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Comparison of Mouthpart Morphology of Three Species of Mexican Oniticellini (Coleoptera: Scarabaeidae: Scarabaeinae) in Relation to Their Trophic Habits

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ABSTRACT

The purpose of this study is to describe the differences in the mouthparts of three Mexican species of Oniticellini that make use of different trophic resources. *Euoniticellus intermedius* (Reiche) is a coprophage *par excellence*, *Attavicinus monstrosus* (Bates) is a specialist in dry particles, and *Liatongus rhinocerulus* (Bates), a saprophage, is sometimes observed in excrement and on small cadavers, but mainly on rotting mushrooms. The results show no substantial structural differences among the species studied, though for each one, particular characteristics are evident.

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Keywords: scarab beetles, *Liatongus rhinocerulus*, *Euoniticellus intermedius*, *Attavicinus monstrosus*, epipharynx, mandibles, maxillae

The research described herein was designed to provide new information on possible variations in the mouthpart morphology of scarabaeinae beetles which are known to make use of trophic resources other than fresh mammal excrement. In this branch of research, some Onthophagini strictly associated with rodent droppings and bat guano have been analyzed (López-Guerrero and Zunino 2007), and there is research on the mouthparts of *Canthon virens* Mannerheim that exhibits marked specialization in terms of feeding and substrate choice for nidification, *i. e* .fertile female Attini ants on which it preys (López-Guerrero 2007).

The tribe Oniticellini (*sensu* Halffter and Edmonds 1982) is represented in Mexico by three species. *Liatongus rhinocerulus* (Bates) and *Attavicinus monstrosus* (Bates) (see Zunino [1982] and Philips and Bell [2008] for phyletic species and their generic attributes) are native in Mexico, whereas *Euoniticellus intermedius* (Reiche) is introduced (see Navarrete-Heredia 2001 and the bibliography therein). The two native species have trophic habits that are quite unusual. *Liatongus rhinocerulus* can be found in excrement and on small cadavers, but is more

commonly observed on rotting mushrooms (Pereira and Halffter 1961; Anduaga *et al.* ,1976; Anduaga 1990; Anduaga and Halffter 1991, 1993)and *A .monstrosus* is associated with the accumulation of detritus in the nests of leaf-cutting ants (*Atta mexicana* Smith) and is restricted to that microhabitat (Halffter and Matthews 1966; Halffter and Edmonds 1982; Halffter and Halffter 2009). *Euoniticellus intermedius* is a strictly coprophagous species.

The genus *Liatongus* Reitter, in which—not without controversy—*L. rhinocerulus* and a closely related species from California and Oregon, *Liatongus californicus* (Horn), are placed, is widely distributed throughout the Old World Tropics. To our knowledge, its feeding habits are characteristic of its group, coprophages. Both in the field and the laboratory, *L. rhinocerulus* adults feed on decomposing mushrooms as well as on carrion and cow dung. Trophic preferences vary with time of year and availability of food source (Anduaga *et al* .1976; Halffter and Edmonds 1982; Anduaga and Halffter 1993; Anduaga 2000).

Euoniticellus intermedius belongs to a genus that is essentially found in the Old World tropics, with three species, *Euoniticellus fulvus* (Goeze), *Euoniticellus pallipes* (F.), and *Euoniticellus pollens* (Olivier), identified in the Palearctic region and one, *Euoniticellus cubiensis* (Castelnau), that is endemic to Cuba (Simonis 1984; Zunino 2005). *Euoniticellus intermedius* primarily feeds on the excrement of large mammals, especially that of cattle (Halffter and Matthews 1966; Cambefort 1982; Halffter and Edmonds 1982). It was introduced into the United States in the 1970s to reduce the accumulation of cattle dung (Montes de Oca and Halffter 1998).

