




## Antennal sensilla in *Cyclocephala literata* Burmeister, 1847 (Coleoptera: Scarabaeidae: Dynastinae)

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**Abstract:** Adults of the beetle *Cyclocephala literata* Burmeister, 1847 are important pollinators to some Magnoliaceae. It is known that insects could find host plants by detecting volatiles through antennal sensilla. *Cyclocephala* has its three distal antennomeres lamellate, and the surface of each lamella has sensilla trichodea, chaetica, placodea, coeloconica, basiconica and ampullacea. Three kinds of sensilla placodea were found (type I, II and III), and two kinds of sensilla coeloconica were observed (type I and II). Females have on average 10,776 sensilla, of which 10,214 are sensilla placodea, 536 are sensilla coeloconica, and 26 are sensilla basiconica. Males have on average 10,386 sensilla, of which 9,873 are sensilla placodea, 464 are sensilla coeloconica, and 49 are sensilla basiconica. Males and females have similar quantities of sensilla, and sensilla placodea are predominant. The differences observed in the number of sensilla of males and females were found in other beetles and were attributed to the detection of conspecific sexual pheromones by one of the sexes, or to the detection of plant volatiles. The antennal sensilla of *C. literata* is described and quantified in present study, and some perspectives about the differences kind of chemical communication, pollination, and antennae dimorphism is discussed.

**Keywords:** chemical receptors; *Cyclocephalini*; masked chafer; morphology; ultrastructure.

## Sensilas antenais em *Cyclocephala literata* Burmeister, 1847 (Coleoptera: Scarabaeidae: Dynastinae)

**Resumo:** Adultos do besouro *Cyclocephala literata* Burmeister, 1847 desempenham importantes funções de polinização em plantas da família Magnoliaceae. É conhecido que muitos insetos encontram plantas hospedeiras pela detecção de voláteis pelas sensilas antenais. *Cyclocephala* possui os três antenômeros distais lamelados e na superfície de cada lamela possuem sensilas trichodea, caética, placódea, coelocônica, basicônica e ampulacea. Foram encontrados três tipos de sensilas placódeas (tipo I, II e III), e dois tipos de sensilas coelocônicas (tipo I e II). Fêmeas apresentam em média 10.776 sensilas, das quais 10.214 são sensilas placódeas, 536 são sensilas coelocônicas e 26 são sensilas basicônicas. Os machos apresentaram em média 10.386 sensilas, das quais 9.873 são sensilas placódeas, 464 são sensilas coelocônicas e 49 são sensilas basicônicas. Machos e fêmeas apresentam quantidades semelhantes de sensilas e as sensilas placódeas são predominantes. As diferenças encontradas nas quantidades de sensilas em machos e fêmeas também foram encontradas em outros besouros e foram atribuídas a detecção de feromônios coespecíficos por um dos sexos, ou para detecção de voláteis de plantas. A sensila antenal de *C. literata* é descrita e quantificada no presente estudo, e algumas perspectivas sobre as diferenças entre os tipos de comunicação química, polinização e dimorfismo antenal é discutido.

**Palavras-chave:** receptores químicos; *Cyclocephalini*; escaravelho; morfologia; ultraestrutura.

## Introduction

Scarab beetles (Coleoptera: Scarabaeidae) are a diverse group with a wide range of adult feeding habits, including phytophagous species that consume leaves, flowers, and fruits of diverse plant species; some species cause damage to cultivated plants (Solís 2004, Maia & Schindwein 2006, Shaughney & Ratcliffe 2015, Rodrigues et al. 2016, Ferreira et al. 2018). Moreover, larvae of some phytophagous scarabs feed on roots and also may cause economic damage to crops (Santos & Ávila 2009, Cherman et al. 2011, Coutinho et al. 2011). The antenna of adult scarab beetles has several minute sensorial structures that detect plant volatiles, gases, and pheromones (Kim & Leal 2000, Larsson et al. 2001). These sensilla are associated with beetle orientation, resource location, aggregation behavior, and mating (Schneider 1964, Leal & Mochizuki 1993, Larsson et al. 2001, Romero-López 2016).

The phytophagous scarab beetles are also known as Pleurosticti (basal spiracles in the connective membrane, partly in the urosternites, the last pair not being covered by the elytra, according to Lima (1953)), a group that includes speciose scarabaeoid subfamilies, such as Cetoniinae, Dynastinae, Melolonthinae, Rutelinae, and other smaller taxa (Morón 2004). Pleurosticti is recovered as monophyletic in cladistic analyses (Browne & Scholtz 1998, Hunt et al. 2007, Ahrens & Vogler 2008, 2011, Bocak et al. 2014, Cherman & Morón 2014, Mckenna et al. 2015, Šípek et al. 2016).

Within this large group, some studies found evidence of the volatiles detection by the antennal sensilla, helping the insect to find potential mating partners, host plant, or other specimens to form an aggregation (Kim & Leal 2000, Larsson et al. 2001, Rodrigues et al. 2014). Regarding phytophagous scarab beetles, it is seemed that both sexual pheromone and plant volatiles are used to guide beetles to sites (the host plant) were mating and feeding occurrences (Gottsberger 1989, Maia et al. 2013, Moore & Jameson 2013), such as in some Rutelinae (e.g., Hansson et al. 1999, to *Phyllopertha diversa* Waterhouse, 1875; Larsson et al. 2001, to *Anomala cuprea* (Hope, 1839)), and in Melolonthinae (e.g., Sun et al. 2014, to *Holotrichia oblita* (Faldermann, 1835); Ruther et al. 2000, to *Melolontha hippocastani* Fabricius, 1801).

The importance of plant volatiles to scarab beetles may elucidate why the host plant flowering and beetle swarming are concomitant processes (e.g., Rodrigues et al. 2014, to the ruteline *Anomala testaceipennis* Blanchard, 1856; Rodrigues et al. 2017, to the melolonthine *Liogenys bidenticeps* Moser, 1919). Sexual pheromones and plant volatiles are also used by Dynastinae beetles, and plant volatiles are especially important to pollinators as some species of the tribe Cyclocephalini (see Schiestl & Dötterl 2012, Vuts et al. 2014).

