



On the natural history of *Pseudochlamys megalostomoides* Lacordaire, 1848 (Coleoptera: Chrysomelidae: Cryptocephalinae)

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Received: 6 August 2025 / Accepted: 28 March 2026 / Published online: 21 April 2026
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Abstract

The subfamily Cryptocephalinae (Coleoptera: Chrysomelidae) is characterized by the behavior of constructing fecal shelters. Despite such a peculiar biology, there are few studies on their natural history. In view of this need, we present here for the first time the natural history of a species of *Pseudochlamys* Lacordaire, 1848. Adults were collected and reared in the laboratory at a temperature of around 25 °C. Eggs produced were individualized, and hatched larvae were fed and monitored daily until adult emergence. Emerged adults were monitored in couples for the reproductive performance of the females. Parasitoidism was also observed on eggs collected in the field. *Pseudochlamys megalostomoides* Lacordaire, 1848 has four larval instars. The preimaginal period lasted 89.95 days: 15.27 in the fecal egg capsule; 46.83 as a larva; and 28 days in the pupal chamber. The active period of the immature was about 39.61% of its development. Females lived for 71.25 days, ovipositing for 41 days. Of the eggs collected in the field, 49.31% were parasitized and only 23.43% were viable. Unlike most Cryptocephalinae taxa, *P. megalostomoides* is a monophagous species that feeds on *Waltheria indica* Linnaeus and *Waltheria rotundifolia* Schrank. This beetle is parasitized by Entedoninae (Hymenoptera: Eulophidae) and Pteromalidae (Hymenoptera). This species of *Pseudochlamys* probably has more than one generation per year.

Keywords Camptosomata · Fecal defenses · Host plants · Leaf beetles · Life cycle · Parasitoids

Introduction

Cryptocephalinae is a group of leaf beetles characterized by adults with an anteriorly flat head retracted into the prothorax, with phytophagous adults and usually saprophagous larvae (Chamorro 2014). This subfamily, along with Lamprosomatinae, forms the clade Camptosomata, whose popular name (casebearers) and monophyly are based on the complex behavior of the female constructing a fecal shelter to protect the egg, and then the larva expanding it with each instar and using it for protection until the adult emerges and leaves (Erber 1988; Brown and Funk 2005; Chaboo et al. 2008; Gómez-Zurita and Cardoso 2021).

Despite such a peculiar biological feature, there is a lack of studies on the natural history of Cryptocephalinae (Chaboo et al. 2008; Agrain et al. 2015). The little information available on the life cycle is usually limited to a single life stage and almost always includes approximate durations (Wood 1966; Flinte and Macêdo 2004; Reu Jr and Del-Claro 2005; Jerez and Briones 2010; Shin et al. 2012). Information on other aspects of life history such as fecundity, fertility and longevity is even scarcer (LeSage 1986; Perecin 2003). Regarding their trophic associations, there are host plant records for 83 genera of Cryptocephalinae and parasitoid records for only eight genera of this subfamily (Chaboo et al. 2016; Agrain et al. 2024).

The same scenario applies to the Fulcidacini (=Chlamisini), cryptocephalines known as warty leaf beetles due to the tubercles on the elytral surface, a tribe that comprises about 500 species in 11 genera (Chamorro 2014). The core of their distribution and origin appears to be the area that currently corresponds to the Neotropical region (Gómez-Zurita and Cardoso 2021). Complete and rigorous data on the life cycle of Fulcidacini are scarce (Brown and

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Funk 2005; Duarte-de-Mélo et al. 2025), with only superficial information and approximations available (Flinte and Macêdo 2004; Reu Jr and Del-Claro 2005; Shin et al. 2012). To date, there are records of 192 host plant species for only eight genera of Fulcidacini, and only eight records of parasitoids on species from four genera of warty leaf beetles (Chaboo et al. 2016; Agrain et al. 2024).

In response to a need for knowledge of the biology of this group, aspects of the natural history of a species of *Pseudochlamys* Lacordaire, 1848 (Cryptocephalinae: Fulcidacini) are presented for the first time. Temporal developmental variables, reproduction and parasitization of eggs are described, in addition to other bioecological information.

Material and methods

Collection

Adult Fulcidacini were collected by hand from Malvaceae plants in November 2018 at the Campus A. C. Simões of the Universidade Federal de Alagoas (−9.557219, −35.775039; 86 m a.s.l.), located in the peri-urban area of the Municipality of Maceió, State of Alagoas, Brazil, approximately 2 km from the Área de Proteção Ambiental do Catolé e Fernão Velho. According to the Köppen-Geiger climate classification, the Maceió area is characterized by a tropical monsoon climate (Am) (Kottek et al. 2006; Beck et al. 2023), with an annual accumulated precipitation of 1808.1 mm (INMET 2024).

Adults of the same beetle species were also collected feeding on a second Malvaceae species in Jacaré dos Homens (−9.577611, −37.255194; 258 m a.s.l.), in the interior of Alagoas. This area has an accumulated annual 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).

Some adults were point-mounted and part of the material was deposited in the Coleção Entomológica Padre Jesus Santiago Moure (DZUP) of the Universidade Federal do Paraná. Beetles were identified using an identification key for Fulcidacini genera (Chamorro-Lacayo and Konstantinov 2009) and then using original species descriptions. Exsiccates of the host plants were prepared and sent to the MAC Herbarium of the Instituto do Meio Ambiente de Alagoas for deposition, where they were identified by the biologist Erlande Lins da Silva.