In terms of taxonomic position, *A. monstrosus* is isolated, although it has certain affinities with the tropical fauna of the Old World. Philips and Bell (2008) maintain that *A. monstrosus* (previously known as *Liatongus monstrosus*) has a completely independent lineage from the species that are considered part of the genus *Liatongus* .According to Zunino (1982) and (Philips and Bell 2008), it has phyletic links to another monotypic genus, *Paroniticellus* Balthasar with the species *Paroniticellus festivus* (Steven), from the southern part of the former Soviet Union and Anatolia. Both in the field and the laboratory, adult *A. monstrosus* consume only the debris produced by the leaf-cutting ant *A. mexicana* (Anduaga *et al* .1976; Halffter and Edmonds 1982; Navarrete-Heredia 2001).

It is noteworthy that in the adults of all three species, the mouthparts and intestines are highly evolved, as are their trophic habits. They are capable of retaining only the most nutritious part of food (Halffter and Edmonds 1982 and literature mentioned therein). The purpose of this study was to compare the epipharynges, mandibles, and maxillae of *L. rhinocerulus*, *E. intermedius* ,and *A. monstrosus* to detect possible variations in the general pattern of Scarabaeinae mouthparts, as they may relate to preferential feeding on different types of food: rotting mushrooms, carrion, excrement, and the detritus found in leaf-cutting ant nests.

MATERIAL AND METHODS

The study was carried out using dried samples collected from localities indicated here for each species. *Liatongus rhinocerulus* :Mexico, Durango, Reserva de la Biosfera “La Michilía”, 4 July to 4 September 1986, pine-oak forest, 2,450 m, R. Terrón collector, NTP-80 (2 males and 3 females); Mexico, Durango, Piedra Herrada, Reserva de la Biosfera “La Michilía”, 12 August 1992, in decomposing fungi, S. Anduaga collector (5 males and 4 females). *Attavicinus monstrosus* :Mexico, Jalisco, Ajijic, 26 July 1977, in *A .mexicana* nest, H. Carrasco and R. Halffter collectors (2 females); Mexico, Jalisco, Tequila, Volcán de Tequila, 24 June 1995, 1,800 m, in *A. mexicana* detritus, J. L. Navarrete-Heredia collector (1 female); Mexico, Jalisco, Tonalá, 12 July 2001, in *A .mexicana* detritus, J. L. Navarrete-Heredia collector (1 male). *Euoniticellus intermedius* :Mexico, Durango, Reserva de “Mapimí” El Daguillo, Mat. Desert, 25 August 1992, in cow dung, Montes de Oca collector (7 females and 4 males). Specimens came from the collections of Enrique Montes de Oca, J. L. Navarrete-Heredia, the author, and the Instituto de Ecologia, Xalapa, Mexico.

Specimens were softened in distilled water for 40 min, after which they were boiled for 15 min. Mouthparts were removed intact, treated with 5% potassium hydroxide for 8–10 min, rinsed with distilled water, and passed through a series of graduated alcohol concentrations to dehydrate them. Epipharynx width and length were measured using an ocular micrometer. For scanning microscope photographs, the pieces were passed through acetone and carbonic gas before being metalized with gold. Microphotographs were taken using a Jeol JMS-5600 LV scanning electron microscope.

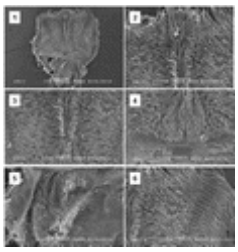
RESULTS

Liatongus rhinocerulus

Epipharynx (Figs. 1–7). As in all Scarabaeinae, the epipharynx of *L. rhinocerulus* (Fig. 1) is a complex, membranous structure that is horizontally positioned and forms the dorsal wall of the preoral cavity chamber, located directly under the clypeus. It is roughly square in shape (1.52 mm long × 1.50 mm wide). The anterior edge of the epipharynx (acroparia) has two sinuosities that make the apex of the central rod stand out (Fig. 2). The acroparia is covered with long, thin, abundant setae that have tiny lateral spines and an apex that bends slightly forward (Fig. 2). The sides of the epipharynx are subrectilinear near the front and moderately curved up to the transverse suture; in the posterior section, they are curved. Bilateral symmetry is marked, with the entire length of lateral margins convergent. The transverse suture is rectilinear and well defined when viewed dorsally. On the medial line of the central region, there is a claviform rod (Halffter 1952), labrum (Edmonds 1972), or medial process (Medina *et al* .2003). Its structure is

