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ORIGINAL ARTICLE

The biology of *Oncideres humeralis* Thorms (Coleoptera: Cerambycidae: Lamiinae) and new Cerambycidae–Melastomataceae host-plant associations

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Abstract
Beetles in the genus *Oncideres* (Cerambycidae: Lamiinae) are girdlers and borers that can cause plant mortality and alterations in the recruitment and age structure of their host-plant populations. Host-plant association, oviposition behavior, development and insect associates of *Oncideres humeralis* were studied in southeastern Brazil. *Oncideres humeralis* Thorms used four species of Melastomataceae as host plants. Females oviposited in forks of branches and their larvae fed on the parenchyma tissue of the forks. Histological analyses showed that these sites were the softest parts of the branches and provided an entrance for newly hatched larvae. Females prepared their oviposition sites with their mandibles, and inserted their ovipositors into the slits to deposit one to three eggs under the bark. We found about six oviposition slits per branch and a mean of eight eggs per branch. The larvae bored into and grew inside the girdled branches. Larval development took 10–12 months. Another cerambycid, *Temnopsis megacephala* Germ, developed in the thinner sections of branches that had been girdled by *O. humeralis* and was thus considered a secondary colonizer.

Resumo
Besouros do gênero *Oncideres* (Cerambycidae: Lamiinae) são serradores a brocadores e podem provocar mortalidade de plantas, alterações no recrutamento e na estrutura estária de populações de plantas hospedeiras. Associação com plantas hospedeiras, comportamento de oviposição, desenvolvimento e insetos associados a *Oncideres humeralis* foram estudados na Sudeste do Brasil. Fêmeas colocaram ovos nas bifurcações dos ramos e suas larvas alimentaram-se do parênquima da forquilha do ramo. Análises histológicas mostraram que este local é a região mais mole da forquilha do ramo e proporciona uma porta de entrada para larvas de primeiro estágio. Fêmeas prepararam estes locais de oviposição com suas mandíbulas e inseriram seus ovipositores dentro da fenda para depositar de um a três ovos sob a casca. Encontramos cerca de seis sítios de oviposição e média de oito ovos por ramo. As larvas brocaram o interior e se desenvolveram dentro dos ramos serrados. O desenvolvimento larval requereu de 10 a 12 meses. *O. humeralis* Thorms. usaram quatro espécies de Melastomataceae como plantas hospedeiras. Outro cerambicídeo, *Temnopsis megacephala* Germ. desenvolveram em ramos mais finos não colonizados por *O. humeralis*, e foi considerado um colonizador secundário.

Keywords: Biology, Brazil, insect–plant interactions, Melastomataceae, *Oncideres humeralis*, wood anatomy

Introduction

In most cerambycid species, females oviposit in cracks and bark crevices of tree branches (Hanks et al., 1991b, 1993a, 1993b), but a more specialized behavior occurs in some species of the subfamily Lamiinae. In these species, the females use their mandibles to perforate the bark and chew a slit through which they lay the eggs under the bark (Linsley, 1961; Rice, 1989, 1995; Paulino Neto, 2004). Lamiines in the genus *Oncideres* have an even more elaborate behavior: they actually girdle living branches prior to oviposition. Depending on the intensity of their attack, they can cause plant mortality, as well as alterations in the recruitment and age structure of the host-plant populations (Caraglio et al., 2001; Romero et al., 2005). Plant

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qualities such as branch diameter, age, height, vigor and nutritional value are important parameters for the choice of infestation site by these beetles, because they affect the development of offspring (Coulson, 1979; Rice, 1995; Paulino Neto et al., 2005). Some plants are able to resist colonization by Cerambycidae due to low nutritional value of the tissue (Coulson, 1979; Hanks et al., 1995), the presence of deterrent compounds (Berkov et al., 2000), or the lack of oviposition stimulants (Hanks et al., 1995).

