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New Host Record for *Megacerus flabelliger* Fåhraeus (Coleoptera: Chrysomelidae: Bruchinae) and Some Notes about its Life History

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Abstract

Larvae of *Megacerus flabelliger* Fåhraeus were found in Venezuela feeding in seeds of *Merremia macrocalyx* (Ruiz and Pavon) O'Donnell, a convolvulaceous weed about which little is known regarding its natural enemies. In the study locality, *M. macrocalyx* produces fruits with one to four seeds. The bruchid oviposited more frequently on fruits with multiple seeds but only one seed was attacked, although in some fruits with multiple seeds almost all seeds had eggs. Oviposition occurred most frequently on seeds still on the plant. Only *M. flabelliger* eggs were noted on the seeds of *M. macrocalyx*. While on a few seeds there was more than one egg attached, most seeds held only a single egg and only one adult emerged from a seed. Wasps belonging to the families Braconidae, Eupelmidae, Eurytomidae and Eulophidae emerged from seeds not destroyed by the bruchid.

Megacerus Fåhraeus is a distinct genus of Bruchinae that merits being the sole member of the tribe Megacerini in the subfamily Bruchinae, with more than 50 species distributed from U.S.A. and Canada to Chile and Argentina (Terán and Kingsolver 1977, 2003; Terán and Johnson 2002; Kingsolver 2004; McNamara 2004). Because of the lack of understanding of the genus by early taxonomists, there are about 38 junior synonyms due primarily to the diligent studies of Terán and Kingsolver (1977). These bruchids have been reported to feed only on the seeds of the morning glory family (Convolvulaceae), with an occasional unconfirmed exception (Center and Johnson 1974; Maes and Kingsolver 2003). This plant family comprises 55 genera and *ca.* 1200 species mainly distributed pantropically, although some species are found in temperate zones (Austin 1997, 1998). Some of the genera have been extensively studied, including in some cases the record of their seed predators, because their species are economically important (Austin 1997; Randall 2001).

Austin (1997) points out that often a single species of *Megacerus* is associated with one plant species, but there are exceptions such as *Megacerus discoidus* Say reared from seeds of *Calystegia* R. Br., *Convolvulus* L. and *Ipomoea* L. (Wang and Kok 1986), *Megacerus cubicus* Motschulsky in seeds of *Ipomoea*, *Merremia* Dennst. ex Endl. and *Argyreia* Lour. (Maes and Kingsolver 2003), and *Megacerus baeri* Pic and *Megacerus porosus* Sharp with several reported species of host plants in *Ipomoea* and *Merremia* (Terán and Kingsolver 1977, 2003; Terán and

Johnson 2002; Scherer and Romanowski 2005). To date, *Megacerus callirhipis* Sharp, *Megacerus deceptor* Terán and Kingsolver, *Megacerus leucospilus* Sharp, *Megacerus ricaensis* Pic, *Megacerus similibus* Terán and Johnson and *Megacerus tricolor* Suffrian have been reared only from seeds of *Ipomoea*, and *Megacerus capreolus* Jekel and *Megacerus bifloccosus* Motschulsky only from *Merremia* (Austin 1997; Maes and Kingsolver 2003).

Little research has been conducted on the life histories of species of *Megacerus*. The species are univoltine, except for *M. baeri* which is multivoltine (Terán and Kingsolver 1977), and only one larva develops in one seed (Terán and Kingsolver 1977, 2003; Scherer and Romanowski 2005). Oviposition occurs mainly on the sepals or in the capsule of the fruit, although occasionally a few species lay eggs on seeds after the valves of the fruit have opened while the fruit is still on the plant (Terán and Kingsolver 1977, 2003; Muruaga de L'Argentier and Terán 1980; Pfaffenberger 1980; Pfaffenberger *et al.* 1984). Some studies on the morphology and larvae of several species of *Megacerus* include information about the methods of attachment of the eggs to the seeds (Pfaffenberger 1980; Pfaffenberger *et al.* 1984). There is not much information available regarding damage caused by *Megacerus* species to seeds of Convolvulaceae. Of these, only scarce reports of studies on species of *Ipomoea* reveal predation values ranging from very low ($<$10%) to considerable ($>$70%) seed destruction (Keeler 1980; Devall and Thien 1989; Frey 1995; Scherer and Romanowski 2005).