elongate, sclerotized, and well developed; it crosses the epipharynx. The apical portion has numerous smooth setae that are thick, of average size, and cone-shaped at the apex (corypha-zygum) where they come together (Dellacasa 1983) (Fig. 2); these setae are also distributed all along the medial process in the form of a jagged row, without reaching the distal limit of the nesium (Fig. 3). Each seta has a small fovea at its base, and thick setae are interspersed with those on the surface of the epipharynx (Figs. 3, 4). In its posterior section, the medial process ends in a triangular structure (nesium) that is short and slightly wide. The entire internal surface of the nesium is smooth, without setae, and has the peculiarity that on either side of its base, there is an ample area consisting of four or five rows of structures that are approximately rectangular with rounded tips, abundant, wide, and of two sizes, short and medium (Fig. 4). On either side of the base of the triangular structure is the phlegmatic area, a roughly circular, small cavity that lies in the most sclerotized transverse zone. Under each area, the central and two lateral (tormae) sections of the triangular structure appear; they are also triangular and covered with abundant pilosity (Fig. 5).

Covering the epipharynx are setae arranged as described herein. On the lateral parts, there is a well defined comb of setae approximately halfway across the width of the epipharynx. Where the comb begins, setae are large and of medium thickness. Setae become smaller nearer the base of the epipharynx, with their tips pointed toward the central region (Fig. 6) and tiny, lateral, non-continuous small spines along their entire long. The parts found between the medial process and the comb of larger setae are completely covered with thin, abundant setae. There are also thicker, medium-sized setae that appear in a line, interspersed with thinner setae. As is characteristic of this group, the part closest to the wall has thin setae and those on its floor are very tiny, triangular, and abundant (Fig. 6).



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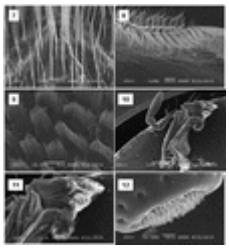
Figs. 1–6. Epipharynx of *Liatongus rhinocerulus*. **1)** Dorsal view; **2)** Detail of the anterior area of the medial process and the distribution of setae on its surface; **3)** Distribution of setae on the medial process (arrow) near the distal end; **4)** Posterior area of the medial process; note the structures on either side of the base of the nesium and the lack of setae on the nesium (arrow); **5)** Lateral tormae of the epipharynx; **6)** Detail of the distribution and different types of setae (arrow).

The entire posterior cephalic part of the epipharynx is covered with a dense layer of thin, long, spiny setae; interspersed among them are small, also abundant, triangular setae with acute tips. This combination of two types of setae continues along approximately half of the area's length (Fig. 7).

Mandibles (Figs. 8, 9): The mandibles, characteristic of Scarabaeidae in general, have highly developed, sclerotized molar surfaces and membranous incisors. Each mandible consists of a basal section that supports the joint, a distal incisor lobe, and an internal molar lobe. Viewed laterally, the basal area appears as a sharp triangle with a projection and ventral condyle; the latter articulates with the corresponding head structures. The incisor lobe is a thin lamina that juts out horizontally; the part closest to the wall has a band featuring abundant setae and at its apical tip is an area densely covered with long, thin setae (sensillae) with curved apices (Fig. 8). Underneath this part is a layer of short setae arranged in small clumps (Fig. 9). The molar lobe is solid and projects out toward the central part of the mandible on a vertical plane and has a smooth area in the middle, which lies opposite the other mandible. The space separating the molar and incisor lobes is an area characterized by corrugated folds that form thick areas of rigid support as well as flexible regions. The basal area of the mandibles is asymmetrical—convex to the right and concave to the left—except at its middle part.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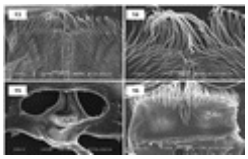
Figs. 7–12. *Liatongus rhinocerulus*. **7)** Detail of two types of setae on their posterior end of the epipharynx; **8)** Distribution of setae on the incisor lobe of the mandible; **9)** Detail of setae on the basal incisor lobe of the mandible; **10)** Maxilla; **11)** Detail of setae on the galea and lacinia; note the scaly structures on the stipital sclerites (arrow); **12)** Apex of the fourth segment of the maxillary palp.