First instar cerambycid larvae usually feed on subcortical tissues, consuming primarily xylem and phloem (Haack & Slansky, 1987; Hanks et al., 1991b). The more mature larvae bore into the sapwood and construct individual galleries (Hanks et al., 1990; Paulino Neto, 2004), and final instar larvae prepare pupal chambers by plugging the tunnel with frass (Hanks et al., 1991b, 1993a, 1993b; Paulino Neto, 2004). Larval mortality is related to the quantity and quality of available food, environmental conditions, inter- and intra-specific competition, parasitism and predation (Coulson, 1979). High larval densities result in competition for food resources and may increase mortality (Powell, 1978; Rice, 1989; Hanks et al., 1991a) or reduce the weight of adults (Hanks et al., 1991a). Larval cannibalism sometimes occurs when the competition is intense (Powell, 1978).

Because the choice of oviposition site clearly influences both the quantity and quality of food available to the developing larvae, we studied the internal characteristics of the plant to detect a possible correlation between preferred oviposition sites and wood anatomy. To understand the interactions between cerambycids and their host plants, we report here on the reproductive behavior and development of *O. humeralis*, and describe the wood anatomy at the oviposition sites.

Materials and methods

Study site

This study was performed from 30 July 2000 to 28 February 2002 along the margins of three trails (Mirante, Paraíso I and Paraíso III, at 400, 700 and 800 m above sea level (a.s.l.), respectively) in the Serra do Japi Ecological Reserve (23°11′S, 46°52′W), a semideciduous mesophyte forest in southeastern Brazil (Leitão-Filho, 1992). This area is hilly, with an altitude between 400 and 1300 m a.s.l. (Pinto, 1992). The climate is seasonal, with mean monthly temperatures varying from 13.5°C in July to 20.3°C in January, and the driest period from June to September (Pinto, 1992).

Field observations

Observations were made every 2 weeks throughout the study in order to determine the emergence and activity periods of adult *O. humeralis*. After detection of the season's first adults, observations were made daily. We recorded host-plant identity, behavior on the host plant, mating sites, duration of oviposition, incubation time, and presence of natural enemies and insect associates. The oviposition sites were determined by direct field observations since the host trees are 3–5 m tall when adult.

Rearing of immatures in the laboratory

Each oviposition was registered and eggs were periodically inspected following partial removal of the bark. Eggs were measured with a micrometric lens. To determine the period of the larval development, branches sawn at the beginning of 2000 were collected, transported to the laboratory and placed in PVC tubes (diameter 100 mm, length 2 m) that were plugged at both ends. The branches were kept humid during storage by periodically adding a wet piece of cotton.

Analysis of wood anatomy

Intact and recently sawn branches of *Miconia sellowiana* Naudin. (Melastomataceae), the plant species most frequently used by *O. humeralis*, were collected along with branches in different stages of larval boring. These branches were used to determine the tissues on which different instars fed and the relationship between oviposition site, feeding site and branch anatomy. Branches in the same diameter class as those used by the beetles (1–3 cm; Paulino Neto et al., 2005) were cut into segments 1.0–1.5 cm long, fixed in FAA 50 solution and stored in 70% ethanol.

Branch segments up to 1 cm long were boiled in 66% glycerin to soften them prior to inclusion in historesin. Thicker segments were cut into four parts. All segments were dehydrated in ethanol as described by Gerrits (1991), but with modifications that included 2 days for pre-infiltration and 5 days for infiltration. The embedded material <1.0 cm in diameter was cut on a rotating microtome, stained with 0.05% toluidine blue in acetate buffer pH 4.7 (O'Brien et al., 1965) for 3 min, washed in running water for 5 min, dried at 37°C and mounted in Permount. Thicker segments were cut on a gliding microtome, clarified in a 5% chlorine solution, washed in running water, stained with Astra-Safranine blue (Bukatsch, 1972) for 15 s, and washed again in distilled water before mounting in glycerinated gelatin. Stained sections were

examined and photographed using an Olympus BX40 photomicroscope.