The genus *Cyclocephala* Dejean, 1821 (Dynastinae: Cyclocephalini) is a group of New World phytophagous scarabs, of which 123 species are known to occur in Brazil (Grossi & Vaz-de-Mello 2019). Adults sometimes swarm on plant and consume leaves and flower parts (Oliveira & Ávila 2011, Moore & Jameson 2013, Dias & Rodrigues 2018), and they use the plant as a mating site (Gottsberger 1989, Munin et al. 2008, Maia et al. 2013, Costa et al. 2017). Within the genus, the antennal sensilla is known to and undetermined species (Bohacz et al. 2020) and to *Cyclocephala putrida* Burmeister, 1847 (Saldanha et al. 2020).

Within the genus, *Cyclocephala literata* Burmeister, 1847 was registered to São Paulo, Rio de Janeiro, and Santa Catarina States, in the Atlantic Forest and Cerrado (Brazilian Savanna), mainly in gallery

forests (Endrödi 1985; Gottsberger 1986). This specie is the only known pollinator of *Magnolia ovata* (A.St.-Hil.) Spreng. and an occasional flower visitor to *Annona crassiflora* Mart. (Magnoliaceae; Gottsberger 1986, Gottsberger et al. 2012). Gibbs et al. (1977) provisionally identified the pollinator of *M. ovata* as the cyclocephaline beetle *Augoderia nitida* Burmeister, 1847 or *Cyclocephala* aff. *emarginata* Endrödi, 1966 but Seymour et al. (2010) named the species as *C. literata* based in personal communication with two dynastine specialists. *Magnolia ovata* (“bagaçu”) is an important plant to Brazilian forest ecology specially in gallery forests (Cazetta et al. 2002), a medicinal plant (Stefanello et al. 2005, Kassuya et al. 2009), used in several human activities (to building constructions, craftsmanship, and other usages) and is an endangered species (Carvalho 2003).

Gottsberger et al. (2012) described the attraction of *C. literata* to volatiles produced by *M. ovata*. To Seymour et al. (2010) the floral thermogenesis could increase the volatilization of plant odorants and the heat itself is an attractant (energy reward). Regarding the above-mentioned biological importance of the *Cyclocephala literata*, the present work aims to describe the antennal sensilla of the beetle.

## Material and Methods

This study was conducted at the Universidade Estadual de Mato Grosso do Sul (UEMS), Campus of Cassilândia, MS, Brazil. Adults of *C. literata* were obtained by using two methods: 1) collecting and rearing larvae and 2) capturing adults attracted to a light trap model “Luiz de Queiroz” (Silveira Neto & Silveira 1969). Larvae were collected from decomposing organic matter in the soil from January to December 2018. A total of 161 larvae was collected and reared in laboratory. Each larva was kept separately in a plastic container (500 mL) filled with the original substrate (2/3 of the container volume). A total of 35 adults were obtained, 18 males and 17 females. Furthermore, 40 adults (15 males and 25 females) were collected using a light trap in a pasture area dominated by *Urochloa decumbens* (Stapf) Webster (Poaceae).

Males and females were sexed by the dimorphism of the protarsi (Figure 1): males have tarsomere V enlarged and claws strongly curved regarding females. The specimens were preserved in 70% ethanol and are deposited in the UEMS entomological collection, campus Cassilândia. Adult reared voucher specimens were sent to Prof. Dr. Paschoal Coelho Grossi (Universidade Federal Rural do Pernambuco, Recife, Brazil) for species identification. The antennae of 10 males and 10 females were detached from the head and prepared according to the procedures described by Tanaka et al. (2006). Each sample (lamella) was successively dehydrated in 80% ethanol and 90% ethanol for 15 minutes each and 100% ethanol for 20 minutes. The samples were dried by CO<sub>2</sub> critical point drying with a Leica® CPD300 dryer before imaging was taken with a Zeiss® EVO LS15 scanning electron microscope (SEM) at the Departamento de Física e Química da Universidade Estadual Paulista, campus Ilha Solteira, state of São Paulo, Brazil. Were taken images of the external surface of lamellae when it is closed and also the inner surface contact between lamellae. Images were obtained with magnifications of 100, 20 and 10 μm. Sensilla terminology follows Keil (1999). The images obtained in SEM were subjected to image enhancement filters available in the software Image-Pro Plus 6.0. The sensillae were quantified in the images obtained by SEM.



Figure 1. *Cyclocephala literata* Burmeister, 1847. A) male B) female.

## Results

The outer surface of the lamellae of *C. literata* have several sensilla chaetica and sensilla trichodea (Figure 2A, C, D, E and F, Figure 3A, C and E). Both sensilla are hair-like, but sensilla chaetica are short and grouped on inner surface of proximal lamella and sensilla trichodea are long. The inner surface of proximal and distal lamella, and both sides of medial lamella have sensilla placodea, sensilla ampullacea (= pores) (Figure 3F), sensilla basiconica, sensilla coeloconica, and some fovea that enclose sensilla placodea I and sensilla basiconica (Figure 2–3).

Three types of sensilla placodea are identified (Figure 3B and F). Type I (Meinecke 1975: G2; Bohacz et al. 2020: placodea F) is a plate surrounded by a furrow, the surface is irregularly reticulate, and mean diameter is 7.67  $\mu\text{m}$  (5.51–9.28  $\mu\text{m}$ ). Type II (Meinecke 1975: G1; Bohacz et al. 2020: placodea A) is similar to type I but has a smooth surface and mean diameter of 12.34  $\mu\text{m}$  (5.71–17.85  $\mu\text{m}$ ). Type III (Meinecke 1975: J4; Bohacz et al. 2020: placodea A) is almost smooth, the peripheral furrow (or ditch) is absent, and mean diameter is 11.51  $\mu\text{m}$  (6.89–15.17  $\mu\text{m}$ ).

The sensilla coeloconica are divided into type I (with pointed apex; Meinecke 1975: L1) and II (with blunt apex; Meinecke 1975: L2). Both sensilla are sparsely distributed (Figure 3F). Sensilla basiconica (Meinecke 1975: L4) resemble minute setae enclosed in a depressed pit, with the apex projected outside the pit. They are sparse (Figure 3F), mainly grouped in foveae on the medial lamella, and present on

distal margins of lamellae (Figure 3B and D). The sensilla basiconica present in foveae are bigger than those placed in surface. The sensilla ampullacea are noted as pores and are sparsely distributed on lamellae surface.