Terminology for biological data

Knowing that much of the development of immature Campsosomata occurs within a fecal shelter, caution must be exercised in the use of terms that should be more general to refer

to what would be typical stages of an insect's life cycle. The terms must encompass the developmental stage itself and the observable biological phenomena that indicate its occurrence. Additionally, it is essential to utilize terms that mirror structures with separate origins and forms, that is, in a broad sense: (1) the encapsulated construction of the mother for her egg; (2) the expanding construction of the larva for itself; and (3) the enclosed shelter of the larva for pupation.

The observable biological phenomena in the life cycle of species in this group are: (1) rupture of the egg capsule; (2a) cessation of feeding and (2b) resumption of feeding; (3) final sealing of the larval case; and (4) exit from the pupal chamber.

The demarcation of such biological phenomena has made it possible to characterize the following periods of preimaginal development: (i) within the egg capsule, covering embryonic development; (ii) during larval feeding activity and inactivity, marking and covering a larval instar at each process of feeding stop (molting); and (iii) within the pupal chamber, including the prepupal and pupal stages.

Rearing for life history study

In the laboratory (24.4–26.8 °C; 55.2–74.5% RH; 12-h photophase), beetles were sexed and separated into couples for rearing in cages made of polyethylene terephthalate bottles ($\approx 300 \text{ cm}^3$) (Lima and Carvalho 2017). These couples were fed fresh branches of the host plant, whose turgor was maintained by immersing the stem base in water in a microtube with the opening sealed with paper towels.

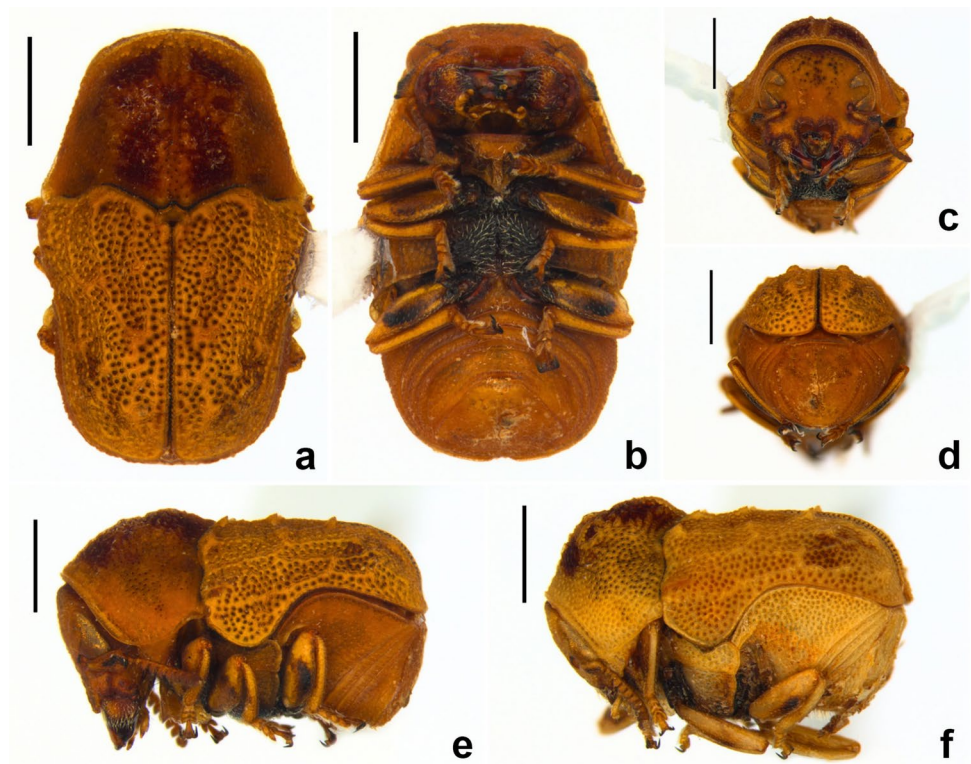
The eggs produced were removed daily from each cage and separated into a container labeled with the date of oviposition. The hatched larvae were individually reared in an acrylic container ($\approx 140 \text{ cm}^3$) under the same feeding conditions as described above until pupation, and each observable biological phenomenon was recorded.

Couples of individuals with similar pupal chamber exit dates were grouped from the adults that emerged in the laboratory. These couples were monitored daily and maintained under the same laboratory conditions described above. Oviposition dates were recorded, and eggs were collected and counted daily for each couple, placed in microtubes labeled by origin and date, until the death of the females. The viability of the eggs produced by each female was also recorded.

The adult phase of a fertile female was considered to be formed by the pre-oviposition, oviposition, and post-oviposition periods. Fecundity (total number of eggs laid), fertility (total number of fertile eggs) and infertility were considered as oviposition variables.

