basal tooth; 6) third antennomore dilated distally, bearing a prominent conical sensory organ (Fig. 30); 7) pronotum with acute anterior angles, shields poorly sclerotized; 8) legs each two-segmented, each terminated by a small, sometimes darkly sclerotized, elongate tubercle bearing two distal setae (Fig. 33); 9) venter of tenth abdominal segment bearing an indistinct raster, consisting of at least a narrow transverse patch of very short setae; 10) anal lobes variable.

Eurysternus magnus (Lap.)

Material examined: one 3rd instar larva, progeny of adults collected at Montebello, Chiapas (G. Halffter, coll.)

THIRD INSTAR LARVA

General: Total length along dorsal surface: 30 mm.

Head capsule (Fig. 29: Maximum width 4 mm; epicranial suture extending beyond frontal suture, very weakly forked distally; frontal suture almost omega-shaped, on each side almost parallel in median portion of head. Cranial setae sparse: 3 dorsoepicranials on each side, a single prominent anterior frontal on each side; other setae lacking. *Labrum* symmetrical, trilobed distally, 4-5 setae on each lateral lobe, 6 setae on middle of median lobe. *Clypeus* with 3 exterior setae on each side. Epipharyngeal surface of labrum (Fig. 32): phobae somewhat asymetrical, right phoba least developed; two large macrosensilla on haptomerum; chaetopariae each with 3-5 setae; mesophoba V-shaped; tormae somewhat asymmetrical.

Head appendages: *Antennae* four-segmented; third segment dilated distally, bearing a prominent conical sensory organ (Fig. 30). *Mandibles*: left tridentate, right bidentate; setation of both as follows: scrobis reduced to a single la-

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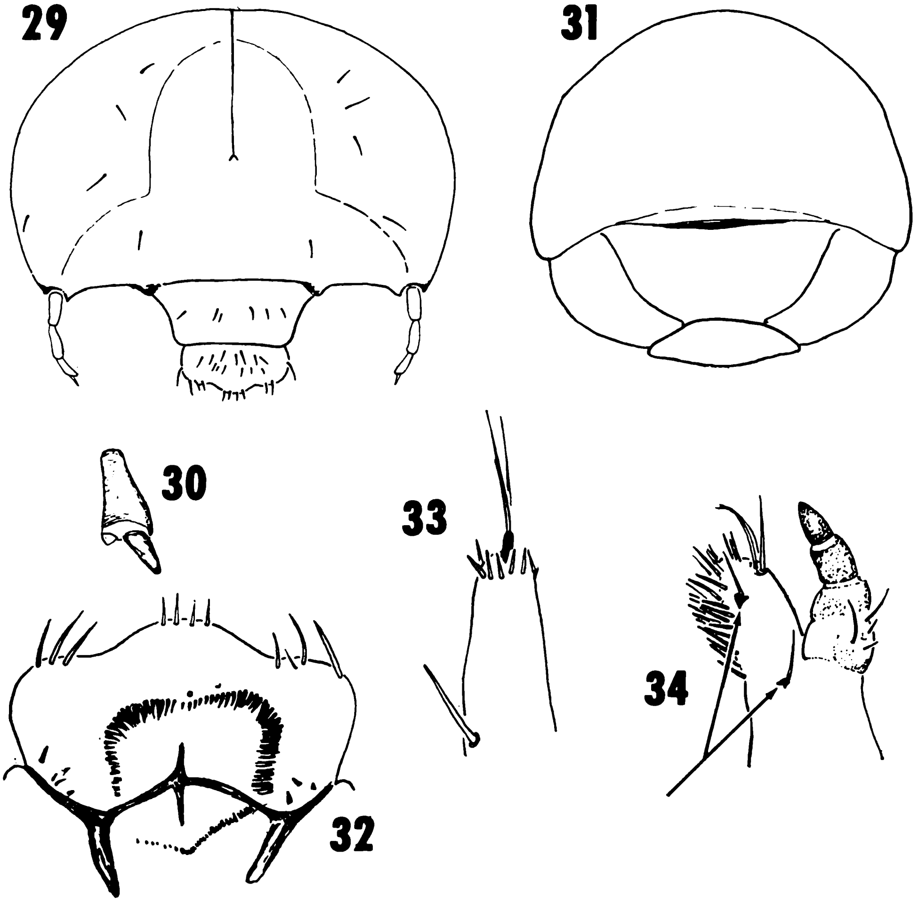
[4] Assigned to a separate tribe, Eurysternini, by Vulcano, Martinez and Pereira, 1960.

teral seta; ventromolar seta tuft present; brustia inconspicuous. *Maxillae*: stipes with 6 or 7 stridulatory teeth; uncus of lacinia without basal tooth; uncus of galea dentiform; ventral surface of galea with two, prominent sclerotized tubercles, each bearing a stout seta (Fig. 34 arrows); palpus four-segmented. *Labium*: glossa without prominent transverse row of stout setae anterior to oncyli; two irregularly shaped oncyli; palpus two segmented.