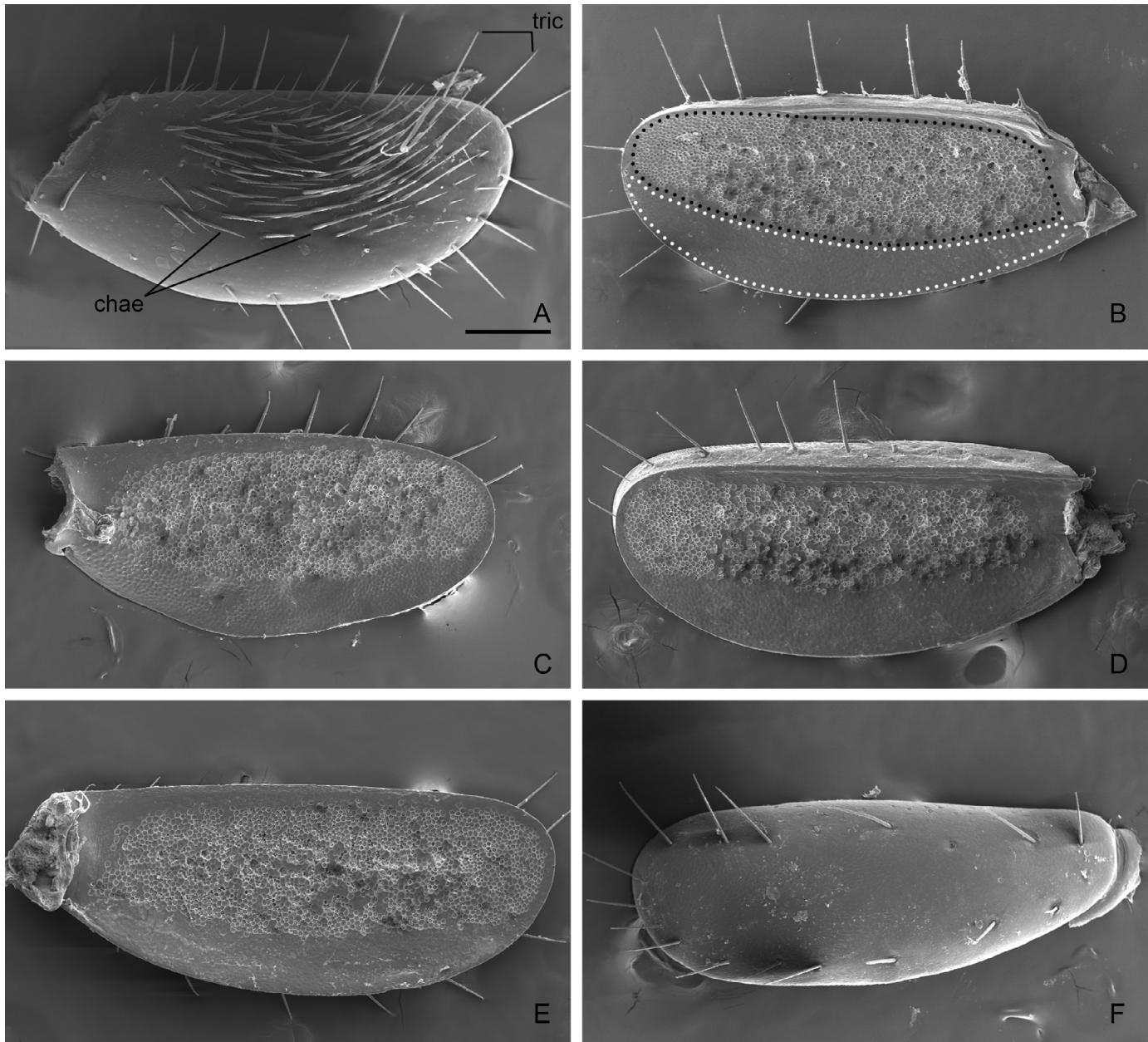
The inner surface of proximal and distal lamella and both surfaces of medial lamella have two well defined area (Figure 2B), the posterior area mainly formed by sensilla placodea type III, and the anterior area with heterogeneously distributed sensilla basiconica, sensilla coeloconica (type I and II), and sensilla placodea (type I and II).

Females have on average 10,776 sensilla on all lamellae, of which 10,214 (94.8%) are sensilla placodea, 536 (5.0%) are sensilla coeloconica, and 26 (0.2%) are sensilla basiconica (Table 1). Males have on average 10,386 sensilla in lamellae, of which 9,873 (95.0%) are sensilla placodea, 464 (4.5%) are sensilla coeloconica, and 49 (0.2%) are sensilla basiconica (Table 1). There is a slightly difference on the number of sensilla between sexes, but the dimorphism is inconspicuous.

## Discussion

Sensilla trichodea are found on the outer side of the proximal and distal lamellae and on the edges of the medial lamella, whereas sensilla chaetica are mainly distributed in a brush-like structure in outer (proximal) side of proximal lamella. A similar distribution of these sensilla is found in *Cyclocephala putrida* Burmeister, 1847 (Saldanha et al. 2020). An undetermined species of *Cyclocephala*