Maxillae (Figs. 10–12): The maxillae are heavily sclerotized appendages that articulate with a plane parallel to the mandibles. The entire piece is covered with spiniferous setae that are long and sturdy, arranged in a radial formation. Each maxilla (Fig. 10) is formed basally by the triangular cardo, which has two articulate projections and attaches to the cephalic capsule. The distal area, which makes up the largest part of the maxilla, is roughly rectangular and formed by four sclerites situated on the cardo; the second, third, and fourth sclerite permit the insertion of different structures. On the lateral part of the second sclerite is a lobe, the lacinia, with a row of abundant setae on its ridge. The third sclerite has a cephalic lobe, the highly developed galea,

which is similar to a cushion and has a layer of abundant setae. The third and fourth sclerites feature a series of structures similar to scales that are abundant and pointing forward (Fig. 11). The maxillary palp articulates with the fourth sclerite. The palp is formed by four segments, the fourth of which is approximately the same size as the other three together. The fourth palpal segment is made up of corrugated folds that are similar to scaly plates; between them are pores with short, thick setae (Fig. 12).

Euoniticellus intermedius

Epipharynx (Figs. 13–16). The epipharynx (Fig. 13) is almost square (1.42 mm long x 1.40 mm wide), with marked bilateral symmetry and rounded lateral margins. The transverse suture is rectilinear and well defined on its posterior face. The anterior edge of the epipharynx is almost straight, with only two small clefts that come together centrally; the medial process does not jut out from this apical border. The cephalic region of the epipharynx (acroparia) is covered with long, thin, sparse setae with apices facing forward. The medial process appears as an elongated structure that is thin and sclerotized, with a smooth surface; its posterior part ends in the nesium, which is small, semi-circular, and features ovoid structures (Fig. 14). The nesium has a small cavity on each side (Fig. 15) that is roughly ovate-circular, resting on a transverse, sclerotized thickening from which the triangular structures arise, two lateral and one central (tormae), covered with abundant pilosity. The phlegmatic area is comprised of these two ovate-circular cavities.



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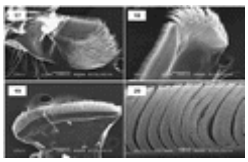
Figs. 13–16. Epipharynx of *Euoniticellus intermedius*. **13)** Dorsal view; **14)** Detail of setae on the proximal end (arrow); **15)** Detail of the phlegmatic area; **16)** Distribution of setae on the dorsal side; note the long setae become sparser and start to form a line as they near the medial suture.

There is a well defined comb of setae on each side of the epipharynx, located approximately on the medial part; the setae decrease in size apically (Fig. 13). Similar setae appear on the part nearest the lateral edge, without well defined rows.

Posteriorly, the epipharynx is completely covered with long, thin, abundant setae with small spines; they become less abundant near the middle, where they form a row and continue to be sparse (4–5) (Fig. 16). Among them, tiny setae are interspersed; these setae are triangular with pointy tips and extend to the lateral margins and continue to the transverse suture (Fig. 16).



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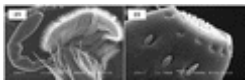
Figs. 17–20. *Euoniticellus intermedius*. **17)** Mandible; **18)** Detail of the tip of the incisor lobe of the mandible; note the type of setae covering the basal surface; **19)** Molar lobe of the mandible; **20)** Detail of fine transverse ridges of the molar lobe.

Mandibles (Figs. 17–20): In general, mandibular morphology is similar to that described for *L. rhinocerulus* ,although in *E. intermedius* ,development is more longitudinal. The incisor lobe (Fig. 17) is highly developed, with two main types of setae: some thin, medium-sized, feathery, and abundant; and others sharing these characteristics but smaller, occupying the basal part of the lobe (Fig. 18). The molar lobe has a peculiar structure consisting of fine, transverse ribs that serve to grind up food (Figs. 19, 20). (For further details on the mandibles, see Hata and Edmonds [1983]).



