

**Research article**

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**The life cycle of a Brazilian *Chlamisus* leaf beetle on its Malvaceae host plants (Coleoptera: Chrysomelidae, Cryptocephalinae, Fulcidacini)**

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**Abstract**

The Fulcidacini (Coleoptera: Chrysomelidae, Cryptocephalinae) is a group of beetles in which the females build a shelter of feces around their eggs and the hatched larvae maintain and expand this shelter with their own feces. *Chlamisus* Rafinesque, 1815 is the largest genus in the Fulcidacini, but immatures of only 25 of the ~400 recognized species have been reported. This paper presents, for the first time, the complete and detailed life cycle of a *Chlamisus* species. Adults were found feeding on Malvaceae (Hermannieae) in the semi-arid region of Brazil; some were collected for laboratory rearing and observation. Captive adults oviposited in individual containers. These eggs were kept in individual containers and after hatching, the larvae were fed and monitored daily until the adults emerged. The pre-imaginal period lasted 87.0 days, with four larval instars, each building on the fecal case from the previous instar. The period from egg fecal capsule to larval emergence was 14.75 days. The larval period lasted approximately 46.54 days. The period in the pupa fecal chamber lasted for 28.5 days. The active period of the immature represented about 45% of its total development time. This *Chlamisus* sp. appears to be monophagous in a broader sense, completing its development on related species and genera of Malvaceae (Hermannieae) and probably having more than one generation per year. The larvae exhibit a novel behavior in their case-construction, cutting off and discarding part of the case before pupation. The pupal chamber appears to be a novelty, mimicking the dried inflorescence of its Malvaceae host plants (in the genera *Waltheria* Linnaeus and *Melochia* Linnaeus).

**Key words:** Behavior, immatures, *Melochia*, *Waltheria*, warty leaf beetles.

**Introduction**

The Fulcidacini (= Chlamisini), one of five tribes of Cryptocephalinae, comprises about 500 species in 11 genera (Chamorro 2014; Gómez-Zurita & Cardoso 2021). Like the rest of the subfamily, adults have an anteriorly flattened hypognathous head that is almost or completely retracted into the prothorax (Chamorro 2014). Cryptocephalinae and Lamprosomatinae together are called the Camptosomata, a clade within Chrysomelidae, recognized by the construction of fecal shelters by the female for her eggs [fecal capsules], and by the offspring throughout its immature phase carrying these cases [larva fecal case and pupa fecal chamber]. Hence, Camptosomata are popularly called “case-bearers”

(Erber 1988). These cases have been hypothesized to function as a hard barrier that protects the offspring from extreme abiotic conditions and from natural enemies (Root & Messina 1983). They mimic buds and other host-plant structures (LeSage 1984), as well as plant debris or insect feces (LeSage 1982).

The Fulcidacini are commonly called “warty leaf beetles”, because of their tuberculate dorsal surface. They occur mostly in the Americas, except for *Aulacomela* Doweld, 2014, which also occurs in Africa and Asia; the nearly cosmopolitan *Chlamisus* Rafinesque, 1815; *Exema* Lacordaire, 1848, which also occurs in Asia; and *Hymetes* Lacordaire, 1848, which is endemic to Asia (Chamorro-Lacayo & Konstantinov 2009). Fulcidacini are thought to have



**Figs 1-3** – Species of *Chlamismus* Rafinesque, 1815 (Coleoptera: Chrysomelidae, Cryptocephalinae, Fulcidacini) from northeastern Brazil, ♀. **1**, dorsal habitus; **2**, ventral habitus; **3**, lateral habitus. Scale bars: 1 mm.

originated in the present Neotropical Region ~110 Ma ago when this landmass was already isolated from Gondwana; other regions were colonized later (Gómez-Zurita & Cardoso 2021).