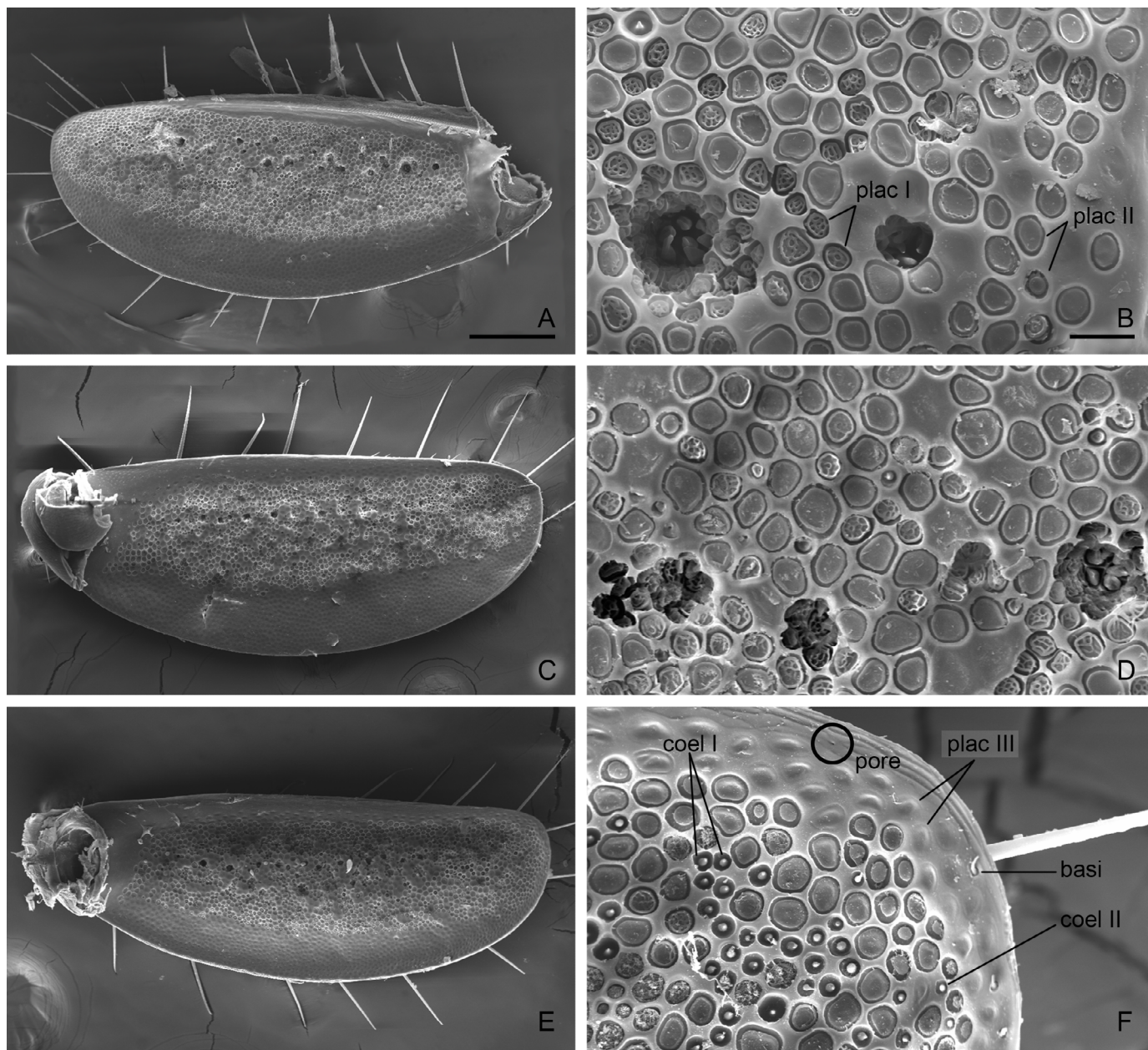


**Figure 2.** *Cyclocephala literata* Burmeister, 1847; antennal lamella of female. A-B) proximal lamella (outer and inner side, respectively) C-D) medial lamella (inner and outer side, respectively). E-F) proximal lamella (inner and outer side, respectively). Anterior area (black dotted line) with sensilla placodea type I and II, sensilla coeloconica type I and II, and sensilla basiconica. Posterior area (white dotted line) with type I homogeneously distributed. Tric = sensilla trichodea; Chae = sensilla chaetica. Scale = 200  $\mu$ m.

studied by Bohacz et al. (2020) was described with a “brush-like sensilla trichodea”. Hair-like sensilla grouped in a brush-like structure (or “field of setae”) occur in Dynastinae (Bohacz et al. 2020) and at least in some Cetoniinae (Bohacz et al. (2020) to *Valgus hemipterus* (Linnaeus, 1758); Costa et al. (2021) to two species of *Hoplopyga*). Otherwise, in other phytophagous scarab as *Anomala inconstans* Burmeister, 1844 (Rutelinae) the proximal lamella have not a brush-like structure and sensilla chaetica are sparse on the outer side of proximal lamella (Rodrigues et al. 2019). Hair-like sensilla were identified as mechanoreceptors (Romero-López et al. 2004, 2010, Mutis et al. 2014), but sensilla trichodea were also identified as gustative sensilla (contact

chemoreceptor; Keil 1999). The function of the brush-like structure is still unknown.

Two types of sensilla coeloconica occur on inner side of antennal club of *C. literata*, and are sparsely distributed over inner side of lamellae (5.0% in females and 4.5% in males). The sparse sensilla coeloconica are common to phytophagous scarab, but they are absent in the lamellae of some melolonthine as Ablaberini, Heteronicini, Liparetrini, Maechidiini, Phyllotocidiini, Sericini, and Sericoidini (Bohacz et al. 2020). Interestingly, these tribes are sometimes recovered as sisters groups to all other phytophagous scarabs (Ahrens & Vogler 2011). This fact must be checked in more species but it

Antennal sensilla in *Cyclocephala literata*

**Figure 3.** *Cyclocephala literata* Burmeister, 1847; antennal lamella of male. A-B) proximal lamella (inner side and detail of area with foveae, respectively). C-D) medial lamella (inner side and detail of area with foveae, respectively). E-F) distal lamella (inner side and detail of distal area, respectively). Basi = sensilla basiconica, Coel I = sensilla coeloconica type I, Coel II = sensilla coeloconica type II, Plac I = sensilla placodea type I, Plac II = sensilla placodea type II, Plac III = sensilla placodea type III; Pore = sensilla ampullacea. Scale of A, C, D = 200  $\mu$ m; scale of B, D, E = 20  $\mu$ m.

could be an important step to the evolution of phytophagous scarabs. To a species of Sericini (*Maladera orientalis* Motschulsky, 1857), the sensilla coeloconica are present in pedicel but not in lamellae, and it was conjectured as hygroreceptors and thermoreceptors by Shao et al. (2019).

Sensilla basiconica are scarce, present in the inner surface of the club, and are predominant in some foveae (see below). Romero-López et al. (2004) suggests that the sensilla basiconica (named as coeloconica) was related with plant volatiles detection. The sensilla basiconica is found in all scarab beetles (Scarabaeoidea) but the foveae in the lamellae are found in Dynastinae, Rutelinae and

some Melolonthinae (Bohacz et al. 2020). Both sensilla coeloconica and sensilla basiconica have similar distribution in *C. literata* and *C. putrida* (Saldanha et al. 2020).

Sensilla ampullacea were associated with detection of  $\text{CO}_2$  in some insects (Keil 1999). The attraction of beetles to  $\text{CO}_2$  released by *M. ovata* is not known yet, but *C. literata* was certainly attracted to *M. ovata* volatiles and probably is also attracted to the heat produced at night by flowers (Gottsberger et al. 2012).

