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## Three New Reports of Subsocial Tortoise Beetles from South America (Chrysomelidae: Cassidinae)

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### Abstract

Subsociality is known in 35 species in 10 genera of the chrysomelid subfamilies Cassidinae and Chrysomelinae. In Cassidinae, the behavior is clustered in two tribes, Eugenyssini and Mesomphaliini, but unknown biologies of many of these species limit fine-scaled resolution of the origins and diversity of this interesting behavior. We report three new records of subsocial Cassidinae, *Eugenysa martae* Borowiec in Colombia, *Omaspides (Omaspides) clathrata* L. in French Guiana, and *Paraselenis (S.) aulica* in Brazil. Females guard larvae and pupae; larvae retain exuvio-fecal shields in some stages. Longer-term study of *P. (S.) aulica* on the host *Ipomoea* (Convolvulaceae) revealed that eggs, larvae, and pupae are gregarious and guarded by the female. Larvae lose the defensive exuvio-fecal shields in older instars. Females will mate despite being occupied with brood care. A wasp, *Emersonella* sp. (Hymenoptera: Eulophidae), and a tachinid fly (Diptera) were observed associated with and reared from juveniles. Our report increases the dataset of documented subsocial cassidines to 26 species, with 23 in Mesomphaliini and three in Eugenyssini.

## Resumo

Em Chrysomelidae a subsocialidade é conhecida para 35 espécies em 10 gêneros nas subfamílias Cassidinae e Chrysomelinae. Em Cassidinae o comportamento é restrito a duas tribos, Eugenysini e Mesomphaliini, mas o desconhecimento da biologia de muitas destas espécies limita uma definição precisa da origem e da diversidade deste comportamento. Neste trabalho apresentamos três novos registros de Cassidinae subsociais, *Eugenysa martae* Borowiec na Colômbia, *Omaspides* (*Omaspides*) *clathrata* L. na Guiana Francesa, e *Paraselenis* (*S.*) *aulica* no Brasil. As fêmeas cuidam das larvas e das pupas, e as larvas mantêm o escudo exúvio-fecal por alguns estádios. Observações mais prolongadas de *P. (S.) aulica* em sua planta hospedeira *Ipomoea* (Convolvulaceae) revelaram que ovos, larvas e pupas são gregários e defendidos pela mãe, que as larvas perdem seu escudo exúvio-fecal em estádios mais adiantados e que as fêmeas podem copular durante o cuidado com a prole. Os parasitoides *Emersonella* sp. (Hymenoptera: Eulophidae) e uma espécie de Tachinidae (Diptera) foram obtidos de imaturos de *P. (S.) aulica*. Nossos registros aumentam para 26 o número de espécies de cassidíneos subsociais, sendo 23 de Mesomphaliini e três de Eugenysini.

**Keywords:** *Ipomoea*, larva, fecal defense, parasitoid

Subsociality, maternal care of offspring, is documented for 35 species in 10 genera of two chrysomelid subfamilies, Chrysomelinae and Cassidinae (see Chaboo et al. 2014 and source citations therein). Subsocial chrysomelines are known in circumtropical and subtropical zones and appear to have originated multiple times in unrelated genera. In Cassidinae (leaf-mining and tortoise beetles), subsociality is a Neotropical phenomenon, with subsocial species ranging from Central America and the Caribbean to Brazil and Bolivia. Most records are in Brazil (eight records) and Peru (five records; Chaboo et al. 2014). The behavior is phylogenetically clustered in closely related genera of two sister tribes, Eugenysini and Mesomphaliini, but we lack finer-scaled taxonomic sampling to determine whether subsociality has single or multiple origins within derived tortoise beetles.

Among the ca. 6,000 Cassidinae species in 325 genera (Chaboo 2007), 23 species in five genera are known to exhibit maternal care. These are known in only two tortoise beetle tribes Mesomphaliini (21 species documented) and Eugenysini (2 species documented; Chaboo et al. 2014). Within the Mesomphaliini, six subsocial species belong to *Acromis* Chevrolat, 10 to *Omaspides* Chevrolat, and five to *Paraselenis* Spaeth.