Dead larvae were preserved in a 70% alcohol solution and adults were point-mounted. Approximately one year after the last cases were sealed by the prepupae, the still-closed pupal

Fig. 1 Adult of *Pseudochlamys megalostomoides* Lacordaire, 1848 (Coleoptera: Chrysomelidae: Cryptocephalinae: Fulcidacini) collected in Maceió, State of Alagoas, Brazil (−9.557219, −35.775039; 86 m a.s.l.). **a** Dorsal view, male. **b** Ventral view, male. **c** Frontal view, male. **d** Caudal view, male. **e** Lateral view, male. **f** Lateral view, female. Scale bars: 1.0 mm



chambers were opened to analyze the potential sex ratio and determine adult mortality.

Egg collection for parasitoidism observation

Manual egg collection was carried out on *W. indica* in the same area of Maceió mentioned above. Eggs were collected in April 2019 and six months later in October of the same year.

The collected material was monitored daily in the laboratory under the same conditions mentioned above to verify the egression of parasitoids. Each egg was individualized in a 0.2 ml microtube to ensure correspondence between individuals and their respective data.

The hatched larvae and emerged parasitoids were preserved in 70% alcohol. The parasitoids were identified using an identification key for Brazilian Hymenoptera (Melo and Dal Molin 2024). Part of the parasitoid material was deposited at DZUP.

Results

The beetle and its host plant

The beetle was identified as *Pseudochlamys megalostomoides* Lacordaire, 1848 (Fig. 1) (DZUP 325051–325062). This species has a generally yellowish body and elytra

strongly punctured with small tubercles and longitudinal ridges; length about 4 mm ($n=6$).

The host plant from which the beetles were collected in Maceió was identified as *Waltheria indica* Linnaeus (Malvaceae) (= *Waltheria americana* Linnaeus) (MAC 65042) (Fig. 2a), and that from the collection in Jacaré dos Homens was identified as *Waltheria rotundifolia* Schrank (MAC 65503) (Fig. 2b).

Bioecological data

Adult *P. megalostomoides* prefer to feed on young leaves of the host plant, where they can be seen copulating (Fig. 2a). When touched, they react with thanatosis (tonic immobility), falling to the ground, or by flying, during hot hours of the day. Females lay a single egg per oviposition event, in a complex process that involves covering the egg with fecal plates and can take about 20 min (Fig. 2c; Online resource). Preferred oviposition sites are the adaxial surface of leaves, the petiole and the stem, almost always on young branches (Fig. 2d, e). It is possible to see many egg capsules (Fig. 2f) deposited in a straight line on a single leaf as the result of multiple oviposition events by a single female. Naked eggs or eggs with an incomplete capsule (partially covered by feces) were found to be non-viable (Fig. 2g).

It is possible to find numerous individuals in different life stages on a single plant. As previously mentioned, adults feed and mate on the young leaves of the plant; therefore,

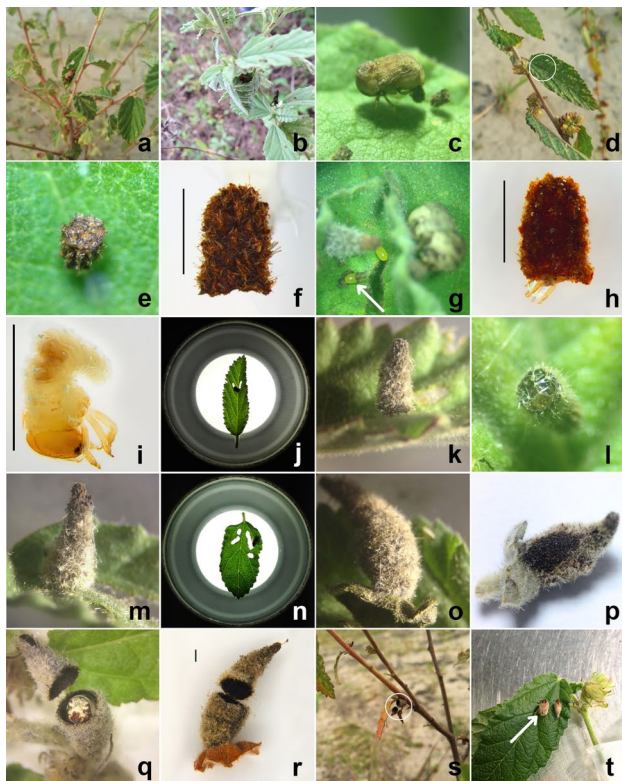


Fig. 2 Bioecological aspects of *Pseudochlamys megalostomoides* Lacordaire, 1848 (Coleoptera: Chrysomelidae: Cryptocephalinae: Fulcidacini) on *Waltheria indica* Linnaeus and *W. rotundifolia* Schrank (Malvaceae). **a** *Waltheria indica* in Maceió, State of Alagoas, Brazil (−9.557219, −35.775039; 86 m a.s.l.). **b** *Waltheria rotundifolia* in Jacaré dos Homens, State of Alagoas, Brazil (−9.577611, −37.255194; 258 m a.s.l.). **c** Oviposition of *P. megalostomoides*. **d** Egg capsule on leaf of *W. indica* (white circumference). **e** Dorsal view of egg capsule on leaf. **f** Lateral view of egg capsule. **g** Naked egg (arrow). **h, i** Lateral view of instar I larva with and without case. **j** Leaf injury caused by instar I larva. **k** Advanced instar I larva just before molting. **l** Instar I larva during molting. **m** Instar IV larva. **n** Leaf injury caused by instars III–IV larvae. **o, p** Pupal chamber. **q** Cut pupal chamber with adult male still inside. **r** Empty pupal chamber. **s** Empty pupal chamber on *W. indica* (white circumference). **t** Similar appearance between adult in dorsal view (arrow) and fallen dried flower of *W. indica*. Scale bars: 1.0 mm

they and their eggs are found at the top of the branches. Larvae in instars I and II are also found on young leaves at the top of the branches. Instars III and IV are more itinerant, and are the ones, including the pupae, that can generally be found on the lower parts of branches, on stems, the base of inflorescences, petioles, or leaves.