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Figs. 21–22. *Euoniticellus intermedius*. **21)** Maxilla; note the two types of setae and the development of the galea; **22)** Apex of the fourth segment of the maxillary palp.

Maxillae (Figs. 21–22): The maxillary structure (Fig. 21) is also similar to that of *L. rhinocerulus* ,although the basal surface of the first and second sclerites features a series of structures similar to scales, abundant and dense, which point forward. The galea is well developed and has two types of setae, both quite abundant: long, thin apical setae; and short, thick, bluntly tipped setae at the base of the cushion (Fig. 21). The lacinia has no observable differences from that of *L. rhinocerulus* .As in *L. rhinocerulus* ,the fourth segment of the maxillary lobe ends in a crown of short, thick setae (Fig. 22). Before reaching this crown, the tip of the fourth segment features a row of small setae (~16); slightly further down, there is another row of larger setae (~8) (Fig. 22). The surface of the fourth segment has short, thick setae that are very sparse.

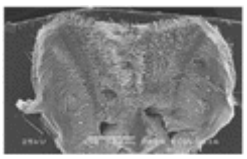

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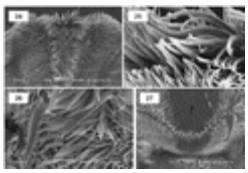
Fig. 23. Epipharynx of *Attavicinus monstrosus* ,dorsal view.



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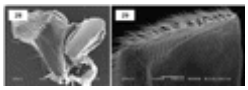
Figs. 24–27. Epipharynx of *Attavicinus monstrosus*. **24)** Setae on the cephalic part of the medial process; **25)** Large, thick setae covering the posterior part, with abundant spines and much thinner setae on the acroparia; **26)** Thick and medium-sized setae interspersed near the nesium; **27)** Detail of ovoid setae on the base of the nesium base; note that the nesium is completely smooth (arrow).

Attavicinus monstrosus

Epipharynx (Figs. 23–27): As in the two previously described species, the epipharynx of *A. monstrosus* (Fig. 23) is roughly square, a little wider than long (2.5 mm long × 2.6 mm wide), with marked bilateral symmetry. The lateral margins are quite pronounced, rounded, and begin to converge near mid-length. The transverse suture is rectilinear and runs across the entire width of the epipharynx. The anterior edge of the epipharynx has two sharp clefts that come together in the middle (acroparia) and is covered with long, thin, apically pointed setae, which are interspersed with setae from the posterior part (Fig. 24). These setae are medium-sized and thicker but densely covered with spines (Figs. 24, 25). The apex of the medial process projects beyond the edge of the epipharynx and has a large clump of thick, medium-length setae, which are interspersed with setae that cover the entire surface of the epipharynx and continue to the tip of the nesium, becoming less dense on either side of it (Figs. 24, 26). The central rod and base narrow near its middle section, becoming somewhat sinewy before reaching the nesium. The large size of the nesium is noteworthy; it is triangular, with a completely smooth surface (Fig. 27). Its basal margin has two rows of ovoid structures that are short and thick, projecting slightly from the base of the nesium base (Fig. 27). The phlegmatic areas are large and roughly ovoid. The other pubescent areas of the epipharynx are similar to those of the two previously described species.



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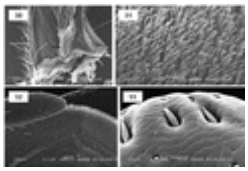
Figs. 28–29. *Attavicinus monstrosus* .**28)** Mandible; **29)** Incisor lobe of the mandible.



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Figs. 30–33. *Attavicinus monstrosus*. **30)** Maxilla; note the cluster of setae at the base of the first and second sclerite (arrow); **31)** Galea with one of the two types of setae present; **32)** Small setae on the galea; **33)** Apex of the fourth segment of the maxillary palp.

Mandibles (Figs. 28–29): Mandibular structure is similar to that of *L. rhinocerulus* and *E. intermedius* .The incisor lobe is well developed.