Results

Activity period of adults

Oncideres humeralis adults emerged during the summer. They were first observed in mid-December and persisted in the forest until early March. They were active diurnally, when they were engaged in mating, feeding or girdling of host-plant branches.

Pre-mating behavior

Three adult females of *O. humeralis* were observed landing on their host plants. They immediately started to feed on the soft bark of the branch tips and on the leaves or flowers of these plants and neighboring melastomes. Females were also observed scratching at the branch tips with their mandibles, and continued scratching for 1 min to more than 1 h.

Mating, girdling and egg-laying behavior and oviposition site

Six *O. humeralis* copulations were observed during the day on the branches of melastome species between mid-December and early March. After mating, the females examined the branches and forks of the host plants by touching the surfaces with their antennae. Once the choice was made, females started to girdle the branches ($n=12$). They positioned themselves upside down to start cutting the branch, and used their mandibles to remove slivers of wood up to 0.5 cm long that were thrown to the ground (Figure 1A). The females started girdling in the morning ($n=7$), and girdling took at least 7 h per branch.

Females only started ovipositing after completely girdling the branches at least once. No eggs were laid on plants with incomplete girdles ($n=7$). Oviposition sites were prepared by inserting both mandibles into the bark and cutting a slit. This took between 20 and 126 s ($n=3$). Females then inserted their ovipositors through the slits under the bark to lay eggs ($n=8$) (Figure 1B). In a single slit, one to three eggs were laid ($n=64$) which were then covered with a sticky secretion from the ovipositor. Oviposition lasted from 1 min 46 s to 43 min ($n=9$). Females laid from one to three eggs per slit and there were three to four oviposition sites (slits) per branch, and the mean number of ovipositions per branch was 5.76 ± 0.42 (mean $\pm$ SE; range 1–12; $n=46$). Hence, an average of eight eggs were deposited per branch. Females were capable of up to 12 ovipositions per branch, interspersed with feeding sessions, and a single egg-laying event could last for up to 7 h. The mean egg length was 3.2 ± 0.03 mm (mean $\pm$ SE; range 2.4–3.5 mm; $n=45$) and the mean width was 0.7 ± 0.01 mm (mean $\pm$ SE; range 0.6–0.8 mm; $n=45$). After depositing eggs, the females resumed girdling the branches until they fell to the ground ($n=9$). Frequently, the branches did not fall on the day they were cut, but broke off later through the action of wind, rain or general weakening.

On one occasion, a female who was still mating started to girdle a branch that already had two oviposition slits. After mating she continued to examine the branch, and proceeded to lay eggs in selected forks.

Duration of the larval phases

In the field, *O. humeralis* eggs hatched after 20–25 days ($n=10$). Larval development required 10–12 months. Adults ($n=12$) emerged between December and February 2001 from branches collected in February and March 2000. Larval development occurred entirely within the branches. Adults emerged by chewing a circular exit hole through the bark.

Relationship between larval development, wood anatomy and wood condition

After eclosion, first instar larvae started boring branches at the fork (Figure 1C), where there were fewer lignified cells because vascular bundles had been diverted from the principal boughs to the lateral branches (Figure 1D). The larvae bored through the bark (periderm, primary and secondary phloem) towards the centre of the principal branch. Initially, the larvae fed on the parenchyma in the branch fork, the softest part of the branch (Figure 1E), but subsequently crossed the primary xylem to reach the pith of the branch, where the tissue was also weakly lignified. There they bored into the pith tissues (parenchyma, intraxillary phloem and primary xylem) (Figure 1F). As they grew, the larvae acquired the ability to feed on secondary xylem and started to construct galleries, which gradually increased in diameter (Figure 1G). At the end of larval development, the galleries were approximately 25 cm long and 1 cm wide. Galleries in the same branch were usually spatially isolated.