*Chlamismus* is the most speciose genus in Fulcidacini, with more than 400 recognized species (Chamorro-Lacayo & Konstantinov 2009). This genus is more similar to *Exema* and *Neochlamismus* Karren, 1972, from which it can be separated by the body usually without iridescence; canthus of eye usually without yellow spots; male ejaculatory guide symmetrical; males without spines or spinulae on first abdominal ventrite; fifth antennomere nearly as large as sixth; sutural serration of elytra usually incomplete; and prosternum posteriorly much narrower than anterior margin (Chamorro-Lacayo & Konstantinov 2009). In Brazil, *Chlamismus* alone comprises 218 species of the 255 recorded species of Fulcidacini; the other 37 species are distributed amongst the other nine genera (Chamorro & Sekerka 2024).

The genus has not been revised, and its taxonomic boundaries are unclear, leading to problems in understanding evolutionary patterns. Data on juveniles are known for 25 *Chlamismus* species, 10 of which are Neotropical (Chaboo et al. 2016). Nine of the Neotropical species with some information on immatures occur in Brazil (Chamorro & Sekerka 2024).

Each immature stage has a specialized morphology for building and carrying the case. The behavior, morphology and case architecture can contribute for taxonomy and phylogeny (Chaboo et al. 2008). Fecal construction behavior has evolved multiple times in Chrysomelidae (Chaboo et al. 2023).

Although host-plant associations help to sort *Chlamismus* species (Brown 1952), and their records provide insight into host choice (Bokermann 1963; Agrain et al. 2024), accurate diagnoses of *Chlamismus* species require a robust accumulation of this type of information.

Despite so many recognized species, little is known about *Chlamismus* biology. Thus, expanding biological information on a greater number of species could help solve fundamental problems of taxonomy and evolution inside this speciose group. This study addresses this challenge by reporting for the first time the life cycle of a *Chlamismus* species from the Brazilian semi-arid region.

## Materials and methods

Adults of a *Chlamismus* species were discovered in July 2019 in the Municipality of Jacaré dos Homens, 9.34.39S, 37.15.18W, 258 m, State of Alagoas, semi-arid region of northeastern Brazil. This area has an annual accumulated rainfall of 586.7 mm (INMET 2024) and is characterized by a hot semi-arid climate (BSh), according to the Köppen-Geiger climate classification (Kottek et al. 2006; Beck et al. 2023). Couples feeding on a species of *Waltheria* L. (Malvaceae) were collected and transported for rearing at the Laboratório de Bioecologia de Insetos (Instituto de Ciências Biológicas e da Saúde, Universidade Federal de Alagoas) in Maceió, a coastal municipality and capital of Alagoas. After the insect rearing was finished, in June 2021, the same beetle species was again sighted and collected in an area close to the first collection site, 9.39.43S, 37.13.60W, 160 m, this time feeding on *Melochia* sp. (Malvaceae).

The rearing began in August 2019 (24–26.1 °C; 62.3–77.3% RH; 12:12 h photoperiod), using a *Waltheria* sp. found nearby. The rearing process took place in two phases, both with daily monitoring, cleaning, and food replacement with the addition of young fresh branches with leaves and inflorescences. In the first phase, for egg production, couples ( $n = 2$ ) were kept in separate cages ( $\approx 300 \text{ cm}^3$ ) made of polyethylene terephthalate bottles (Lima & Carvalho 2017).

In the second phase, for immature rearing, the eggs produced ( $n = 28$ ) were individualized in polypropylene containers ( $\approx 140 \text{ cm}^3$ ) and the hatched larvae were observed until adult emergence. The following biological phenomena were recorded chronologically: (1) oviposition; (2) rupture of the egg fecal capsule (or egg capsule); (3) beginning and end of moulting processes; (4) cessation of feeding; and (5) exit from the pupa fecal chamber (or pupal chamber).

The dead reared larvae ( $n = 26$ ) were preserved in a container with a 70% ethanol solution. Vouchers of adults (DZUP 325063-325069) were mounted, using the double-mount technique, and deposited in the Coleção Entomológica Padre Jesus Santiago Moure, Universidade Federal do Paraná (DZUP), Curitiba, Paraná, Brazil. An identification key for Fulcidacini (Chamorro-Lacayo & Konstantinov 2009) was used to identify the beetle genus. The beetle was also compared with specimens in DZUP identified by Werner Bokermann. The host plants are deposited in the MAC Herbarium, Instituto do Meio Ambiente de Alagoas, Brazil, and identified by the biologist Erlande Lins da Silva.