In this paper, we present three novel records of subsocial cassidine species from Brazil, French Guiana, and Peru. We describe the biology of *Paraselenis* (*S.*) *aulica* Boheman, first noted on an *Ipomoea* species (Flinte et al. 2008), based on our field and laboratory study. We also comment on the biology of *Eugenysa martae* Borowiec in Colombia and *Omaspides* (*Omaspides*) *clathrata* L. in French Guiana, based on data shared by colleagues. Subsociality is documented already in other species of these genera.

## Materials and Methods

### Study Site

*Paraselenis* (*S.*) *aulica* was studied at Serra dos Órgãos National Park (22°26'56"S and 42°59'05"W), at ca. 900 m elevation, city of Teresópolis, State of Rio de Janeiro, Brazil, in two periods: September to October 2009 and January to March 2015. Host plant can be

found exposed to sun along the main trails of the park. The species was also recorded at Parque Estadual da Pedra Branca in the municipality of Rio de Janeiro. The other two species reported here were one-time observations of colleagues in Colombia and French Guiana and details are more limited.

#### ***Specimen Collections and Lab Study***

In 2009, we first recorded two females guarding clusters of eggs of *P. (S.) aulica* on different plants of the same species and counted their eggs. In March 2015 at about 900 m altitude, we observed three more females guarding offspring. Two females were with clusters of eggs on the same plant; the third female was with her group of larvae on another plant of the same species. The three groups and their mothers were collected and brought to the Laboratório de Ecologia de Insetos at Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil, and reared at room temperature for daily observations of biology and behavior. The two egg-guarding mothers were intentionally disturbed by touching them from different directions (back, front, sides, and above) with the tip of a pen. Each time, the duration of the disturbance was gradually increased up to 30 s. This probing procedure was conducted at least twice on different days for each female. After 1 wk, two males collected from the same area were placed in the rearing container with one female and her larval brood for 5 d. Parasitoids were collected over adult beetles in the field and also obtained from parasitized egg masses.

#### ***Specimen Identifications***

*Paraselenis (S.) aulica* was identified by Lech Borowiec (University of Wrocław, Poland), the host plant was identified by Rosângela Simão-Bianchini (Instituto de Botânica, São Paulo, Brazil) and the parasitoid wasp by Thiago Marinho Alvarenga (Universidade Estadual de Campinas). Chaboo identified the other species reported here.

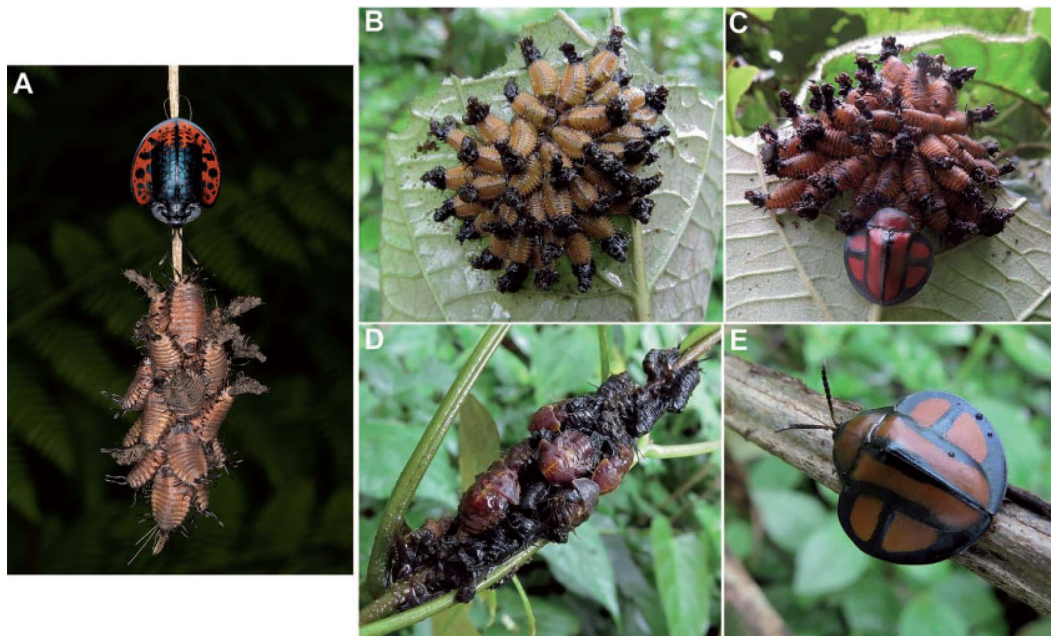
#### ***Vouchers***

Specimens of *P. (S.) aulica* and their parasitoids are deposited in the collection of the Laboratório de Ecologia de Insetos, Instituto de Biologia, Universidade Federal do Rio de Janeiro, State of Rio de Janeiro, Brazil.