Maxillae (Figs. 30–33): Although similar to those of the two previously described species, in *A. monstrosus* the maxillae have a clump of setae at the base of the first and second sclerites (Fig. 30); these setae are barely visible in *L. rhinocerulus* and *E. intermedius* .The galea is quite large and well developed with two types of setae, one thin and long with the apex bent forward (Fig. 31) and the other small, triangular, and with sharp tips (Fig. 32). The fourth segment of the maxillary palp has corrugated folds along its entire surface; similar to scales, they feature small, sparse setae distributed across the surface. As is the case for *L. rhinocerulus* and *E. intermedius* ,the tip of the fourth segment has a crown of short, thick, abundant setae. On the basal section of this crown, there is a row of small, short (~8 µm) setae and slightly below it another row of large setae (Fig. 33).

DISCUSSION

From my observations, it can be concluded that the mouthparts of *E. intermedius* (coprophage *par excellence*), *L. rhinocerulus* (with its varied eating habits: decomposing mushrooms, carrion, and excrement), and *A. monstrosus* (very specialized, feeding only on ant detritus) do not exhibit major morphological differences from dung roller beetles in general. However, peculiarities are noted for each species.

The epipharynx of *L. rhinocerulus* has setae on the corypha and zygum (at the apex of the medial process lies a patch of thick, medium-sized setae) that do not reach the nesium (Figs. 3, 4), where they end as thin, abundant setae; these setae are quite long with forward-facing tips. Interspersed among these setae are other setae that are thick and long (Fig. 2). The setae that predominate on the entire surface of the epipharynx are medium-sized. On each side of the nesium is an area covered with thick, short setae that do not go beyond it, and others a little larger but also thick (Fig. 4) that differ somewhat from those of *E. intermedius* (Fig. 13) and *A. monstrosus* (Fig. 27). The epipharynx of *E. intermedius* lacks this patch of large, thick setae on the medial process (Fig. 14). The setae that cover the entire surface of the epipharynx of *E .intermedius* are sparse. In its posterior section, long, thin setae continue almost to the transverse suture but become smaller and much sparser (Fig. 16).

Like that of *L. rhinocerulus* ,the epipharynx of *A. monstrosus* has thick, medium-sized setae that form a patch on the apex of the medial process (Fig. 24). On the entire surface, there are also thick, large setae interspersed with long, thin setae (Figs. 24, 26). Setae on the posterior surface of the epipharynx are thick, long, and spiny (Fig. 25); although this is also the case for *L. rhinocerulus* and *E. intermedius* ,in *A. monstrosus* these setae are larger and extremely abundant.

In the case of *A .monstrosus* ,it must be emphasized that substantial differences related to its trophic specialization (detritus from ant nests) were expected. However, the mandibles of the three species studied do not have noteworthy differences. The most marked difference is that on the incisor lobe of *E. intermedius* ,where there are rows of small anterad setae (Fig. 18) along with thin, long, abundant setae.

Significant differences among the maxillae of *E. intermedius, A. monstrosus* ,and *L. rhinocerulus* are also lacking. The galea of all three species is well developed. In *A. monstrosus* ,there are a larger number of setae at the base of the second and third sclerites (Fig. 30), a characteristic that is not noticeable in the other two species. The fourth maxillary palpal segment of *A .monstrosus* is formed by numerous folds that give the appearance of scales and numerous pores with short, thick setae (Fig. 33). In all three species, the apex of the fourth segment has a crown of short, abundant, translucent setae (Figs. 12, 22, 33), the function of which probably relates to olfactory perception.

López-Guerrero and Zunino (2007) conducted a study on the evolution of mouthparts of Onthophagini (Scarabaeinae). They observed no substantial difference among the different species of *Onthophagus* Latreille, regardless of whether they were free living or found in caves and dens. Furthermore, López-Guerrero (2007) studied a predatory species, *C. virens* ,and reported finding no substantial differences with the mouthparts of coprophagous species. The observations made herein confirm that mouthpart morphology of coprophages is similar to that of species that feed on specialized resources. It must be clarified, however, that in the case of *A .monstrosus* ,the detritus from leaf-cutter ant nest is composed of fine fragments of fungus grown by the ants and also pieces of the ants themselves, material that accumulates outside the nest where dead ants tend to decompose. Therefore, the food source consists of fairly hard particles and is different from the purely vegetative detritus that has been associated with other dung beetle species studied (Halffter and Halffter 2009).