The egg capsule is shaped like a bell. The rounded base is attached to the substrate by a stalk, and the other end is truncated with a flattened fecal seal (Fig. 2e, f). After hatching, the larva expands the egg capsule with its feces, as well as leaf and stem trichomes from the host plant (Fig. 2h–p). The larva also uses the trichomes to temporarily close the case when adhering to the substrate to molt (Fig. 2l). When

the larva is in instar IV, three regions can be observed in its case: (1) the region corresponding to the maternal capsule in the apical area, which has a different color and texture, and it lacks attached trichomes; (2) the basal part corresponding to the larval construction, with numerous attached trichomes; and (3) a longitudinal, bare scar of a darker color, that appears at the back of the case from instar III onwards, when the larva needs to enlarge the internal space to accommodate its larger body (Fig. 2p). During emergence, the adult is positioned at a 180° angle relative to the larval position and makes a transverse cut at the top of the pupal chamber in the boundary region built by the instar II larva. Through this opening, one can see that, at some point, the larva reverses its position and creates an internal fecal seal just above the area where the adult will make the transverse cut.

The instar I larvae (Fig. 2h, i), upon opening their capsules, feed on the leaves closest to the oviposition site, leaving damage in the form of irregular holes (Fig. 2j); as they grow, they seek new places on the plant to feed. Before each ecdysis, the larva attaches the opening of the case to the leaf surface and stop feeding for a period that includes the molting process (Fig. 2k, l). Instars III and IV (Fig. 3m, n) are more voracious, even feeding on the outer stem tissue. The larva could be seen moving around while carrying a relatively large case, with only its legs and head exposed. When threatened, the larva retracts its entire body into the case, firmly fixing the opening to the leaf surface. The instar IV larvae usually attach the case to the stem surface of the host plant and seal its opening definitively with a denser fecal material, forming the pupal chamber. Then, the prepupae invert its position at an angle of 180° and only then pupate (Fig. 2o, p). Upon emergence, adults leave the chamber after making a transverse cut at the apex of the shelter with its mandibles (Fig. 2q–s). The dorsal habitus of adults of *P. megalostomoides* resembles the appearance of a dried fallen flower of *W. indica* (Fig. 2t).

Life history

Pseudochlamys megalostomoides had a preimaginal period of 89.95 days ($n=22$) when feeding on *W. indica* under laboratory conditions (Table 1). The period in the egg capsule was 15.27 days ($n=51$). Four larval instars were observed in *P. megalostomoides*.

The larval period of *P. megalostomoides* was 46.83 days ($n=44$). The first three larval instars lasted 10.76 ($n=51$), 9.18 ($n=50$) and 10.62 ($n=48$) days, respectively. The fourth instar of *P. megalostomoides* lasted 16.27 days ($n=44$). The active larval period of *P. megalostomoides* lasted 35.63 days ($n=44$), 39.61% of the total developmental time.

Fig. 3 Hymenoptera parasitoids of *Pseudochlamys megalostomoides* Lacordaire, 1848 (Coleoptera: Chrysomelidae: Cryptocephalinae: Fulcidacini). **a** Entedoninae species (Hymenoptera: Eulophidae) on *P. megalostomoides* eggs. **b** Empty egg capsules of *P. megalostomoides* with the exit hole made by the parasitoid Eulophidae (arrow). **c** Pteromalidae species (Hymenoptera) on *P. megalostomoides* larvae. **d** Empty fecal case of *P. megalostomoides* with the exit hole made by the parasitoid Pteromalidae (arrow). Scale bars: 1.0 mm