We report here on a new host record for *Megacerus flabelliger* Fåhraeus in Venezuela and its success feeding in the seeds of its host. Additionally, some features of the life history of the insect and the damage done to the seeds are described. *Megacerus flabelliger* is a widespread Latin American species with a reported seven species of host plants (Janzen 1977, 1978, 1980; Terán and Kingsolver 1977, 2003; Terán and Johnson 2002). According to Terán and Kingsolver (1977), it is distributed from Mexico to northern Argentina.

Material and Methods

Field work was conducted in the Los Guayabitos forest, southeast of Caracas, on the environs of the Universidad Simón Bolívar (Estado Miranda, Venezuela, 10°24′N–66°52′W, 1,200–1,430 m above sea level). Formerly, the area was regarded as a cloud forest with evergreen trees and lush vegetation (Aristeguieta and Matos 1959). Today, only fragments of the original forest remain, mainly replaced by disturbed areas populated by a large variety of weeds, among them *Merremia macrocalyx* (Ruiz and Pavon) O'Donnell.

Merremia macrocalyx (=*M. glabra* Hallier F.) is a very large vine that grows naturally in thickets and open areas of evergreen lowland to montane forests. It is used as an ornamental plant, but is cited also as a weed in important crops such as coffee (Austin 1998; Groth 2001; Randall 2001). Flowers of *M. macrocalyx* are campanulate, mainly white with a light-yellow center, grouped in few-flowered inflorescences. The ovary is 4-ovulate, with one ovule per locule. The fruits are capsules with a very thin and membranous pericarp which is fragile and easily opened by wind and other factors in the environment when mature. The fruits are longitudinally dehiscent by as many segments as locules in the fruit (septifragal capsule), permitting the dispersal of individual seeds. The seed coat is densely pubescent. The average dimensions of the spherical seeds (n = 30) were: $4.1 \pm 0.2 \times 4.0 \pm 0.3 \times 3.9 \pm 0.3 = 63.7 \pm 7.8$ mm^3. In the study area *M. macrocalyx* produces flowers and fruits from August through March.

Predispersal seed predation was measured in a group of mature fruits collected at random from plants during the fruiting period in 2003–2004. These fruits had the pericarp partially opened but the seeds were still in them. In the laboratory, the pericarp was carefully examined to verify the presence of eggs. The fruits were opened manually, and the number of seeds per fruit was counted, recording the presence of eggs on the seeds. The number of seeds with attached egg(s) in each fruit and the number of eggs on each seed were assessed. In order to determine differences in the usage of fruits for oviposition according to the number of seeds per fruit, a contingency table based on a test of independence was applied (Sokal and Rohlf 1995). Significance was established at $\alpha \leq 0.05$.

All the seeds were taken out of the fruits and placed in rearing chambers. These were mantained in the laboratory at room temperature. Some seeds from already opened fruits where also included in this procedure. The rearing chambers consisted of plastic baskets covered with mesh bags for the aeration of the seeds. They were periodically monitored to verify the emergence of adult insects. When an insect was seen to emerge from a seed, both the insect and the seed were removed from the chamber. The following calculations were made based on the total number of analyzed seeds: (1) the number of seeds not fed upon and without eggs on them, (2) the number of seeds fed upon, and (3) the number of seeds with eggs on them but no insects emerging; these latter ones were observed for several days until it became evident that no insect would emerge from them. Additionally, the number of insects emerging from each seed was counted.

Results

All reared bruchids were identified as males and females of *M. flabelliger*. The emergence of these insects was through characteristic circular exit holes in the seed coat (Fig. 1a). Only one adult emerged from each seed, even in the few cases with more than one egg per seed. Some of the eggs had a transparent chorion while others were opaque. A larva could be seen inside the transparent eggs prior to their burrowing into seeds. Eclosion from the eggs occurred ventrally, evidenced by holes in the seed beneath the eggs that were made when the larva entered the seed. The emergence of bruchids was limited to seeds with a transparent egg attached to their surface as no bruchids emerged from seeds with opaque eggs. The bruchid larvae destroyed almost the entire seed content, leaving the seed hollow but with its coat complete. Damage by the bruchids to the seeds was such that no seed content remained to allow another bruchid to complete its development. No cocoon formation was observed inside the seeds, whereas a pupation chamber surrounded by compressed frass and some remains of seed content were always seen. The damage to a seed does not seem to restrict the dispersal of the other seeds in the same fruit, as it solely affected the interior of the seed.