## **Results**

#### ***Maternal Care in Eugenysa martae (Eugenysini; Fig. 1A)***

A single brood was photographed by R. Oelman in Colombia: Upper Anchicayá, Valle del Cauca, 28.II.2015, with a female guarding about 16 mature larvae. The larvae exhibit mixed behaviors, with some retaining the exuvio-fecal shield but others lacking the shield. This may be a situation where the older larvae tend to lose the shield (e.g., as in *P. (S.) aulica* described herein), and the pupa is anticipated to retain only the fifth larval exuviae as in other *Eugenysa* (Chaboo 2002). This single observation of subsociality in *E. martae* fits with the prediction of our phylogenetic hypotheses that all *Eugenysini* may be subsocial, but more field data are critical to identifying species-level variations of behaviors.



**Figure 1.** New subsocial cassidinae. (A) Female of *Eugenysa martae* (Tribe Eugenysini) guarding mature larvae on twig in Colombia (Photo: Robert Oelman). (B–E) *Omaspides* (*O.* *clathrata* L. (Tribe Mesomphaliini) in French Guiana (Photos: Pascal Bonin). (B) Unguarded younger larval brood in cycloalexic arrangement. (C) Female guarding brood of older larvae. (D) Gregarious pupae on host plant stem. (E) Mature adult female.

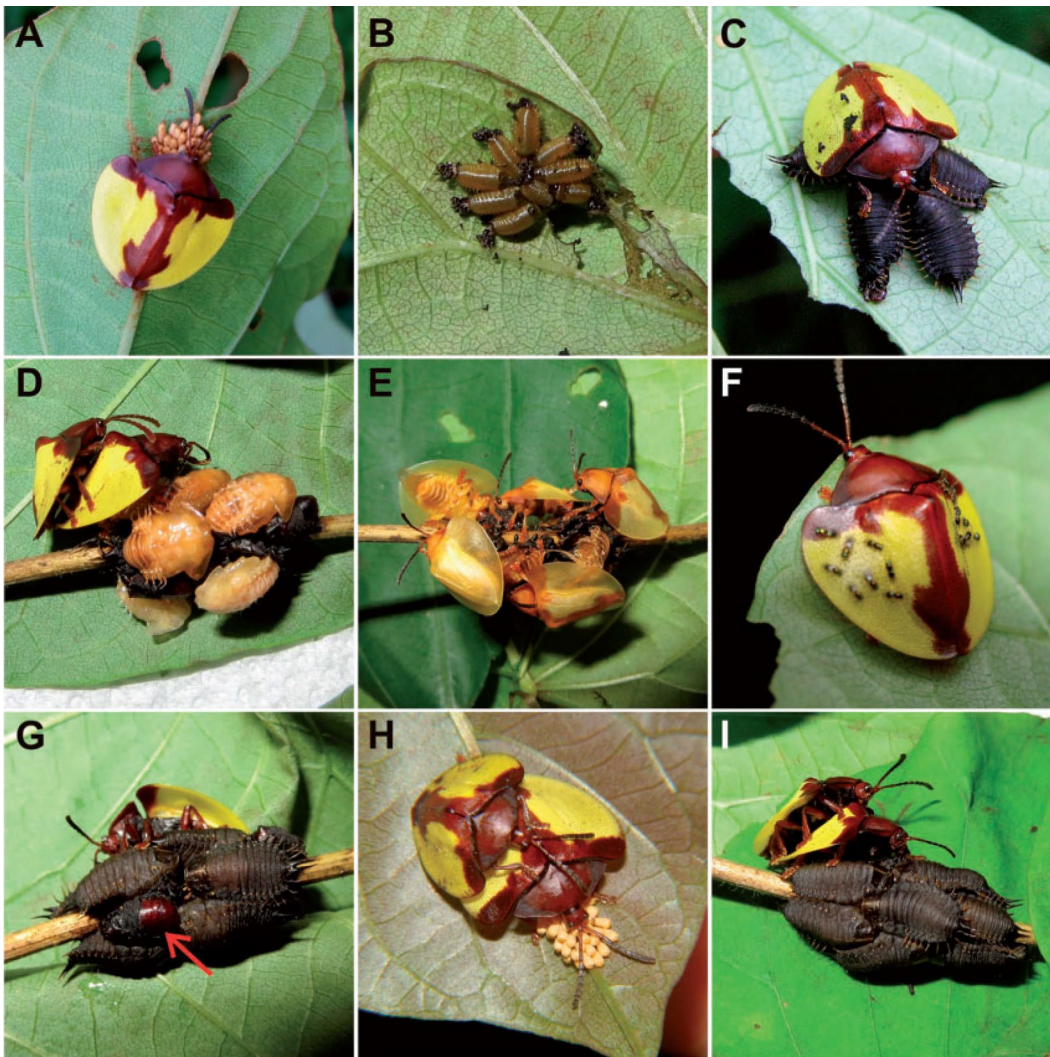
**Maternal Care in *Omaspides* (*O.*) *clathrata* (Mesomphaliini; Fig. 1B–E)**