Natural enemies

Ants (Formicidae: Myrmicinae: *Cephalotes* sp.) were seen feeding on *O. humeralis* eggs and larvae in any

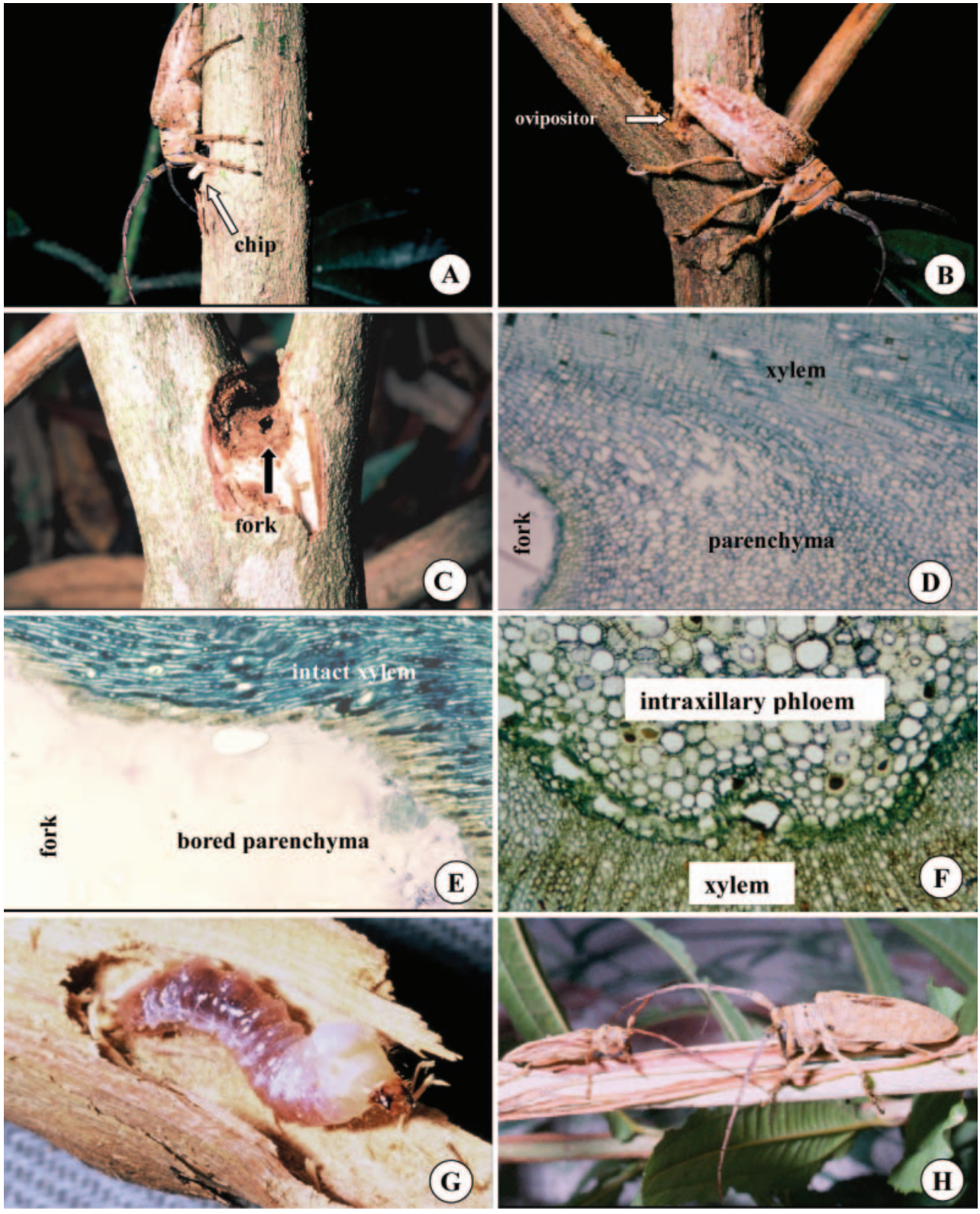

Figure 1. Cerambycid beetles on Melastomataceae. (A) *Oncideres humeralis* female girdling a host plant with a sliver of branch in its mandibles; (B) *Oncideres humeralis* female ovipositing in the fork of a host plant; (C) bored fork of the main branch with a secondary branch containing an oviposition site; (D) anatomy of an intact fork; (E) anatomy of a branch fork of *Miconia sellowiana* bored by *O. humeralis* initial instar larvae; (F) transverse section of a *M. sellowiana* stem; (G) last larval stage of *O. humeralis* in bored branch; (H) *Oncideres humeralis* (right) and *Temnopsis megacephala* (left) on the extremity of a branch of *M. sellowiana*.

instar on branches in the field ($n=4$). *Camponotus crassus* (Formicidae: Formicinae) colonized branches containing late instar *O. humeralis* larvae devouring the larvae and occupying their galleries ($n=6$). In the laboratory, parasitoid wasps (Braconidae, $n=3$) emerged from branches containing *O. humeralis* larvae.

Secondary colonist

A smaller cerambycid, *Temnopsis megacephala* Germ (Lamiinae; Figure 1H, left), also used *M. sellowiana* as a host. This species was never observed girdling branches of *M. sellowiana* or any other plant species. All individuals ($n=5$) emerged from, or were collected while feeding, mating or ovipositing on branches of *M. sellowiana* recently girdled by *O. humeralis*. *Temnopsis megacephala* developed in secondary twigs with diameters <0.7 cm that were not occupied by *O. humeralis*, which only used branches >0.7 cm in diameter. The color and speckled pattern of the elytra of *O. humeralis* resembled that of the bark on the basal parts of the branch, while the streaked pattern of clear and dark brown of adult *T. megacephala* matched well with the branch tips where they were found most commonly (Figure 1H).

Discussion

Life cycle and activity

The life cycle of *O. humeralis* is univoltine (one generation per year), with the period of adult activity in the summer. Adults were diurnal, as is the case with many species in this family (Goldsmith, 1987). The adults of many diurnal cerambycid species feed on flowers (Matter, 1997; Matter et al., 1999), and a similar behavior was observed in *O. humeralis* adults.