Verdú and Galante (2004) studied the morphological adaptations and behavior of dung beetles associated with European rabbit droppings in semi-arid and arid habitats in Iberian ecosystems. They observed highly developed setae on the zygum, strongly curved setae on the acroparia, and mandibles with well developed molar areas in the mouthparts of *Onthophagus (Relictonthophagus) punctatus* (Illiger), *Onthophagus (Relictonthophagus) emarginatus* Mulsant, and *Onthophagus (Amphionthophagus) latigena* d'Orbigny. They also found

modification patterns similar to those of other species of Scarabaeoidea, such as those of the genus *Thorectes* Mulsant (Geotrupidae) in which the epipharynx has less hair and a rolled paraglossa. The mandibles feature strongly developed denticles and molar areas that are also modified, being well developed in order to grind up dry feces. They also observed this in some species of *Aphodius* Illiger (Aphodiinae), another genus that feeds on rabbit droppings. Thus, the results of my study are consistent with those obtained from previous research on beetles that make use of special trophic resources.

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REFERENCES CITED

Anduaga, S. 1990. Etología de la nidificatión de *Liatongus monstrosus* (Bates) (Coleoptera: Scarabaeinae, Oniticellini) [pp. 167–168]. *In* :Memoria XXV Congreso de Entomología, Oaxaca, Oaxaca. Sociedad Mexicana de Entomología, Mexico.

Anduaga, S. 2000. Escarabajos coprófagos (Coleoptera: Scarabaeoidea) asociados a hongos en la Sierra Madre Occidental, Durango, Mexico: con una compilación de las especies micetófagas. *Acta Zoológica Mexicana (n.s.)* 80: 119–130.

Anduaga, S., and G. Halffter. 1991. Micofagia en Scarabaeidae [pp. 151–169]. *In* :Memorias del Simposio Nacional sobre la Interacción Insecto-Hongo (J.L. Navarrete-Heredia y G.A. Quiroz-Rocha, editors). Sociedad Mexicana de Entomología, Facultad de Ciencias, IGU, Veracruz, Mexico.

Anduaga, S., and G. Halffter. 1993. Nidificación y alimentación en *Liatongus rhinocerulus* (Bates) (Coleoptera: Scarabaeidae: Scarabaeinae). *Acta Zoológica Mexicana* 57: 1–14.

Anduaga, S., V. Halffter, and G. Halffter. 1976. Etograma de *Liatongus monstrosus* (Bates) (Coleoptera, Scarabaeidae). *Folia Entomológica Mexicana* 36: 48–49.

Cambefort, Y. 1982. Nidification behavior of Old World Oniticellini (Coleoptera: Scarabaeidae) [pp. 141–145]. *In* :The Nesting Behavior of Dung Beetles (Scarabaeinae): An Ecological and Evolutive Approach (G. Halffter and W. D. Edmonds, editors). Instituto de Ecología, Mexico.