Sensilla placodea are the main sensilla of lamellae and represent about 95% of all sensilla in males and females of *C. literata*. The dominance of sensilla placodea is usual to scarab beetles (Meinecke



**Table 1.** Mean number of three sensilla types on the antennal lamellae of adult *Cyclocephala literata*.

Sensillum	proximal lamella		medial lamella		distal lamella	
	outer	inner	outer	inner	outer	inner
Female ( <i>n</i> = 10)						
Placodea	0	2,475 ± 19.40	2,461 ± 20.68	2,478 ± 25.23	0	2,800 ± 23.73
Coeloconica	0	147 ± 2.10	108 ± 1.78	114 ± 4.21	0	167 ± 4.16
Basiconica	0	3 ± 0.21	6 ± 0.5	8 ± 0.59	0	9 ± 0.47
Total	0	2,625 ± 20.69	2,575 ± 20.27	2,600 ± 27.6	0	2,976 ± 23.12
Male ( <i>n</i> = 10)						
Placodea	0	2,714 ± 30.84	2,436 ± 22.85	2,512 ± 23.15	0	2,211 ± 24.16
Coeloconica	0	91 ± 1.67	92 ± 2.91	81 ± 2.41	0	200 ± 3.71
Basiconica	0	10 ± 0.57	0	0	0	39 ± 1.47
Total	0	2,815 ± 29.93	2,528 ± 22.99	2,593 ± 24.07	0	2,450 ± 25.84

1975, Romero-López et al. 2004, 2010, Tanaka et al. 2006, Mutis et al. 2014, Martínez-Bonilla et al. 2015, Rodrigues et al. 2019, Bohacz et al. 2020) and the sensilla is related to pheromone detection in *Popillia japonica* Newman, 1841 (Kim & Leal 2000) or related both with sexual attractants (peripheral ones) and plant volatiles detection (central ones) in *Anomala cuprea* (Hope, 1839) (Larsson et al. 2001). *C. literata* do not have an evident sexual dimorphism in antennae, and the amount of sensilla placodea is similar between sexes. It could be evidence that the beetle uses plant volatiles (and possibly heat and CO<sub>2</sub> as discussed in above sentence) as the main attractant, and sexual pheromones could have a minor role or even be entirely absent. *C. literata* is a pollinator as above mentioned and does not have the sexual dimorphism regarding the amount and pattern of lamellar sensilla. Otherwise, *C. putrida* have an evident antennae dimorphism, females have more sensilla than males, and the beetle is not seemed as a pollinator (Saldanha et al. 2020).

Kim & Leal (2000) suggested that the sexual dimorphism in antennae is related to the detection of sexual attractant. Hallett et al. (1995) and Renou et al. (1998) show that a dynastine beetle (*Oryctes rhinoceros* L., 1758) does not have antennal dimorphism, and uses aggregative semiochemicals, not pheromones to find potential partners.

It is not known how many variables are involved on the attraction of beetle pollinator to flower chamber of host plants, but it is accepted that the flower attractants (odorants, heat, gases) play the main role in the beetle aggregation, and the conspecific sexual pheromones are partially or entirely suppressed, at least to cyclocephaline pollinators (Beach 1982, Pellmyr & Thien 1986, Dieringer et al. 1999, Gibernau et al. 1999). Otherwise, not pollinators cyclocephaline, that usually matting on the ground, grass leaves or shrubs, used sexual pheromones as attractant (Haynes & Potter 1995).

The relationship between dimorphism, pollination, and the kind of chemical communication in *Cyclocephala* must be checked and the rules of sexual pheromones or aggregative odorants must be clarified in the genus.

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Cleicimar Gomes Costa: Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision.

Juarez Fuhrmann: Contribution in the analysis and interpretation of data, also assisting in article revision; Contribution to critical revision, adding intellectual content.

Sérgio Roberto Rodrigues: Contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

## Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

## References

- AHRENS, D. & VOGLER, A.P. 2008. Towards the phylogeny of chafers (Sericini): Analysis of alignment-variable sequences and the evolution of segment numbers in the antennal club. *Mol. Phyl. Evol.* 47: 783-798. <https://doi.org/10.1016/j.ympev.2008.02.010>
- AHRENS, D. & VOGLER, A.P. 2011. The phylogeny of monkey beetles based on mitochondrial and ribosomal RNA genes (Coleoptera: Scarabaeidae: Hopliini). *Mol. Phyl. Evol.* 60: 408-415. <https://doi.org/10.1016/j.ympev.2011.04.011>