Pre-mating behavior

Since males were seen only during copulation, the females probably arrived at the host plants before the males. The scratching of branches with the mandibles prior to oviposition, a behavior also observed by Wang et al. (1998) for *Oemona hirta* (F.), may be related to feeding, although bark has a lower nutritional value than plant pith (Hanks et al., 1999). However, it is possible that *O. humeralis* females scratch these twigs to release plant chemicals that attract sexual partners, as reported for other cerambycid species as in *Phoracantha semipunctata* (F.) (Powell, 1978), or to stimulate oviposition, as observed for *P. semipunctata* (F.) (Hanks et al., 1995).

Girdling behavior and oviposition site

Many cerambycid species in the subfamily Lamiinae show behaviors similar to that of *O. humeralis*, such as cutting a slit into the bark (Linsley, 1961; Rice, 1989; Hanks, 1999), ovipositing under the bark through this slit, and covering the eggs with material from the ovipositor, which then hardens (Hanks, 1999). This egg-laying behavior is considered the most specialized among cerambycids (Linsley, 1961). According to Paulino Neto (2004) and Paulino Neto et al. (2005), the behavior of *O. humeralis* is so specialized that females select branches for oviposition based on their diameter (1–3 cm) and the number of secondary branches (about seven).

The observation that females cut around the host branch at least once before preparing the oviposition site and laying eggs, and afterwards finish the girdle, suggests that this primary cut is vital to the successful development of the offspring. This conclusion is strengthened by the observation that no eggs were laid on plants with an incomplete girdle, and corroborates the idea that girdling weakens a part of the living host for the benefit of the larvae (Hanks, 1999). The eventual death and desiccation of the girdled branch is also important to the reproductive success of girdler cerambycids (Cannon & Robinson, 1982; Hanks et al., 1991b, 1999).