Dellacasa, G. 1983. *Sistematica e nomenclatura degli Aphodiini italiani (Coleoptera: Scarabaeidae: Aphodiinae).* Monografie I, Museo Regionale di Scienze Naturali, Torino, Italy.
Edmonds, W. D. 1972. Comparative skeletal morphology, systematics and evolution of the Phanaeine dung beetles (Coleoptera: Scarabaeidae). *The University of Kansas Science Bulletin* 49: 731–874.
Halffter, G. 1952. Notas sobre el género *Phanaeus* .1. *Phanaeus quadridens* Say (Coleoptera: Scarabaeidae). *Ciencia (Mexico), Revista Hispano Americana de Ciencias Puras y Aplicadas* 12(3–4): 79–86.
Halffter, G., and W. D. Edmonds. 1982. *The Nesting Behavior of Dung Beetles (Scarabaeinae): An Ecological and Evolutive Approach.* Instituto de Ecología, Mexico.
Halffter, G., and V. Halffter. 2009. Why and where coprophagous beetles (Coleoptera: Scarabaeinae) eat seeds, fruits or vegetable detritus. *Boletín de la Sociedad Entomológica Aragonesa* 45: 1–22.
Halffter, G., and E. G. Matthews. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). *Folia Entomológica Mexicana* 12–14: 1–312.
Hata, K., and W. D. Edmonds. 1983. Structure and function of the mandibles of adult dung beetles (Coleoptera: Scarabaeidae). *Journal of Insect Morphology and Embryology* 12(1): 1–12. CrossRef
López-Guerrero, I. 2007. Análisis de las piezas bucales en *Canthon virens* Mann. (Coleoptera: Scarabaeinae: Canthonina) en relación con sus hábitos tróficos [pp. 131–142]. *In* :Escarabajos, Diversidad y Conservación Biológica. Ensayos en Homenaje a Gonzalo Halffter M. Zunino and A. Melic, editors). Vol. 7, Monografías Tercer Milenio, Sociedad Entomológica Aragonesa, Zaragoza, Spain.
López-Guerrero, I. and M. Zunino. 2007. Consideraciones acerca de la evolución de las piezas bucales en los Onthophagini (Coleoptera: Scarabaeidae) en relación con diferentes regímenes alimenticios. *Interciencia* 32(7): 482–489.
Medina, C. A., C. H. Scholtz, and B. D. Gill. 2003. Morphological variation and systematics of *Canthon* Hoffm. 1817, and related genera of New World Canthonini dung beetles (Coleoptera: Scarabaeinae). *Mitteilungen aus dem Museum für Naturkunde in Berlin: Deutsche Entomologische Zeitschrift* 50(1): 23–68. CrossRef
Montes de Oca, E., and G. Halffter. 1998. Invasion of Mexico by two dung beetles previously introduced into the United States. *Studies on Neotropical Fauna and Environment* 33: 37–45. CrossRef, CSA
Navarrete-Heredia, J. L. 2001. Beetles associated with *Atta* and *Acromyrmex* ants (Hymenoptera: Formicidae: Attini). *Transactions of the American Entomological Society* 127(3): 381–429. CSA
Pereira, C. M. F., and G. Halffter. 1961. Nuevos datos sobre Lamellicornia mexicanos con algunas observaciones sobre saprofagia. *Revista Brasileira de Entomologia* 10: 53–66.

Philips, K., and K. L. Bell. 2008. *Attavicinus* ,a new generic name for the myrmecophilous dung beetle *Liatongus monstrosus* (Scarabaeidae: Scarabaeinae). *The Coleopterists Bulletin* 62(1): 67–81. BioOne

Simonis, A. 1984. Note sugli *Euoniticellus* della fauna italiana (Coleoptera, Scarabaeidae). *Bolletino del Museo Regionale di Scienze Naturali* 2: 545–554.

Verdú, J. R., and E. Galante. 2004. Behavioural and morphological adaptations for a low-quality resource in semi-arid environments: dung beetles (Coleoptera, Scarabaeoidea) associated with the European rabbit (*Oryctolagus cuniculus* L.). *Journal of Natural History* 38: 705–715. CrossRef

Zunino, M. 1982. Aspectos taxonómicos y biogeográficos del poblamiento americano de Oniticellini (Coleoptera, Scarabaeidae) [pp. 1083–1089]. *In* :Zoología Neotropical (P. J. Salinas, editor). Tomo 2, Actas del VIII Congreso Latinoamericano de Zoología, Mérida, Venezuela.

Zunino, M. 2005. Corotipos y biogeografía sistemática en el Euromediterráneo [pp. 181–187]. *In* :Regionalización Biogeográfica en Iberoamérica y Tópicos Afines (J. Llorente-Bousquets and J. J. Morrone, editors). Facultad de Ciencias, Universidad Autónoma de México, Distrito Federal, Mexico.