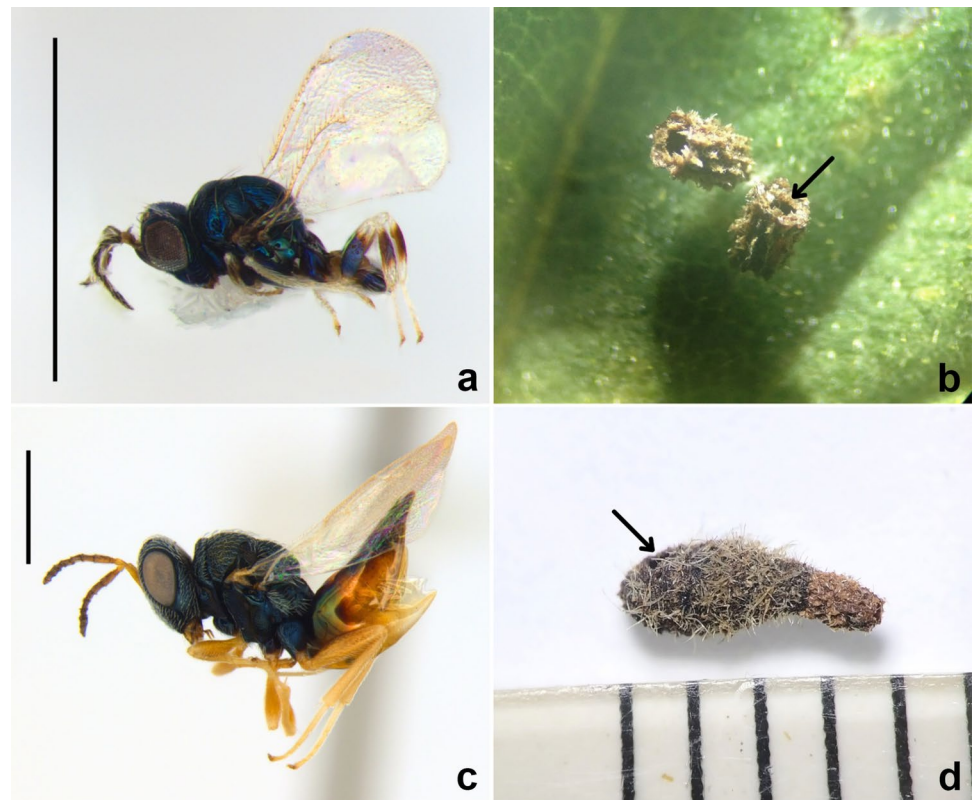


Table 1 Preimaginal stages (in days) in the life cycle of *Pseudochlamys megalostomoides* Lacordaire, 1848 (Coleoptera: Chrysomelidae: Cryptocephalinae: Fulcidacini) feeding on *Waltheria indica* Linnaeus (Malvaceae), under laboratory conditions (24.4–26.8 °C; 55.2–74.5% RH; 12-h photophase)

Life cycle stages	X ± SD	Relative use of time (%)	Minimum–Maximum	Mode	Median	CV (%)
Egg capsule ^a	15.27 ± 1.45	16.97	13–20	14	15.0	9.5
Larva I ^a	10.76 ± 2.26	11.96	8–20	9	10.0	21.0
active	7.78 ± 1.91	8.64	6–16	7	7.0	24.6
immobile	2.98 ± 0.61	3.31	2–5	3	3.0	20.5
Larva II ^b	9.18 ± 6.25	10.20	7–52	8	8.0	68.1
active	6.16 ± 6.25	6.84	3–49	5	5.0	101.5
immobile	3.02 ± 0.51	3.35	2–5	3	3.0	16.9
Larva III ^c	10.62 ± 6.07	11.80	8–39	9	9.0	57.2
active	6.89 ± 6.09	7.65	4–36	5	5.0	88.4
immobile	3.72 ± 0.49	4.13	3–5	4	4.0	13.2
Larva IV ^d	16.27 ± 7.51	18.08	10–37	12	13.0	46.2
Active larva ^d	35.63 ± 10.67	39.61	26–78	30	31.5	29.9
Prepupa + pupa ^e	28.00 ± 2.48	31.12	24–34	27	27.5	8.8
Preimaginal ^e	89.95 ± 15.55	100.00	59–133	77	86.5	17.28

X = mean, SD = standard deviation, CV = coefficient of variation. ^an = 51; ^bn = 50; ^cn = 48; ^dn = 44; ^en = 22

A total of 16 females and six males emerged from their pupal chambers, for a sex ratio of 0.72. Approximately one year after the start of the sealing of the larval cases, no adults had emerged from 27 pupal chambers; however, some chambers showed traces of unfinished cuts made by the mandibles of adults, suggesting that an attempt had been made to exit. Considering the total number of adults, i.e. the sum

of those that left their chambers plus the dead adults that emerged and did not leave their chambers, it was found that the “potential sex ratio” of this cohort was 0.53: 16 females and six live males plus seven females and 14 dead males equal 23 females and 20 males.

Regarding the longevity of *P. megalostomoides*, 71.25 days were obtained for females (n = 16) and 56.5 days

Table 2 Mean number of eggs produced by females of *Pseudochlamys megalostomoides* Lacordaire, 1848 (Coleoptera: Chrysomelidae: Cryptocephalinae) feeding on *Waltheria indica* Linnaeus (Malvaceae) under laboratory conditions (24.4–26.8 °C; 55.2–74.5% RH; 12-h photophase), per imaginal day and per oviposition day

Female	Eggs per imaginal day	Eggs per oviposition day
I	1.91	2.79
II	0.61	1.92
III	0.73	1.30
IV	1.25	2.05

Table 3 Stages (in days) within the longevity of females ($n=4$) of *Pseudochlamys megalostomoides* Lacordaire, 1848 (Coleoptera: Chrysomelidae: Cryptocephalinae: Fulcidacini) feeding on leaves of

Stage	$X \pm SD$	Relative use of time (%)	Minimum–Maximum	Median	CV (%)
Preoviposition	21.0 ± 4.08	31.3	18–27	19.5	19.4
Oviposition	41.0 ± 16.38	60.6	23–62	39.5	40.0
Postoviposition	5.5 ± 1.26	8.1	4–7	5.5	22.9
Fertile period (preoviposition + oviposition)	62.0 ± 3.14	91.9	50–80	59.0	21.2
Longevity	67.5 ± 3.45	100.00	54–85	65.5	5.1

X =mean, SD =standard deviation, CV =coefficient of variation

for males ($n=6$), *i.e.* the longevity of the male is approximately 79.30% of the longevity of the female. During her lifetime, the female tends to lay very few eggs per day of the oviposition period (Table 2).