- BEACH, J.H. 1982. Beetle pollination of *Cyclanthus bipartitus* (Cyclanthaceae). Amer. J. Bot. 69(7): 1074-1081. <https://doi.org/10.1002/j.1537-2197.1982.tb13352.x>
- BOCAK, L., BARTON, C., CRAPTON-PLATT, A., CHESTERS, D., AHRENS, D. & VOGLER, A.P. 2011. Building the Coleoptera tree-of-life for >8000 species: composition of public DNA data and fit with Linnaean classification. Syst. Entomol. 39: 97-110. <https://doi.org/10.1111/syen.12037>
- BOHACZ, C., HARRISON, J.G. & AHRENS, D. 2020. Comparative morphology of antennal surface structures in pleurostict scarab beetles (Coleoptera). Zoomorphology 139: 327-346. <https://doi.org/10.1007/s00435-020-00495-0>
- BROWNE, J. & SCHOLTZ, C.H. 1998. Evolution of the scarab hindwing articulation and wing base: a contribution toward the phylogeny of the Scarabaeidae (Scarabaeoidea: Coleoptera). Syst. Entomol. 23: 307-326. <https://doi.org/10.1046/j.1365-3113.1998.00059.x>
- CARVALHO, P.E.R. 2003. Bagaçu. Embrapa Floresta, Circular Técnica 72: 11 p. <http://www.infoteca.cnptia.embrapa.br/infoteca/handle/doc/293841>
- CAZETTA, E., RUBIM, P., LUNARDI, V.O., FRANCISCO, M.R. & GALETTI, M. 2002. Frugivoria e dispersão de sementes de *Talauma ovata* (Magnoliaceae) no sudeste brasileiro. Ararajuba 10(2): 199-206.
- CHERMAN, M.A. & MORÓN, M.A. 2014. Validación de la Familia Melolonthidae Leach, 1819 (Coleoptera: Scarabaeoidea). Acta Zool. Mex. (n.s.) 30(1): 201-220.
- CHERMAN, M.A., GUEDES, J.V.C., MORÓN, M.A., DALPRA, E., PERINI, C.R. & JUNG, A.H. 2011. First record of species of *Liogenys* (Coleoptera: Melolonthidae) associated with winter grain crops in Rio Grande do Sul (Brazil). Rev. Bras. Entomol. 55(4): 618-620. <https://doi.org/10.1590/S0085-56262011005000052>
- COSTA, M.S., SILVA, R.J., PAULINO-NETO, H.F. & PEREIRA, M.J.B. 2017. Beetle pollination and flowering rhythm of *Annona coriacea* Mart. (Annonaceae) in Brazilian cerrado: Behavioral features of its principal pollinators. PlosOne 12: 1-14. <https://doi.org/10.1371/journal.pone.0171092>
- COSTA, C.G., RODRIGUES, S.R. & FUHRMANN, J. 2021. Morphology of the antennal sensilla of two species of *Hoplopyga* Thomson, 1880 (Coleoptera, Scarabaeidae, Cetoniinae). Rev. Bras. Entomol. 65(1): 1-8. <https://doi.org/10.1590/1806-9665-RBENT-2020-0078>
- COUTINHO, G.V., RODRIGUES, S.R., CRUZ, E.C. & ABOT, A.R. 2011. Bionomic data and larval density of Scarabaeidae (Pleurosticti) in sugarcane in the central region of Mato Grosso do Sul, Brazil. Rev. Bras. Entomol. 55(3): 389-395. <https://doi.org/10.1590/S0085-56262011005000038>
- DIAS, B.M.R. & RODRIGUES, S.R. 2018. Floral association of adult *Cyclocephala tucumana* Brethes and *Cyclocephala melanocephala* (Fabricius) with passion flowers (*Passiflora edulis* Sims). Entomobrasiliis 11 (2): 144-146. <https://doi.org/10.12741/ebrazilis.v11i2.738>
- DIERINGER, G., CABRERA-R., L., LARA, M., LOYA, L. & REYES-CASTILLO, P. 1999. Beetle pollination and floral thermogenicity in *Magnolia tamaulipana* (Magnoliaceae). Int. J. Plant Sci. 160(1): 64-71. <https://doi.org/10.1086/314099>
- ENDRÖDI, S. 1985. The Dynastinae of the world. Series Entomologica 28: 1-800.
- FERREIRA, K.R., GOMES, E.S. & RODRIGUES, S.R. 2018. Description of the third instar and mating behavior of *Liogenys suturalis* (Blanchard) (Coleoptera: Scarabaeidae). Coleop. Bull. 72(3): 457-464. <https://doi.org/10.1649/0010-065X-72.3.457>
- GIBBS, P.E., SEMIR, J. & CRUZ, N.D. 1977. Floral biology of *Talauma ovata* St. Hill. (Magnoliaceae). Ciênc. Cult. 29(12): 1437-1441.
- GIBERNAU, M., BARABÉ, D., CERDAN, P. & DEJEAN, A. 1999. Beetle pollination of *Philodendron solimoesense* (Araceae) in French Guiana. Int. J. Plant Sci. 160(6): 1135-1143. <https://doi.org/10.1086/314195>
- GOTTSBERGER, G. 1986. Some pollination strategies in Neotropical savannas and forests. Plant System. Evol. 152: 29-45. <https://doi.org/10.1007/BF00985349>.
- GOTTSBERGER, G. 1989. Beetle pollination and flowering rhythm of *Annona* spp. (Annonaceae) in Brazil. Plant System. Evol. 167: 165-187. <https://doi.org/10.1007/BF00936404>