Only *Megacerus* eggs were noted on the seeds (Fig. 1b). Of the 411 fruits that were examined, only four (1.0%) had eggs attached to the pericarp, 72 (17.5%) had at least one egg attached to the surface of the seed and the remaining had no egg on the fruit nor on the seeds. There were 105 fruits with one seed, 84 with two seeds, 122 with three seeds and 100 with four seeds (Table 1). The greater proportion of all these fruits had no eggs on any seed. In the fruits with more than one seed and some of them with eggs, these were mainly observed only on one of the seeds. Nevertheless, a weak but significant relationship was detected between oviposition and the number of seeds per fruit (test of independence, $X^2 = 7.82$, df $= 3$, $P \leq 0.05$).

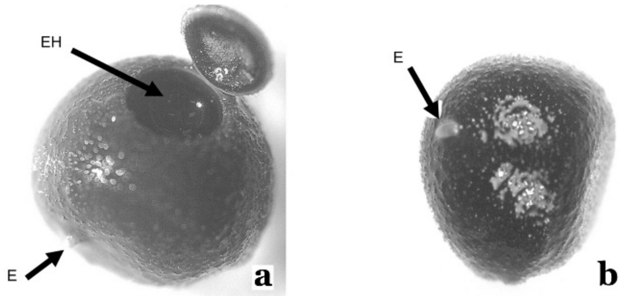

Fig. 1. Seeds of *Merremia macrocalyx* with evidence of bruchid infestation **a**) exit hole (EH) left by emerging *Megacerus flabelliger* adult, and egg (E) on the seed surface; **b**) egg (E) on the seed surface.

Of the 1,893 seeds examined, 1,534 (81.0%) were not fed upon nor showed any indication of an egg attached to their surface. Bruchids emerged from 164 seeds (8.7%) and another 144 seeds (7.6%) had eggs attached to their surface but no bruchids emerged from them. Various Hymenoptera emerged from 51 seeds (2.7%). The adults were recognized as belonging to four families (M. El Souki, pers. comm.) with parasitoid or with parasitoid and phytophagous habit (Table 2). In some cases, two morphotypes were distinguished in a single family, which may represent two separate species. The largest number of captured wasps corresponded to one of the two morphotypes of Eulophidae (Figs. 2a, b). The damage in the seeds from which these wasps emerged was less than that seen in the seeds with bruchids, as only the cotyledons were partially affected. Nevertheless, the seeds from which wasps had emerged were more frequently attacked by fungal mycelia. The wasps emerged through small exit holes in the seed coat (Fig. 2c). A single small exit hole could be seen on each seed. No wasps emerged from seeds from which bruchids emerged, yet they did so from seeds with eggs attached to their surface. Dead bruchid larvae were not observed in these last seeds.

Discussion

This description of the attack of *M. flabelliger* on the seeds of *M. macrocalyx* constitutes the first record of predispersal seed predators on this plant species and widens the host record of the bruchid, which had already been captured on other *Merremia* and on *Ipomoea* species (Terán and Kingsolver 1977, 2003;

Table 1. Number of fruits with bruchid eggs on the seeds in relation to the number of seeds per fruit (percentages over the total for each kind of fruit in parentheses; n = number of samples).

Number of seeds per fruit with eggs	Number of seeds per fruit			
	1 (n = 105)	2 (n = 84)	3 (n = 122)	4 (n = 100)
0	94 (89.5%)	72 (85.7%)	96 (78.7%)	77 (77.0%)
1	11 (10.5%)	11 (13.1%)	23 (18.9%)	16 (16.0%)
2	-	1 (1.2%)	2 (1.6%)	6 (6.0%)
3	-	-	1 (0.82%)	1 (1.0%)
4	-	-	-	0 (0.0%)

Table 2. Hymenoptera which emerged from the seeds of *Merremia macrocalyx*. For each of the first two families two morphotypes were observed, which possibly represent different species.