There is a strong negative correlation ($r = -0.838$) between the pre-oviposition and oviposition periods, indicating a tendency for females with a shorter pre-oviposition period to have a longer oviposition period (Table 3). Comparisons between the oviposition and post-oviposition periods and the pre-oviposition and post-oviposition periods showed weak correlations. The pre-oviposition period and fertility (egg viability) show a strong negative correlation ($r = -0.758$), indicating that females with a shorter pre-oviposition period tend to produce a greater number of fertile eggs (Tables 3, 4). There is a very strong positive correlation ($r = 0.973$) between female longevity and oviposition period, *i.e.* the longer a female lived, the longer was her oviposition period.

Egg parasitoidism

The first sample of collected eggs ($n=101$) showed that 19 egg capsules were opened by larvae, 41 contained parasitoids, and another 41 were not opened, revealing a viability rate of only 18.81% and a parasitoidism rate of more than 40%. The second sampling ($n=266$) showed similar data

Table 4 Ovipositional variables of females ($n=4$) of *Pseudochlamys megalostomoides* Lacordaire, 1848 (Coleoptera: Chrysomelidae: Cryptocephalinae: Fulcidacini) feeding on *Waltheria indica* Linnaeus (Malvaceae), under laboratory conditions (24.4–26.8 °C; 55.2–74.5% RH; 12-h photophase)

Ovipositional variables	$X \pm SD$	Minimum–Maximum	Median	CV (%)
Fertile eggs	20.00 ± 15.49	2–38	20	77.45
Unfertile eggs	27.50 ± 17.71	14–52	22	64.40
Fecundity	47.25 ± 29.78	17–78	47	63.02

X =mean, SD =standard deviation, CV =coefficient of variation

Table 5 Stages (in days) within the longevity of females ($n=4$) of *Waltheria indica* Linnaeus (Malvaceae), under laboratory conditions (24.4–26.8 °C; 55.2–74.5% RH; 12-h photophase)

Stage	$X \pm SD$	Relative use of time (%)	Minimum–Maximum	Median	CV (%)
Preoviposition	21.0 ± 4.08	31.3	18–27	19.5	19.4
Oviposition	41.0 ± 16.38	60.6	23–62	39.5	40.0
Postoviposition	5.5 ± 1.26	8.1	4–7	5.5	22.9
Fertile period (preoviposition + oviposition)	62.0 ± 3.14	91.9	50–80	59.0	21.2
Longevity	67.5 ± 3.45	100.00	54–85	65.5	5.1

to the first: more than half of the capsules contained parasitoids, a total of 140, or 52.63% of the eggs; 67 capsules, 25.18%, were opened by larvae, and 59, *i.e.* 22.18%, not.

The complete analysis of the data revealed a very high rate of parasitoidism in the eggs. Considering the two egg samples ($n=367$), 49.31% were parasitized, 27.26% were infertile and only 23.43% of the eggs were viable.

The egg parasitoids are all from a single species of Entedoninae (Hymenoptera: Eulophidae) (DZUP 328714–328,719). They are solitary egg parasitoids (only one per egg) with a generally metallic green body coloration and less than 1 mm in length (Fig. 3a).

After egression, the parasitoids open the egg capsule at the apical portion (Fig. 3b). This region is visually distinct from the basal and lateral portions and corresponds to the site where the female seals the construction of the first shelter of the immature, as well as the site where larva break the fecal capsule after hatching from the egg. However, these openings are different: the larva of *P. megalostomoides* completely eliminates the maternal seal, while the parasitoid makes a small circular hole in the region of the seal.

From some of the larvae collected in the field and brought to the laboratory for observation, it was possible to record the parasitoidism of the larvae by Pteromalidae (Hymenoptera) (DZUP 328709) (Fig. 3c, d). The parasitized larva had

its development interrupted, as indicated by the reduced size and premature sealing of the case.

Discussion

Pseudochlamys is one out of eleven genera of the tribe Fulcidacini; it has five species, with four occurring in Brazil: *Pseudochlamys bellicosus* Monrós, 1953 in Bahia; *P. megalostomoides* in Ceará, Bahia and Minas Gerais; *Pseudochlamys rufescens* Bowditch, 1913 in Santa Catarina; and *Pseudochlamys seminigra* (Jacoby, 1904) in Goiás (Lacordaire 1848; Jacoby 1904; Bowditch 1913; Monrós 1953; Chamorro-Lacayo and Konstantinov 2009). *Pseudochlamys semirufescens* (Karren, 1972) is the only non-Neotropical species and is found in Arizona, United States (Karren 1972). Females and males have the same size and can be distinguished by the sexual dimorphism, which is diagnostic of this genus: males have larger heads and mandibles than females (Chamorro-Lacayo and Konstantinov 2009) (Fig. 1).

Both host plants are native to Brazil and can be easily found because they grow in dense populations in their habitats, intermingling with other shrub and tree species. *Waltheria indica* is a sub-shrub that occurs in different types of phytogeographic areas and vegetation in all Brazilian geographic regions and *W. rotundifolia* occurs exclusively in the Northeast Region of Brazil, from the Atlantic Forest to the Caatinga (Coutinho et al. 2025).