- GOTTSBERGER G. & SILBERBAUER-GOTTSBERGER, I. 1991. Olfactory and visual attraction of *Erioscelis emarginata* (Cyclocephalini, Dynastinae) to the inflorescences of *Philodendron selioum* (Araceae). Biotropica 23(1): 23-28. <https://doi.org/10.2307/2388684>
- GROSSI, P.C. & VAZ-DE-MELLO, F.Z. 2019. Melolonthidae in catálogo taxonômico da fauna do Brasil. fauna.jbrj.gov.br/fauna/faunadobrasil/145460 (Accessed 23 September 2020).
- HALLETT, R.H., PEREZ, A.L., GRIES, G., GRIES, R., PIERCE Jr., H.D., YUE, J., OEHLISHLAGER, A.C., GONZALEZ, L.M. & BORDEN, J.H. 1995. Aggregation pheromone of coconut rhinoceros beetle, *Oryctes rhinoceros* (L.) (Coleoptera: Scarabaeidae). J. Chem. Ecol. 21: 1549-1570. <https://doi.org/10.1007/BF02035152>
- HANSSON, B.S., LARSSON, M.C. & LEAL, W.S. 1999. Green leaf volatile-detecting olfactory receptor neurons display very high sensitivity and specificity in a scarab beetle. Physiol. Entomol. 24: 121-126. <https://doi.org/10.1046/j.1365-3032.1999.00121.x>
- HAYNES, K.F. & POTTER, D.A. 1995. Chemically mediated sexual attraction of male *Cyclocephala lurida* (Coleoptera: Scarabaeidae) and other scarabaeid beetles to immature stages. Environ. Entomol. 24(5): 1302-1306. <https://doi.org/10.1093/ee/24.5.1302>
- HUNT, T., BERGSTEN, J., LEVKANICOVA, Z., PAPADOPOULOU, A., JOHN, O.S., WILD, R., HAMMOND, P.M., AHRENS, D., BALKE, M., CATERINO, M.S., GÓMEZ-ZURITA, J., RIBERA, I., BARRACLOUGH, T.G., BOCAKOVA, M., BOCAK, L. & VOGLER, A.P. 2007. A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. Science 318, 1913-1916. <https://doi.org/10.1126/science.1146954>
- KASSUYA, C.A.L., CREMONEZE, A., BARROS, L.F.L., SIMAS, A.S., LAPA, F.R., MELLO-SILVA, R., STEFANELLO, M.E.A. & ZAMPRONIO, A.R. 2009. Antipyretic and anti-inflammatory properties of the ethanolic extract, dichloromethane fraction and costunolide from *Magnolia ovata* (Magnoliaceae). J. Ethnopharmac. 124(3):369-376. <https://doi.org/10.1016/j.jep.2009.06.003>
- KEIL, T.A. 1999. Morphology and development of the peripheral olfactory organs. In: Insect olfaction (B. Hansson, ed.). Springer, Berlin, p. 6-44.
- KIM, J.Y. & LEAL, W.S. 2000. Ultrastructure of pheromone-detecting sensillum placodeum of the Japanese beetle, *Popillia japonica* Newmann (Coleoptera: Scarabaeidae). Arthrop. Struc. Develop. 29(2): 121-128. [https://doi.org/10.1016/S1467-8039\(00\)00022-0](https://doi.org/10.1016/S1467-8039(00)00022-0)
- LARSSON, M.C., LEAL, W.S. & HANSSON, B.S. 2001. Olfactory receptor neurons detecting plant odours and male volatiles in *Anomala cuprea* beetles (Coleoptera: Scarabaeidae). J. Insect Physiol. 47(9): 1065-1076. [https://doi.org/10.1016/S0022-1910\(01\)00087-7](https://doi.org/10.1016/S0022-1910(01)00087-7)
- LEAL, W.S. & MOCHIZUKI, F. 1993. Sex pheromone reception in the scarab beetle *Anomala cuprea*: enantiomeric discrimination by sensilla placodea. Naturwissenschaften 80: 278-281. <https://doi.org/10.1007/BF01135914>
- LIMA, A.C. 1953. Insetos do Brasil. 8º Tomo. Capítulo XXIX. Coleópteros 2ª parte. Escola Nacional de Agronomia Série didática. n. 10, 323p.
- MCKENNA, D.D., FARRELL, B.D., CATERINO, M.S., FARNUN, C.W., HAWKS, D.C., MADDISON, D.R., SEAGO, A.E., SHORT, E.Z., NEWTON, A.F. & THAYER, M.K. 2015. Phylogeny and evolution of Staphyliniformia and Scarabaeiformia: forest litter as a stepping stone for diversification of nonphytophagous beetles. Syst. Entomol. 40: 35-60. <https://doi.org/10.1111/syen.12093>
- MAIA, A.C.D. & SCHLINDWEIN, C. 2006. *Caladium bicolor* (Araceae) and *Cyclocephala celata* (Coleoptera, Dynastinae): a well-established pollination system in the northern Atlantic rainforest of Pernambuco, Brazil. Plant Biol. 8: 529-534. <https://doi.org/10.1055/s-2006-924045>
- MAIA, A.C.D., GIBERNAU, M., CARVALHO, A.T., GONÇALVES, E.G. & SCHLINDWEIN, C. 2013. The cowl does not make the monk: scarab beetle pollination of the Neotropical aroid *Taccarum ulei* (Araceae: Spathicarpeae). Biol. J. Linn. Soc. 108(1): 22-34. <https://doi.org/10.1111/j.1095-8312.2012.01985.x>