A single brood was followed for a few days by P. Bonin in French Guiana in 2015. The larvae and pupae are gregarious (Fig. 1B–D), living on the underside of leaves of the Convolvulaceae host plant vine (probably *Ipomoea* or *Merremia*). Larvae retain the exuvio-fecal shield as fifth instars (Fig. 1C); pupation was observed on the stem, not on the leaf (Fig. 1D). Larvae displayed cycloalexic defense rings, with the head arranged to the center and the “tail” outward, a common behavior in larvae of subsocial leaf beetle species (Santiago-Blay et al. 2012).

**Natural History of *Paraselenis* (*S.*) *aulica* (Fig. 2).**

*Host Plant*

*Paraselenis* (*S.*) *aulica* feeds as both larvae and adults on leaves of *Ipomoea philomega* (Vell.) House (Convolvulaceae). This is a common vine in lower tropical montane forests and flowers high in the canopy.



**Figure 2.** Subsociality in *Paraselenis (S.) aulica* (Tribe Mesomphaliini). (A) Mother guarding egg clutch. (B) Young larvae reared without attending mother in the lab. (C) Mother guarding brood of larvae. (D) Pupae on stem. (E) Teneral adults. (F) Phoretic Eulophid wasps on adult female. (G) Tachinid parasitoid pupa (indicated by arrow) among beetle prepupae. (H) Male mating with guarding mother on eggs and on (I) Prepupa. Photos by Margarete V. Macedo (A–B, D–E, G, I), Marcia Franco (C), Ricardo F. Monteiro (F), and Vivian Flinte (H).

### Eggs

Hard elliptical eggs are arranged in clutches ranging from 30 to 40 eggs (mean = 34;  $n = 4$ ), attached along the ventral main vein near the leaf apex (Fig. 2A). Eggs hatch in 7 d ( $n = 2$  clutches).

*Larvae*

*Paraselenis (S.) aulica* larvae retain loose feces and exuviae as a stacked fecal structure on their mobile urogomphi (caudal process) only during their first stages, turning from the yellow (Fig. 2B) to dark brown in their final stages (Fig. 2C). One group of larvae was reared in the lab since egg hatching and took 23 d to pupate ( $n = 9$  larvae). Larvae display buccal regurgitation when manipulated and present cycloaexy (Fig. 2B).

*Pupae*

They pupate gregariously around a stem of the vine (Fig. 2D) and emerged as adults in 6 and 7 d ( $n = 2$  aggregations with 9 and 10 larvae, respectively). The pupae jerk their abdomens when disturbed. The adults emerged almost simultaneously in the morning, and they are completely cream in color (Fig. 2E), getting darker in a few hours.

*Parasitoids*

We found adult *Emersonella pubipennis* (Hymenoptera: Eulophidae), an egg parasitoid, phoretic on the adult beetles. We observed as many as 14 wasps on the elytra of one single female (Fig. 2F). Parasitism rates on *P. (S.) aulica* eggs can be very high, 56.7% in a 30-egg mass and 71.4% in a 35-egg mass. A tachinid species (Diptera) was reared from *P. (S.) aulica* larvae. The flies pupated outside the body of the final larval instar two days before beetle pupation (Fig. 2G) and emerged as adults one day before beetle emergence. Three flies emerged from a group of 13 larvae.