Four records of Fulcidacini were made on *Waltheria*: *Chlamisus discipennis* (Jacoby, 1901) and *Chlamisus gibbicollis* (Lacordaire, 1848) (= *Chlamys lebasii* Lacordaire, 1848) on *W. indica* in Argentina (Bokermann 1963); *Pseudochlamys* nr. *megalostomoides* on *W. indica* in Costa Rica (Flowers and Janzen 1997); and *Chlamisus* sp. on *W. rotundifolia* in Alagoas State, Brazil (Duarte-de-Mélo et al. 2025). A species of *Lexiphanes* Gistel, 1848 is the only other non-Fulcidacini Cryptocephalinae recorded feeding on *Waltheria* (Duarte-de-Mélo et al. 2023).

In contrast to most genera of the Fulcidacini, *Pseudochlamys*, together with *Aulacomela* Doweld, 2014 (= *Aulacochlamys* Monrós, 1952), is considered monophagous (Agrain et al. 2024), i.e. insect species that feed on plants of only one genus or closely related genera (Biondi 1996; Trigo et al. 2012; Biondi et al. 2013). Until now, only *W. indica* was known to host *Pseudochlamys*, although other species of *Waltheria* were suspected (Bokermann in Karren 1972).

The *Chlamisus* species that was found feeding on *W. rotundifolia* can also be found in all developmental stages on *Melochia tomentosa* Linnaeus (Malvaceae) (Duarte-de-Mélo et al. 2025). Similar to what occurs between *P. megalostomoides* and *W. indica*, adults, eggs, and instars I and II of *Chlamisus* sp. are found at the tops of branches where the youngest leaves are located, while instars III

and IV are more itinerant, moving throughout the plant; however, the pupae of this *Chlamisus* species are almost exclusively found attached to the stems of the branches, camouflaging themselves as part of the dried inflorescence (Duarte-de-Mélo et al. 2025).

The egg capsule of this *Chlamisus* species is similar to that of *P. megalostomoides* in that the arrangement of the fecal plates gives the capsule surface a pinecone-like appearance, but its shape is closer to that of a honey pot (Duarte-de-Mélo et al. 2025).

Like that of *P. megalostomoides*, *Chlamisus* larva adhere trichomes from their host plants to the walls of its case; however, from instar II onwards, the larva also begins to adhere sepals and petals of flowers, culminating in a cross-section of the apical portion that corresponds to what was built by instars I and II, hence the final appearance resembles a dry inflorescence when the larva definitively adheres to the stem to pupate (Duarte-de-Mélo et al. 2025). At no point does the fecal case of the *P. megalostomoides* larva appear capable of camouflaging itself on *W. indica*.

The *Chlamisus* sp. collected on *W. rotundifolia* require 87 days ($n=2$) to complete the same developmental period when also reared in the laboratory on *W. indica* (Duarte-de-Mélo et al. 2025). The preimaginal period of *Neochlamisus bimaculatus* (Karren, 1972) and *Neochlamisus platani* (Brown, 1952) ranges from 54 to 70 days (Hyche 1996; Brown and Funk 2005); *Neochlamisus gibbosus* (Fabricius, 1777) requires 74 to 125 days (Shin et al. 2012). Under natural conditions, *Fulcidax monstrosus* (Fabricius, 1798) can take eight months to leave the pupal chamber (Flinte and Macêdo 2004); and *Chlamisus minax* (Lacordaire, 1848) takes about nine months (Reu Jr and Del-Claro 2005).

The egg capsule period of *P. megalostomoides* is consistent with that observed for *N. bimaculatus*, *N. gibbosus*, and *N. platani*, lasting one to two weeks (Hyche 1996; Brown and Funk 2005; Shin et al. 2012). *Fulcidax monstrosus* has an egg capsule period of 10 days (Flinte and Macêdo 2004). The period of *Chlamisus* sp. within the egg capsule is 14.75 days (Duarte-de-Mélo et al. 2025).

Four larval instars were also observed in *F. monstrosus*, *N. bimaculatus*, *N. gibbosus*, *N. platani* (Hyche 1996; Flinte and Macêdo 2004; Brown and Funk 2005; Shin et al. 2012). The same amount has also been recorded for *Chlamisus* sp. (Duarte-de-Mélo et al. 2025).

Fulcidax monstrosus larvae seal their cases after four months (Flinte and Macêdo 2004). The larval period lasts three months for *C. minax* (Reu Jr and Del-Claro 2005) and 46.54 days for *Chlamisus* sp. (Duarte-de-Mélo et al. 2025). For *N. bimaculatus* and *N. platani*, this period is about 30 days (Hyche 1996; Brown and Funk 2005), and for *N. gibbosus*, it can be up to 90 days (Shin et al. 2012).

The first three stages of *P. megalostomoides* are compatible with those observed for *N. gibbosus*, 10 to 20 days for each instar, with the fourth instar of *N. gibbosus* lasting at least 30 days (Shin et al. 2012). The four larval stages of *Chlamisus* sp. on *W. indica* are similar to those of *P. megalostomoides*, lasting 11.5, 9.42, 11.84, and 15.69 days, respectively (Duarte-de-Mélo et al. 2025).