Family	Number of adults	Habit of the family*
Braconidae 1	3	Parasitoids of different orders of insects, mainly of larvae; phytophagous as seed predators or as gall formers
Braconidae 2	1	
Eulophidae 1	Several	Parasitoids of different orders of insects, mainly of eggs or larvae; phytophagous as gall formers
Eulophidae 2	1	
Eupelmidae	Few	Mainly egg parasitoids
Eurytomidae	1	Parasitoids of eggs, larvae or pupae; phytophagous as seed predators or as gall formers

* http://www.sel.barc.usda.gov/hym/chalcid.html

Pfaffenberger *et al.* 1984; Terán and Johnson 2002; Maes and Kingsolver 2003). With regard to its geographical distribution range, the presence of *M. flabelliger* in Venezuela had already been established as well as that of many other species of this genus (Terán and Johnson 2002; Maes and Kingsolver 2003; Terán and Kingsolver 2003).

Once inside a seed, the larva of *M. flabelliger* destroys the entire seed content, *i.e.* both the cotyledons and the embryo axis, generating a large amount of frass but leaving the seed cover intact. Hence, the seed is left hollow and probably losing its germinative capability. This kind of damage agrees with that described for almost all species of *Megacerus* attacking diverse convolvulaceous species (Terán and Kingsolver 1977, 2003; Pfaffenberger 1980; Pfaffenberger *et al.* 1984; Wang and Kok 1986; Devall and Thien 1989; Terán and Johnson 2002; Scherer and Romanowski 2005). Together with the frass, the rest of the seed content is used to construct a pupal chamber inside the seed in which the insect completes its development to adult. This feature is variable in the species of *Megacerus* because

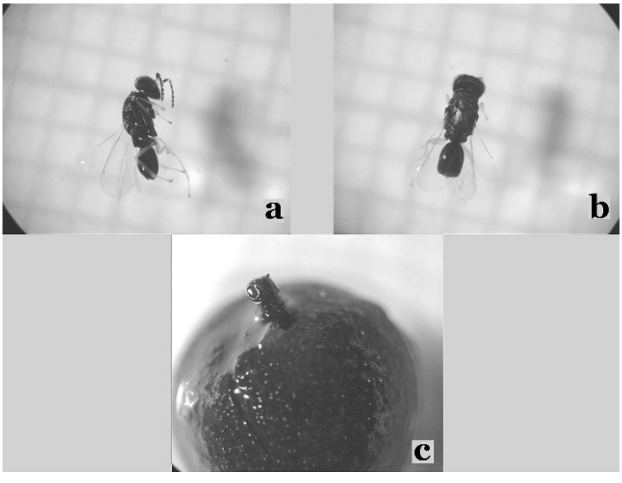

Fig. 2. Adults of the most numerous morphotype of Eulophidae that emerged from seeds of *Merremia macrocalyx* **a**) lateral view; **b**) dorsal view; **c**) adult wasp emerging from the seed.

although most resemble *M. flabelliger*, in some cases a well defined cocoon becomes evident (Pfaffenberger *et al.* 1984). Following pupation, adults emerge through a circular exit hole in the seed cover. The exit hole appears to be perforated by the larva, and this is in itself a distinctive feature of the genus (Pfaffenberger *et al.* 1984; Scherer and Romanowski 2005).

In the subfamily Bruchinae, to which *Megacerus* belongs, it is usual that a single larva develops in each seed (Terán and Kingsolver 1977, 2003; Southgate 1979; Pfaffenberger 1980; Pfaffenberger *et al.* 1984). In the case of *M. flabelliger*, this seems to be the consequence of the oviposition of a single egg per seed, but in other species, such as *M. cubicus*, *M. discoidus* and *Megacerus eulophus* (Erichson), cannibalism occurs when eggs are laid in multiples on a single seed (Pfaffenberger 1980; Pfaffenberger *et al.* 1984; Wang and Kok 1986). The laying of eggs individually, as observed for *M. flabelliger*, might be a means of avoiding competitive interactions between larvae, because a single seed seems to be not enough for the development of more than one adult.