## Results

The beetle was confirmed as a member of *Chlamisus* (Figs 1-3); in similar genus *Exema*, fifth antennomere is much smaller than sixth, and sutural serration of elytra is complete (Chamorro-Lacayo & Konstantinov 2009). Due to unresolved taxonomic issues of the group, it was not possible to identify the beetle species at this time, even when compared with expert-identified specimens deposited in DZUP. Although being thus far unidentified, comparisons with DZUP specimens suggest that this species is similar, and probably closely related, to *Chlamisus melochiae* Monrós, 1952. The sexes of the studied species are externally similar, with size varying from 4.08 mm to 4.56 mm. Females are slightly larger than males and have a fovea in the middle of the fifth abdominal ventrite.

The plant from which adult beetles were collected in field was identified as *Waltheria rotundifolia* Schrank (MAC 65503) (Malvaceae, Hermannieae). The second plant from which they were collected was identified as *Melochia tomentosa* Linnaeus (MAC 65504) (Malvaceae, Hermannieae). Plant used as food for rearing *Chlamisus* sp. in laboratory was identified as *Waltheria indica* Linnaeus (= *Waltheria americana* L.) (MAC 65042).

In nature, larvae and adults of the here studied unidentified *Chlamisus* species feed on Malvaceae, on leaves of *Waltheria rotundifolia* (Fig. 4) and *Melochia tomentosa* (Fig. 5). This beetle does not defoliate the plant, but its feeding behavior causes large irregular holes. Feeding on stems, flowers and fruits has not been observed. *Waltheria indica* is scarce in the area where beetles were collected and there were no sightings on this plant of the *Chlamisus* sp. reported here.

The rearing allowed to determine duration of each life stage and number of larval instars. Pre-imaginal development, from oviposition to adult emergence, lasts 87.0 days ( $n = 2$ ). The period from egg capsule (egg wrapped in maternal feces) and its opening by larva lasts 14.75 days ( $n = 28$ ). The larval period has four stages and lasts approximately 46.54 days ( $n = 11$ ). The pupal chamber period (prepupa and then pupa wrapped in larval feces) lasts 28.5 days ( $n = 2$ ). The larval activity period represents approximately 45% ( $n = 11$ ) of the total pre-imaginal development time.

The eggs of this species of *Chlamisus* are generally deposited singly or in small clusters on stems, petioles, and adaxial surfaces of leaves of younger branches of the plant (Figs 6-7). The egg fecal capsule is rounded, shaped like honey pot, with rounded base attached to substrate by a stalk and other end with a flattened fecal seal (Fig. 6); adult female takes up to 15-20 minutes to build each capsule. Instar I lasts 11.5 days ( $n = 22$ ), during which larvae expand maternal egg case using their own feces and add leaf trichomes (Fig. 8). These plants have dense trichomes, appearing almost silvery (Figs 4-5), and larvae use them in their own cases throughout development. Instar II, lasting 9.42 days ( $n = 19$ ), also use sepals and petals of inflorescences, partially adhering them to the wall of their cases. From instar III, which lasts 11.84 days ( $n = 13$ ), use of these floral parts becomes more frequent and culminates in instar IV, which lasts 15.69 days ( $n = 13$ ) (Figs 9-10). These older cases (Fig. 10) exhibit three sections: apical rounded maternal egg case, central younger case with a few floral parts and some trichomes, and wider basal section with many floral parts and thick trichomes.