The prepupal and pupal periods combined last four months for *F. monstrosus* (Flinte and Macêdo 2004), four times longer than that observed for *P. megalostomoides* (28 days). The pupal period of *N. gibbosus* (the last larval ecdysis was directly observed) has a duration of one to three weeks (Shin et al. 2012). The pupal chamber period of *Chlamisus* sp. lasts 28.5 days (Duarte-de-Mélo et al. 2025).

The prepupal and pupal periods of other *Neochlamisus* species in the *gibbosus* group have been effectively observed by the invasive technique of opening the pupal chamber, which allowed the determination of a prepupal period of five days and a pupal period of seven days (Brown and Funk 2005). However, the data may have suffered from some interference (e.g. light conditions).

The greater number of males (twice as many females) among *P. megalostomoides* adults that did not leave their chambers may have two explanations: (1) males become active in nature only after females; or (2) because they have much larger mandibles, males may have some difficulty using them to “cut their way out” of the pupal chamber.

The presence of well-formed adults still confined in the pupal chambers may indicate pupal or imaginal diapause of *P. megalostomoides* (Kaur-Gill et al. 2017). This phenomenon has also been suggested for *C. minax* and *F. monstrosus*, as these species spend long periods in the pupal chamber (Flinte and Macêdo 2004; Reu Jr and Del-Claro 2005).

Comparing the sex ratio obtained with the potential one, and considering the attempt to leave the chambers indicated by the observation of unfinished cuts, it is hypothesized that males of *P. megalostomoides* must have difficulty leaving their pupal chambers, possibly because their mandibles are much larger than those of females, a sexual dimorphism that morphologically characterizes the genus.

According to Perecin (2003), the only study on the longevity of Cryptocephalinae, the life span of *Metallactus mosei* (Schöller, 2003) is 135.28 days for females and 141.67 days for males in a cohort with a sex ratio of 0.52.

The low number of eggs deposited daily by females of *P. megalostomoides* may be due to the energetic effort required during oviposition: after deposition, the naked egg is continuously rotated with the hind legs while fecal plates are placed on its surface until the capsule is complete, which can take 20 to 30 min (Erber 1988; Chaboo et al. 2008).

There are few studies that address parasitoid rates in cryptocephaline eggs. Forbes and Funk (2013) suggest high levels of nonviable eggs due to parasitoid action.

Flinte and Macêdo (2004) reported 65% mortality [non-viability] of *F. monstrosus* eggs.

Parasitoid records have been made for four genera of the Fulcidacini: *Chlamisus* Rafinesque, 1815; *Diplacaspis* Jakobson, 1924; *Exema* Lacordaire, 1848; and *Neochlamisus* Karren, 1972 (Chaboo et al. 2016). There was only one record for Fulcidacini eggs: *Baryscapus chlamytis* (Ashmead, 1896) (Hymenoptera: Eulophidae) in *N. platani* eggs (Neal 1989).

Conclusions

As seen, in Camptosomata all development is linked to the construction of fecal shelters, from the costly egg oviposition by females to the concealment of the larvae in the pupal chamber. Life history studies are therefore essential to characterize and better understand the biological phenomena associated with the life cycle and reproduction of Camptosomata species in their close relationships with host plants. The use of time during reproduction and immature development, the shape and structure of fecal shelters, and the behaviors associated with each life stage can provide valuable information for solving problems in the systematics of this group of beetles. It is believed that this adaptive trait of constructing fecal shelters, which unites the Camptosomata, arose in response to strong evolutionary pressure resulting from the diversification of angiosperms and the emergence of ants (Gómez-Zurita and Cardoso 2021). Finally, unlike what was observed for *P. megalostomoides*, most Cryptocephalinae taxa are expected to be polyphagous (Agrain et al. 2024), which suggests different survival strategies on their host plants, ranging from more refined and dependent to more generalized and opportunistic.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11756-026-02185-6>.

Acknowledgements The authors are grateful to the Museu de História Natural of the Universidade Federal de Alagoas (Jorge Luiz Lopes da Silva), for providing the equipment for the initial analysis of the material obtained from the rearing, to the MAC Herbarium of the Instituto do Meio Ambiente of the State of Alagoas (Erlande Lins da Silva and Rosângela Lira Lemos) for the plants identification. The authors would also like to thank André Luis Martins from the Universidade Federal do Rio Grande do Sul for identifying the Eulophidae parasitoid subfamily. The authors thank the Fundação de Amparo à Pesquisa of the State of Alagoas for the scientific initiation fellowship to the third author at the time of the study, through the 2019–2020 cycle of the Programa Institucional de Bolsas de Iniciação Científica, and to the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior of the Ministry of Education of Brazil for the current doctoral fellowships to the first (88887.931875/2024-00) and second (887.931876/2024-00) authors. The authors also thank the reviewers for their valuable comments, which improved the initial version of the manuscript.

Authors contribution Conceptualization: JDM, IMML. Data curation: JDM. Formal analysis: JDM, SC, IMML. Investigation: JDM, SC. Methodology: JDM, SC, IMML. Supervision: IMML. Visualization: JDM, SC, IMML. Writing—original draft: JDM. Writing—review and editing: JDM, SC, IMML.

Funding The Article Processing Charge (APC) for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614).

Data availability Not applicable.

Declarations

Ethical approval Not applicable.

Conflict of interest The authors declare no competing interests.

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