Thorax: Prothoracic shields weakly sclerotized, anterior angles distinct. Legs each two segmented, terminated by small tubercle bearing two long setae and surrounded by a crown of 7 or 8 short, stout setae (Fig. 33) (in the specimen examined, some legs bore nothing distally or a simple, sclerotized tubercle; these conditions probably due to wear). Methatoracic spiracle indicated, but not definitely observed.



FIGS. 29-34. *Eurysternus magnus* (Lap.), 3rd instar larva. 29—Frontal view of head (mouthparts removed). 30—Apical two antennomeres. 31—Posterior view of 10th abdominal segment. 32—Epipharyngeal surface of labrum. 33—Tip of leg. 34—Ventral view of apex of left maxilla (arrows indicate tubercles on galea).

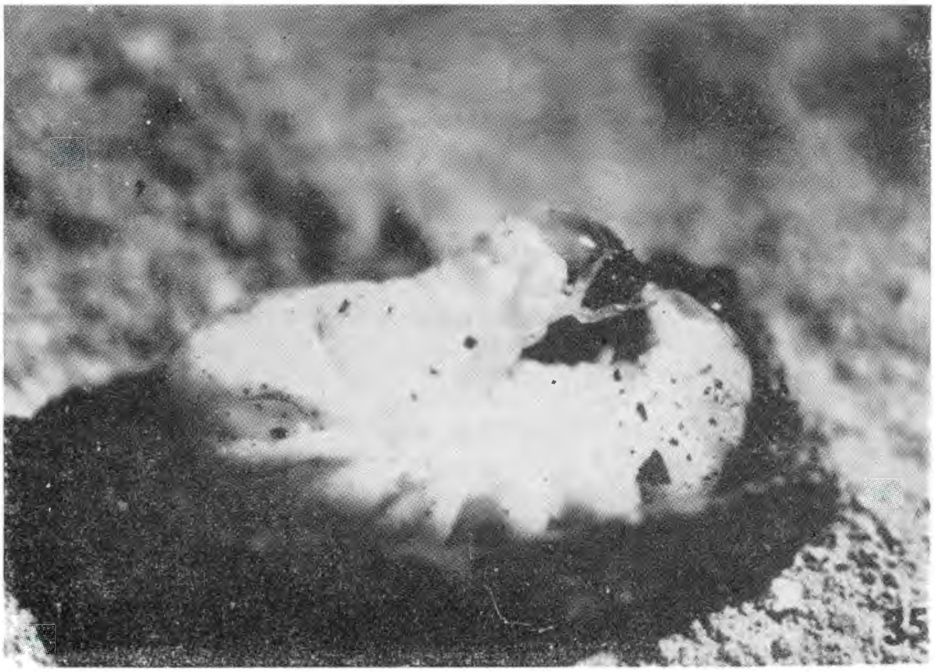


FIG. 35. *Liatongus monstrosus* (Bates), third instar larva in cutaway pupation cell. Note C-shaped body and consequent juxtaposition of head and anal near.

Abdomen: No dorsal gibbosity on dorsum of third segment; diameter of anterior segments abruptly larger than that of thorax (see comment below). Raster inconspicuous, consisting of a transverse palidium of short setae paralleling posterior margin of segment. Inconspicuous row setae along posterior margin of terga 6—9.

Comment: A peculiar feature of this specimen is the abrupt increase in diameter of the body between the torax and abdomen. In specimens of *E.* sp. *n.*, this change is gradual. The accentuation of the size of the first few abdominal segments is probably due to an accumulation of feces in the posterior portion of the gut, which is located in this part of the abdomen. A similar development change has been noted in *Chironitis irroatus* (Goidanich, 1961: 253) and in *Scarabaeus sacer* (Goidanich and Malan, 1964). We can only guess that a similar change in body shape occurs in the development of this species toward the end of the third stadium.

BIOLOGY

The biology of this and the following species is currently under study by Gonzalo Halffter and will be published a later date.

layer of hardened larval excrement. The structure containing this cavity is here called a pupation cell, the nature of which is determined by the nidification behavior of the group involved.