**Maternal Care in *Paraselenis (S.) aulica***

Females guard their broods from eggs until adult emergence. When disturbed, the female turned her body toward the source of disturbance and moved her body laterally and forwards (“jerking”) while remaining over her brood. With prolonged disturbance, we observed the two females leaving their young once, going to the other side of the leaf, and returning a few seconds later. This is consistent with behaviors seen in other intensely observed cassidine species: *Acromis sparsa* Boheman (Upton, 1996: online at <https://www.youtube.com/watch?v¼EsS-OfPjOCg>; Trillo 2008; Chaboo, personal observation), *Acromis spinifex* (L.) (Chaboo, personal observation), and *Eugenysa columbiana* Boheman (Chaboo 2002). One egg-guarding female was observed with a male in the field (Fig. 2H). Under laboratory conditions, another female that was caring for her brood also mated (Fig. 2I) at least five times with two different males presented into the rearing container during the 5 d.

**Discussion**

Our three new reports increase the dataset of subsocial Chrysomelidae to 38 species and in Cassidinae to 26 species, with 23 in Mesomphaliini and 3 in Eugenysini. Table 1 summarizes and compares some of the major hallmarks of cassidine subsocial behaviors for the three new records. These features may provide phylogenetic information at the species, generic, and tribal levels; Chaboo (2007) used some as phylogenetic characters (her characters 14–17, 19–20). Undoubtedly many more aspects of subsociality can be formulated as

phylogenetic character hypotheses to further resolve species-level relationships and clarify evolutionary steps in the complex defense repertoire of Cassidinae.

**Table 1.** Comparison of behaviors in three new records of subsociality

Taxon	Eggs, grouped	Larvae, gregarious	Larvae, fecal annex present	Larvae, cycloaexy	Pupae, gregarious	Pupae, fecal annex present
<i>Eugenysa martae</i>	?	+	±	?	?	?
<i>Omaspides</i> (O.) <i>clathrata</i>	?	+	+	+	+	—
<i>Paraselenis</i> ( <i>S.</i> ) <i>aulica</i>	+	+	±; + in 1st stage; lost later	+	+	—

“+” — present; “—” — absent; “?” — unknown. These features may provide phylogenetic information at the species, generic, and tribal levels.

We document *P. (S.) aulica* being attacked by parasitoids already known to parasitize cassidines—wasps and tachinid flies (Cox 1994). The phoretic habit was found to be common in *Emersonella* species parasitizing Panamanian cassidine eggs (Cuignet et al. 2008); however, the authors did not find as many wasps riding on a single female elytra as we found in *P. (S.) aulica*. The phoretic wasps are waiting probably for the female to lay eggs which they will parasitize. Author Macedo has observed that females of *Mecistomela marginata* (Chrysomelidae: Cassidinae) that have more phoretic wasps on their bodies tend to lay eggs in a shorter time than those ones with fewer wasps.

A second interesting observation about *P. (S.) aulica* is the absence of the exuvio-fecal shield in older instars; this is unusual in tortoise beetles but is known in the tribe Ischyrosomychini (Chaboo, personal observation). In subsocial *Acromis* Chevrolat (Mesomphaliini), the shield is small but present in all instars (Chaboo 2001).

A third observation, the courtship and mating of tortoise beetle mothers with broods, is also known in *Acromis*, *Eugenysa*, and *Omaspides* (Chaboo et al. 2014). Broods with different fathers have been documented only for *A. sparsa* (Trillo 2008), but this may be a broader pattern in light of our field observations.

Chaboo et al. (2014) evaluated hypothetical models developed by Reid et al. (2009) and VencI and Srygley (2012) about the origins of chrysomelid subsociality. It is not surprising that the new records presented herein belong to the genera *Eugenysa*, *Omaspides*, and *Paraselenis* where many other subsocial species are documented. Our new data add further support to the phylogenetic clustering of subsocial species—within two sister tribes as determined in previous phylogenetic work (e.g., Hsiao and Windsor 1999, Chaboo 2007) and within these few genera (see Chaboo et al. (2014): Fig. 8). Field work will certainly uncover more subsocial Cassidinae, but deeper phylogenetic sampling of species around these nodes (tribes and genera) and generic revisions are now the crucial next step in our study of cassidine subsociality.



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