- MARTÍNEZ-BONILLA, O.K., ROMERO-LÓPEZ, A.A. & BENÍTEZ-HERRERA, L.N. 2015. Morfometría corporal y antenal *Macroductylus mexicanus* y *Macroductylus nigripes* (Coleoptera: Scarabaeoidea: Melolonthidae) y descripción de sus sensilas lamelares. Bol. Soc. Mex. Entomol. (nueva serie) número especial 1: 81-87.
- MEINECKE, C.C. 1975. Riechensillen und Systematik der Lamellicornia (Insecta, Coleoptera). Zoomorphologie 82: 1-42.
- MORÓN, M.A. 2004. Melolontídeos edafícolas. In: Salvadori, J.R., Ávila, C.J., Silva, M.T.B. (Eds.), Pragas de Solo no Brasil. Embrapa Trigo, Passo Fundo, Brazil, p. 133-166.
- MOORE, M.R. & JAMESON, M.L. 2013. Floral associations of cyclocephaline scarab beetles. J. Insect Sc. 13(100): 1-43.
- MUNIN, R.L., TEIXEIRA, R.C. & SIGRIST, M.R. 2008. Esfingofilia e sistema de reprodução de *Bauhinia curvula* Benth. (Leguminosae: Caesalpinioideae) em cerrado no Centro-Oeste brasileiro. Rev. Bras. Bot. 31(1): 15-25. <https://doi.org/10.1590/S0100-84042008000100003>
- MUTIS, A., PALMA, R.P.L., ALVEAR, M., ISAACS, R., MORÓN, M.A. & QUIROZ, A. 2014. Morphology and distribution of sensilla on the antennae of *Hylamorphia elegans* Burmeister (Coleoptera: Scarabaeidae). Neotrop. Entomol. 43: 260-265. <https://doi.org/10.1007/s13744-014-0208-y>
- OLIVEIRA, H.N. & ÁVILA, C.J. 2011. Ocorrência de *Cyclocephala forsteri* em *Acronomia aculeata*. Pesq. Agrop. Trop. 41(2): 293-295. <https://doi.org/10.5216/pat.v41i2.8769>
- PELLMYR, O. & THIEN, L.B. 1986. Insect reproduction and floral fragrances: keys to the evolution of the angiosperms? Taxon 35(1): 76-85. <https://doi.org/10.2307/1221036>
- RENOU, M., TAUBAN, D. & MORIN, J.P. 1998. Structure and function of antennal pore plate sensilla of *Oryctes rhinoceros* (L.) (Coleoptera: Dynastinae). Int. J. Insect Morphol. Embryol. 27(3): 116-122. [https://doi.org/10.1016/S0020-7322\(98\)00014-2](https://doi.org/10.1016/S0020-7322(98)00014-2)
- RODRIGUES, S.R., GOMES, E.S. & BENTO, J.M.S. 2014. Sexual dimorphism and mating behavior in *Anomala testaceipennis*. J. Insect. Sci. 14: 210-210. <https://doi.org/10.1093/jisesa/ieu072>
- RODRIGUES, S.R., MORÓN, M.A., GOMES, E.S. & BENTO, J.M.S. 2016. Morphology of immature stages and mating behavior in *Liogenys fusca* (Blanchard) (Coleoptera, Melolonthidae, Melolonthinae). Rev. Bras. Entomol. 60(4): 284-289. <https://doi.org/10.1016/j.rbe.2016.06.005>
- RODRIGUES, S.R., FUHRMANN, J., GOMES, E.S. & AMARO, R.A. 2017. Description of immatures and mating behavior of *Liogenys bidenticeps* Moser, 1919 (Coleoptera: Melolonthidae: Melolonthinae). Rev. Bras. Entomol. 61: 339-348. <https://doi.org/10.1016/j.rbe.2017.07.006>
- RODRIGUES, S.R., FUHRMANN, J. & AMARO, R.A. 2019. Aspects of mating behavior and antennal sensilla in *Anomala inconstans* Burmeister, 1844 (Coleoptera: Scarabaeidae: Rutelinae). Biota Neotrop. 19(3): 1-7. <https://doi.org/10.1590/1676-0611-bn-2018-0664>
- ROMERO-LÓPEZ, A.A. 2016. Comunicación química de coleópteros Melolonthidae distribuidos en México: a una década de distancia. Dugesiana 23(1): 59-73. <https://doi.org/10.32870/dugesiana.v23i1.5748>
- ROMERO-LÓPEZ, A.A., ARZUFFI, R., VALDEZ, J., MORÓN, M.A., CASTREJÓN-GÓMEZ, V. & VILLALOBOS, F.J. 2004. Sensory organs in the antennae of *Phyllophaga obsoleta* (Coleoptera: Melolonthidae). Ann. Entomol. Soc. Am. 97(6): 1306-1313. [https://doi.org/10.1603/0013-8746\(2004\)097\[1306:SOITAO\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2004)097[1306:SOITAO]2.0.CO;2)
- ROMERO-LÓPEZ, A.A., MORÓN, M.A. & VALDEZ, J. 2010. Sexual dimorphism in antennal receptors of *Phyllophaga ravidia* Blanchard (Coleoptera: Scarabaeoidea: Melolonthidae). Neotrop. Entomol. 39(6): 957-966. <https://doi.org/10.1590/S1519-566X2010000600018>
- RUTHER, J., REINECKE, A., THIEMANN, K., TOLASCH, T., FRANCKE, W. & HILKER, M. 2000. Mate finding in the forest cockchafer, *Melolontha hippocastani*, mediated by volatiles from plants and females. Physiol. Entomol. 25: 172-179. <https://doi.org/10.1046/j.1365-3032.2000.00183.x>
- SALDANHA, F.G., RODRIGUES, S.R., AMARO, R.A. & FUHRMANN, J. 2020. Description of mating behavior, life cycle, and antennal sensilla of *Cyclocephala putrida* Burmeister, 1847 (Coleoptera, Scarabaeidae, Dynastinae). Biota Neotrop. 20(3): e20200973. <https://doi.org/10.1590/1676-0611-bn-2020-0973>
- SANTOS V. & ÁVILA, C.J. 2009. Aspectos biológicos e comportamentais de *Liogenys suturalis* Blanchard (Coleoptera: Melolonthidae) no Mato Grosso do Sul. Neotrop. Entomol. 38(6): 734-740. <https://doi.org/10.1590/S1519-566X2009000600005>
- SCHIESTL, F.P. & DÖTTERL, S. 2012. The evolution of floral scent and olfactory preferences in pollinators: coevolution or pre-existing bias? Evolution 66(7): 2042-2055. <https://doi.org/10.1111/j.1558-5646.2012.01593.x>
- SCHNEIDER, D. 1964. Insect antennae. Ann. Rev. Entomol. 9: 103-122. <https://doi.org/10.1146/annurev.en.09.010164.000535>
- SEYMOUR R.S., SILBERBAUER-GOTTSBERGER, I. & GOTTSBERGER, G. 2010. Respiration and temperature patterns in thermogenic flowers of *Magnolia ovata* under natural conditions in Brazil. Funct. Plant Biol. 37: 870-878. <https://doi.org/10.1071/FP10039>
- ŠÍPEK, P., FABRIZI, S., EBERLE, J. & AHRENS, D. 2016. A molecular phylogeny of rose chafers (Coleoptera: Scarabaeidae: Cetoniinae) reveals a complex and concerted morphological evolution related to their flight mode. Mol. Phyl. Evol. 101: 163-175. <http://dx.doi.org/10.1016/j.ympev.2016.05.012>
- SHAO, K.M., SUN, Y., WANG, W.K. & CHEN, L.A. 2019. SEM study of antennal sensilla in *Maladera orientalis* Motschulsky (Coleoptera: Scarabaeidae: Melolonthinae). Micron 119: 17-23. <https://doi.org/10.1016/j.micron.2019.01.004>
- SHAUGHNEY, J.M. & RATCLIFFE, B.C. 2015. A monographic revision of the genus *Hoplopyga* Thomson, 1880 (Coleoptera: Scarabaeidae: Cetoniinae: Gymnetini). Coleop. Bull. 69(4): 579-638. <https://doi.org/10.1649/0010-065X-69.4.579>
- SILVEIRA NETO, S. & SILVEIRA, A.C. 1969. Armadilha luminosa modelo "Luiz de Queiroz". Solo 61: 19-21.
- SOLÍS, A. 2004. Escarabajos fruteros de Costa Rica. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica, 238 pp.
- STEFANELLO M.E.A., ALVARENGA, M.A., TOMA, I.N. & MELLO-SILVA, R. 2005. Ocorrência de quimiotipos em *Talauma ovata*, uma planta medicinal brasileira. Rev. Bras. Plant. Med. 8: 1-3.
- SUN, H., GUAN, L., FENG, H., YIN, J., CAO, Y., XI, J. & LI, K. 2014. Functional characterization of chemosensory proteins in the scarab beetle, *Holotrichia oblita* Faldermann (Coleoptera: Scarabaeida). PLoS ONE 9(9): e107059. <https://doi.org/10.1371/journal.pone.0107059>
- TANAKA, S., YUKUHIRO, F. & WAKAMURA, S. 2006. Sexual dimorphism in body dimensions and antennal sensilla in the white grub beetle, *Dasylepida ishigakiensis* (Coleoptera, Scarabaeidae). Appl. Entomol. Zool. 41(3): 455-461. <https://doi.org/10.1303/aez.2006.455>
- VUTS, J., IMREI, Z., BIRKETT, M.A., PICKETT, J.A., WOODCOCK, C.M. & TÓTH, M. 2014. Semiochemistry of the Scarabaeoidea. J. Chem. Ecol. 40: 190-210. <https://doi.org/10.1007/s10886-014-0377-5>

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