Halfway through instar IV, after 7.78 days ( $n = 14$ ), larvae use their mandibles to cut off the apex of larval case transversely (Fig. 11). This cut section is dropped off. Discarded part corresponds to fecal shelter built by mother around egg, and sections of fecal case added by instars I-II, which have least number of floral parts adhering to the wall; the hole left behind is sealed with fecal material. When instar IV larvae finally adhere to stem substrate and seal case for pupation, fecal shelter, now without top, takes on appearance of host's dried inflorescence (Figs 12-13).

Survival of lab sample was low, with only 7.14% of immatures (2 of the 28 larvae that hatched from the eggs) becoming active adults.

## Discussion

*Chlamisus* is a polyphagous genus, using hosts from six families: Euphorbiaceae (Friebig 1910); Loranaceae (Reid 1991); Magnoliaceae (Medvedev & Zaitsev 1979 in Chaboo et al. 2016); Malpighiaceae (Reu Jr & Del-Claro 2005); Malvaceae (Friebig 1910; Bokermann 1963; Karren 1972); and Mimosaceae (Reid 1991). A total of 87 species in 52 genera in 26 families of plants are associated

with *Chlamisus* (Agrain et al. 2024). The fact that this *Chlamisus* species feeds on two closely-related genera of the same botanical family is a sign of monophagy (in a broad sense), i.e. an insect species that potentially feeds on genera that are closely related (Biondi 1996; Trigo et al. 2012; Biondi et al. 2013).

It is possible that the plant used for feeding in this study influenced the development of *Chlamisus* sp., since no beetles were found on *W. indica* in the nature. *Waltheria indica* is more common in the coastal region, under a different climate regime, and is rare in the semi-arid region where adults of *Chlamisus* sp. were collected. In turn, this (in a broad sense) apparently monophagous beetle was not found in the coastal region and its food plants seem to be restricted to the semi-arid region.

Other genera of Fulcidacini have been found to have four larval stages (Hyche 1996; Flinte & Macêdo 2004; Brown & Funk 2005; Shin et al. 2012). *Fulcidax monstrosus* (Fabricius, 1798) has an egg capsule period of 10 days (Flinte & Macêdo 2004), while *Neochlamisus bimaculatus* (Karren, 1972), *Neochlamisus gibbosus* (Fabricius, 1777) and *Neochlamisus platani* (Brown, 1952) have an egg capsule period of 1-2 weeks (Hyche 1996; Brown & Funk 2005; Shin et al. 2012).

The larval period of *F. monstrosus* can last up to four months, while that of *N. bimaculatus* and *N. platani* four to five weeks (Hyche 1996; Flinte & Macêdo 2004; Brown & Funk 2005). For *N. gibbosus*, it takes 10 to 20 days for the first three larval instars and up to 30 days for instar IV (Shin et al. 2012). The pupal chamber period lasts approximately 20 days for *N. bimaculatus*, varying from one to three weeks for *N. gibbosus*, and from 17 to 22 days for *N. platani* (Hyche 1996; Brown & Funk 2005; Shin et al. 2012). *Fulcidax monstrosus* remains in the pupal chamber for four months (Flinte & Macêdo 2004).

The only other *Chlamisus* species whose life cycle has been observed is *Chlamisus minax* (Lacordaire, 1848), but not in the detail of the aforementioned studies. Reu Jr & Del-Claro (2005) suggested that this species has six “morphometric stadia”, but the approximate duration of each developmental stage is unknown, because moulting was not observed. *Chlamisus minax* feeds exclusively on *Heteropterys pteropetala* A. Juss. (Malpighiaceae), where the larvae feed on flower buds and petals; adults appear during flowering season and are univoltine with a pupal diapause [or adult diapause reclusive in the pupal chamber] of about six months (Reu Jr & Del-Claro 2005).