Taxa in which the adults construct brood balls (e. g., many Coprini and Scabaeini) have been referred to as behavior Scarabaeinae Gorups II, III and IV by Halffter and Matthews (1966). Groups II-IV nidification behaviors are considered by them evolutionarily advanced provisioning procedures. Developing larvae hollow out the foot supply (usually dung) provided by the parents as brood balls. The result of feeding by the larva is some type of hollow, thin-walled spheroid-now a pupation cell-within which pupation occurs. The composition of the walls of the cell varies but generally at least partially includes uneaten larval food provided by the adult. In the phanaeines (included in Group II) the brood ball consist of an inner spherical core of food capped by a thick outer layer of soil. In the Scarabaeini (Group IV) the brood balls and, later, pupation cells may also be covered by a thin outer layer of soil or soil-food mixture. Nevertheless, there are instances of brood balls without earthern caps which do not receive maternal care (e. g., *Canthon*). When maternal care is usual (Group III, as in *Copris;* see above), an outer earthen cap may be absent. The soil cap probably inhibits fungus formation near developing larvae or pupae; in *Copris* inhibition might be aided by the continual working of the brood balls by the female.

In those groups exhibiting such nidification behavior, the pupation cell is nothing more than hollowed out remains or modified remains of a brood ball constructed by the parente (s), the only larval contribution being an inner coating of excrement. The larval modifications of brood balls capped by an outer soil layer are less than those modifications caused larvae occupying "naked" brood balls since the outer cap lends ridgity to the pupation cell walls.

In groups considered more primitive behaviorally and included in Group I by Halffter and Matthews, adults do not construct brood balls. Provisions for the larva differ little from those destined for adult consumption, usually a sausage-shaped mass of food (usually dung) packed into the blind end of an underground gallery. In these groups a distinct, spheroid pupation cell is constructed by the larva itself, probably near the end to the third stadium. The occurrence and construction of the pupation cell in Group I Scarabaeinae merits analysis here since it was not stressed by Halffter and Matthews (p. 122 ff).

Larva constructed pupal cells have long been known (or suspected) in *Onthophagus.* (Ohaus, 1909; Sim, 1930; Ritcher, 1945; Howden and Cartwright, 1963; Halffter and Matthews, 1966). By far the most complete and lucid account of nidification and larval behavior of *Onthophagus* is that of Goidanich and Malan (1964), an excellent work which deserves summarization here. Working with six european species of *Onthophagus*, these authors describe what, for the moment, we believe can be considered typical Group I behavior. The female *Onthophagus* packs the blind end of a gallery or branched cluster of galleries or spherical chambers with dung usually brought in to her by the male. An egg is laid in a small spherical cavity in the exposed end of sausage-shaped dung mass, which is next covered by a layer of soil isolationing both the egg and adjacent dung. Upon hatching the larva soon begins feeding along the longitudinal axis of the dung mass, filling the cavity created by feeding with its own feces. In time, the dung originally provided by the female is largely replaced by larval feces. On reaching the bottom of the dung mass, the larva reverses its feeding direction and begins to consume its own feces. According to Goidanich and Malan, consumption of larval feces results in the digestion of cellulose-containing element not previously utilized; this more complete utilization of the original food supply is affected by an extensive intestinal flora population of bacteria and yeasts. Finally, the larva consumes all available food, leaving only the walls of the original dung mass as well as particulate soil matter accumulated during packing; this dung-soil mixture produces hard walls. The result is an elongate, tube containing a fully developed larva. At this stage the larval digestive tract (particularly the proctodeum) is swollen with fecal and partially digested matter which gives the body a decidedly more grossly humpbacked appearance than in preceding stages. This accumulation of dense fecal material is expulsed in large quantities which the larva works using the mouthparts, legs and body surface to build up a spherical chamber enclosing itself. The result is a pupation cell housed in the tubular remains of the original food supply. The inner surface of the pupation cell is very smooth; the outer surface remains rough. Oral manipulation of fecal material is facilitated by a doubling over of the body of scarabaeinae larvae (Figc. 11, 35) which brings together the head and anal area. The behavior of *Chironitis,* also studied in detail by Goidanich (1961), differs from *Onthophagus* in that, rather than constructing a complete spherical cell, the larva uses stored fecal matter to partition off a portion of the cavity enclosed by the remains of the original brood mass. The resulting pupation cell is oval with hard, uniformly thick walls.

So far the only reported accounts of the larval construction of pupation cells are those of Goidanich and his associates; their descriptions allow us to guess with reasonable expectation of certainly that the pupation cells of *Dichotomius carolinus* and *Liatongus monstrosus* are constructed as in *Onthophagus* and *Chironitis.* Our understanding of other groups currently thought to exhibit Group I behavior is not yet complete, but we suspect that larval construction of some type of pupation cell will later prove characteristic of this type of behavior. The tribe Oniticellini definitely does not exclusively include species of Group I.