Relationship between larval development, wood anatomy and wood condition

The branch forks offered optimal conditions for the initial development of cerambycid larvae since the lower resistance of this wood allowed easier penetration to the pith. The Melastomatacea host plants have abundant parenchyma and phloem in the central pith (Metcalfe & Chalk, 1950) but the *O. humeralis* females cut deep enough to reach the phloem in the central pith so that the branches dry out and die. This is important for the successful development of *O. humeralis* larvae, because according to Paulino Neto (2004), they require dry branches.

Many studies have shown that competition for food caused by high larval densities can increase mortality (Coulson, 1979; Rice, 1989; Hanks et al., 1991a), lead to a lower adult weight (Hanks et al., 1991a) or provoke larval cannibalism (Powell, 1978). The use of fresh branches might be a strategy to avoid inter- and intraspecific competition, because healthy, intact branches are unlikely to contain larvae from other cerambycid species. In addition, because *O. humeralis* females oviposit in several forks of a girdled branch, the potential for

intra-specific competition among siblings is reduced. If secondary colonizers bore in previously girdled branches, the larvae of the primary colonizers will have the great advantage of already being established. Another advantage of laying eggs on live plants is that females can feed on the host plant without having to move elsewhere for food.

Field observations suggest that deposition of eggs under the bark of fresh branches is essential for insects such as *O. humeralis*, because when the bark dries, oviposition becomes impossible. Immature larvae may need to feed on fresh tissues because of a low capacity to digest desiccated wood. Some species, including *Acalolepta rusticator* (Fabricius), *Plocaederus obesus* (Gahan) and *Olenecamptus bilobus* (Fabricius), acquire this ability during their development (Haack & Slansky, 1987). In many plant species, the tissues of recently girdled branches are also richer in nutrients than ungirdled branches and contain more sugar on which the larvae can feed (Haack & Slansky, 1987).

Natural enemies

The emergence of several braconid wasps from branches containing *O. humeralis* larvae suggests that these wasps parasitized this species. Braconid wasps are known to be important natural enemies of many cerambycids (Austin et al., 1994) and it would be interesting to know whether the wasps only attack *O. humeralis*, or whether they also attack other species of *Oncideres*, or other cerambycids sharing the same host plant. Additional studies are needed to determine the effect of this parasitoid on population dynamics of *O. humeralis*.

Wood-nesting ants were also considered important natural enemies of *O. humeralis* because they prey on all larvae inside the branches. Way et al. (1992) also documented predation of *Phoracantha semipunctata* eggs by wood-nesting ants.

Secondary colonist

Temnopsis megacephala is considered a secondary colonizer of *M. sellowiana* because it bored only in previously girdled branch sections that were thinner than those selected by *O. humeralis*. In our study area, *T. megacephala* seemed to reproduce only in branches of *M. sellowiana*, although Buck (1957) recorded these beetles colonizing other plant species, for example *Acacia decurrens* (Leguminosae) in Porto Alegre, southern Brazil (Buck, 1957; Bertels & Baucke, 1966). Our data corroborate findings that *T. megacephala* is associated with other cerambycids, principally species in the genus *Oncideres* (Martins, 1997), that girdle branches (Buck, 1957).

Further studies are needed to establish if, in the study area, *T. megacephala* uses only *M. sellowiana* as a host plant, whether it colonizes all melastome species used by *O. humeralis*, or whether it also colonizes host plants attacked by other branch-girdling cerambycids. Regional variation also needs to be studied, because *T. megacephala* is widely distributed from Rio Grande do Norte in Brazil to Argentina (Martins, 1997). It is intriguing to speculate that *T. megacephala* may actually turn out to be a specialist dependent upon certain cerambycid species rather than a particular host plant for reproduction.

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