Current knowledge of the immature stages of Fulcidacini is still scarce, so the group is still awaiting a systematics development able to recognize taxa based on eggs, larvae or pupae. However, it is believed that the maternal fecal plates used to build the egg capsule have unique characteristics for each species (Erber 1988). In addition to the rounded, honeypot-like appearance, the egg capsule of *Chlamisus* sp. observed in this study has its fecal plates

arranged in horizontal rows, overlapping from the base to the top, but each one with a pointed distal margin free of contact, giving the capsule surface the appearance of a pine cone (Figs 6-7). The surface of the egg capsules of species of *Neochlamisus* Karren, 1972 is smoother, being difficult to see each fecal plate and its disposition (Brown & Funk 2005; Chaboo et al. 2008). As this *Chlamisus* sp., species of *Pseudochlamys* Larcodaire, 1848 also has a well-marked fecal plates disposition (Duarte-de-Mélo, personal observation), but with a capsule with a bell-like format as in *Neochlamisus* spp. (Chaboo et al. 2008).

In addition to new host plants and life cycle findings, three aspects of the behavior of this *Chlamisus* species are unusual. First, the case is “furry” with trichomes (Figs 8-10), indicating that the larva cuts trichomes and attaches them to the case wall as it builds it; such behavior has not been reported in camptosomates, but it occurs in a *Pseudochlamys* species that also feeds on *Waltheria* spp. (Duarte-de-Mélo, personal observation). Camptosomata larval fecal cases are constructed primarily of feces, but with inclusions of other materials—secretions, soil, plant fragments, trichomes (Packard 1869; Monrós 1953; Karren 1964; Brown & Funk 2005; Chaboo et al. 2008). These structural components may strengthen the case or enhance camouflage and mimicry as a defense. The case wall is hard and forms a protective barrier around the soft, vulnerable larvae (Fig. 14), and the pupae later (Fig. 15).

This study reports that *Chlamisus* sp. has a second unusual feature: the cutting and addition of sepals and petals, not reported in known camptosomate cases. Since these cases resemble the dried inflorescence of the plant (Figs 12-13), a likely hypothesis is that this mimicry may help this insect to hide on the plant and thus avoid enemies.

The preparation of the pupal chamber by cutting and discarding the sections built by the mother and instars I-II is unique amongst Camptosomata (Figs 16-17). Nevertheless, Reu Jr & Del-Claro (2005) point out that the upper part of the case of *C. minax* is broken during the pupation process, leaving only the large base. Certainly, the narrow upper section of the fecal case cannot contain the fat prepupal body and seems to be of little purpose. Brown & Funk (2005) reported the storage of trichomes in this upper part of the case for some species of *Neochlamisus*.

In addition to new information about the life cycle and behavior of adults and immature stages of Fulcidacini, this work reports three more associations between *Chlamisus* and Malvaceae, the fifth record on *Waltheria* (Friebig 1910; Bokermann 1963; Karren 1972) and the second on *Melochia* (Friebig 1910).

The morphology, behavior, and ecology of *Chlamisus* show many intriguing features. The variation in case construction behavior may offer diagnostic and phylogenetic information. Detailed natural history studies and specimen collections are crucial to resolve current problems in taxonomy and phylogeny.



**Figs 4-11** – Immatures of species of *Chlamisus* Rafinesque, 1815 (Coleoptera: Chrysomelidae, Cryptocephalinae, Fulcidacini) on *Waltheria rotundifolia* Schrank, *W. indica* Linnaeus and *Melochia tomentosa* Linnaeus (Malvaceae). 4, larva on *W. rotundifolia* (circle); 5, larva on *M. tomentosa* (circle); 6-7, eggs on *W. rotundifolia*; 8, instar I larva on *W. rotundifolia*; 9, older larvae on *W. rotundifolia*; 10, older larvae on *W. indica*; 11, larval case without apex, after being cut by the larva (arrow). Scale bar: 1 mm.



**Figs 12-17** – Adult and immatures of *Chlamisus* Rafinesque, 1815 (Coleoptera: Chrysomelidae: Cryptocephalinae: Fulcidacini) on *Waltheria rotundifolia* Schrank and *W. indica* Linnaeus (Malvaceae). **12**, adult on *W. rotundifolia* (circle); **13**, pupal chamber (left arrow) next to a dried inflorescence (right arrow) of *W. indica*. **14-17**, instar IV larva. Scale bars: 1 mm.

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