Oniticellus cinctus (Fab.) (Gardner, 1929) and *Liatongus festivus* (Steven) (Medvedev, 1952) reportedly make brood balls. Gardner's observations on *cinctus* are confirmed by Bornemissza (1969), who states that the brood balls are fabricated in a chamber dug in the lower part of a dung heap (behavior that he terms "endocoprid type nidification"). Halffter has observed habits similar to *O. cinctus* in some *Eurysternus.* On the other hand, other Oniticellini are of Group I or strongly suspected of so being. The nidification of *Oniticellus fulvus* (Goeze) is, according to Fabre's description (1897), of the Group I type. The elaborate pupation cells of *Liatongus monstrosus* strongly suggest Group I behavior (see discussion above); we have, moreover, observed dung packed galleries made by *L. rhinocerulus* (Bates) which we suspect were destined for oviposition. As in Oniticellini, the subtribe Dichotomina (Coprini) includes Group I and II species.

Dichotomius carolinus constructs pupation cells very similar to those of *Chironitis* (see discussion above); *D. torulosus* makes brood balls. We can only guess for now that the larval behavior of other groups placed in Group I by Halffter and Matthews (*Ateuchus, Uroxys, Bubas, Onitis*) includes the construction of a pupation cell.

The morphological adaptation of the pupae of Scarabaeinae for development within spherical cavities has been pointed out (Halffter and Matthews, 1966: 184 ff); they have some combination of dorsal projections (ridges, tubercles, etc.) which minimize contac between the pupa and walls of the pupation cell. All pupae so far observed share the following projections: longitudinal and transverse ridging of the abdominal terga, finger-like projections at each side of at least three terga and at least one, usually small pterothoracic tubercle. Other thoracic projections are variable. Functionally, the support projections may reduce the danger of microbial growth, ensure good air circulation around the developing adult and/or prevent deformation of developing adult cuticle. These support projections are definitely *pupal* characters, saliences in addition to any developing adult armature; only occasionally are obvious support projections retained as adult armature; or, stated obversely, only occasionally do developing adult projections function in pupal support.

One explanation for the occurrence of "horns", etc. in the adult has been that these projections serve as pupal support projections which are retained by the adult. Although this explanation may partially account for the functional origin of adult armature, the case of the pupae of male *Phanaeus* suggests that it is certainly not universal. While some pronotal processes retained in adult male *Phanaeus* certainly contact the pupation cell walls, a special pair, which are lost in the adult, obviously prevents contact between the walls and the developing cephalic process ("horn"). On the other hand, the erect developing

RESUMEN

En este trabajo se describen la larva, la pupa y se incluyen comentarios sobre la biología de las siguientes especies, en su mayor parte mexicanas, de *Scarabaeinae* (Coleoptera-Scarabaeidae); *Liatongus monstrosus* (Bates), *Copris armatus* Har., *C. lugubris* Bohem., *Phanaeus dapnis* Har., *Ph. mexicanus* Har., *Ph. palliatus* Sturm. *Canthon huemctus humectus* (Say), *Eurysternus magnus* (Lap.) y *Eurysternus* sp. n. Asimismo se discute la biología de *Dichotomius carolinus* (L.) y *Glaphyrocanthon viridis leechi* Martínez, Halffter y Halffter.

Las descripciones de larvas y pupas aumentan, en aproximadamente un 50%, nuestro aun pobre conocimiento de los estados inmaduros de Scarabaeinae. Se ha prestado una atención especial a la presencia de espiráculos metatorácicos vestigiales, que son descritos por vez primera, a pesar de su existencia evidentemente común. Una sección especial trata de la celda de pupación y de las adaptaciones pupales de los Scarabaeinae. Se aclaran diferencias en el comportamiencephalic process of male *Copris lugubris* does contact the pupation cell wall. to que derivan de la preparación de masas de excremento para la nidificación o de bolas nido. La celda pupal es definida como una estructura (usualmente esferoidal u oval) que contiene una cavidad esférica en la cual ocurre la pupación. Se puede suponer que todos los Scarabaeinae completan su desarrollo en algún tipo de celda pupal, construida por la misma larva (en los taxa que pertenecen al grupo I de comportamiento en la nidificación, como es definido por Halffter y Matthews, 1966) o por los padres (Grupos II, III y IV). Las adaptaciones pupales para el desarrollo en una cavidad cerrada, esférica, incluyen proyecciones de soporte que reducen al mínimo el contacto con la paredes de la celda.

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