Johnson (1981) proposed three oviposition guilds by bruchid beetles: 1) some bruchids oviposit only on fruits while still on the plant, 2) others oviposit on seeds in partially opened fruits, and 3) others oviposit only on seeds on the substrate after they have been separated from the fruit. Descriptions of oviposition behavior in species of *Megacerus* point out that females lay eggs indiscriminately on the sepals or on the pericarp of the fruits as the proposed first guild and, even though direct oviposition on seeds may not be disregarded, some authors believe that this happens only occasionally (Muruaga de L'Argentier and Terán 1980; Pfaffenberger 1980; Pfaffenberger *et al.* 1984; Wang and Kok 1986; Terán and Kingsolver 2003; Scherer and Romanowski 2005). Nevertheless, *M. flabelliger* ought to be included in the second guild due to the presence of eggs primarily deposited directly on seeds that were still in the fruits and the very scant number of eggs oviposited outside the fruits. *Merremia macrocalyx* fruits have a thin, membranous pericarp, which may be opened easily by wind without becoming loose once the fruit is ripe and remains for long periods on the plant while the seeds are gradually liberated. This might provide easy access to seeds by female bruchids besides diminishing the risk for larvae moving across the pericarp and the seed. The few observed ovipositions on the pericarp of the fruits of *M. macrocalyx* may have been due to the need of the female bruchid to lay its eggs without having reached the seeds or it may have been a mistake, by not entering the thin pericarp to find seeds upon which to oviposit.

Megacerus flabelliger oviposited proportionally more on fruits with multiple seeds. However, although a slight but significant tendency for oviposition on two or more seeds was noted according to the increase in the number of seeds per fruit, it seems odd that the bruchid females frequently lay eggs on only one of the seeds in a single visit to fruits with more than one seed. Southgate (1979) proposed that gravid females are more attracted to fruits when more seeds are available. Nevertheless, in another report of a similar study on *Ipomoea imperati* (Vahl) Griseb., Scherer and Romanowski (2005) did not find any significant difference between the use of fruits with one or two seeds.

The predation rate on seeds of *M. macrocalyx* (8.7%) due to attack by *M. flabelliger* may be regarded as low in comparison with the 38–68% recorded in *Calystegia sepium* (L.) R. Br. by *M. discoidus* (Wang and Kok 1986), the 68% damaged in *Ipomoea imperati* by *M. baeri* (Scherer and Romanowski 2005), or the 77% in *I. leptophylla* Torr. by *M. discoidus* (Keeler 1980). Even one of the highest recorded percentages of seed predation (74%) of *Megacerus* on convolvulaceous species corresponds to *M. flabelliger* on *I. carnea* Jacq. (Frey 1995). Despite this, other studies have reported lower values, such as the damage of *M. leucospilus* on *Ipomoea pes-caprae* (L.) Sweet ranging from 3.6 to 16% (Devall and Thien 1989, 2005). Scherer and Romanowski (2005) found that the predation rate appeared to be related to the amount of fruits and seeds produced, which in turn depended on the density of plants in a given locality, so that probably the magnitude of predation by *M. flabelliger* on *M. macrocalyx* may differ when studying other reproductive seasons or populations.

As many as six species of wasps were reared from the seeds of *M. macrocalyx*, some perhaps parasitizing eggs or other immature stages of both bruchids and/or the other species of wasps, and others maybe feeding on the seeds because at least some species of the families Braconidae and Eurytomidae have been described as seed predators (Macêdo *et al.* 1998; USDA 2001; Flores *et al.* 2005). An observation that leads to believe that some of the wasps are parasitoids of *M. flabelliger* was that both insects never emerged from the same seed but wasps did emerge from seeds with attached eggs. Knowledge about parasitism in bruchids of the genus *Megacerus* is scant because few published works refer to the presence of parasitoids (Muruaga de L'Argentier and Terán 1980; Wang and Kok 1986; Hetz and Johnson 1988). These few articles cite the families Braconidae, Eulophidae and Eupelmidae as parasitoids of *Megacerus* species but do not mention *M. flabelliger*. From this, the present study represents not only the first report of possible parasitoids on this bruchid species but also a possible new finding of wasps as seed predators.

In conclusion, we confirmed once more the high affinity of the genus *Megacerus* with convolvulaceous species. Also, we detected possible parasitoid interactions of some wasp families with this bruchid. A larger number of *M. macrocalyx* populations or this population in other reproductive seasons should be studied in order to verify the values of predation intensity. Such information generated from a weed of important crops, as is *M. macrocalyx*, might serve as a baseline for studies concerning its control using *M. flabelliger* as a biological control agent.

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