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Research

First Evidence of *Thaumastocoris peregrinus* (Heteroptera: Thaumastocoridae) Feeding From Mesophyll of Eucalyptus Leaves

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Abstract

The bronze bug, *Thaumastocoris peregri*nus Carpintero & Dellapé, 2006 (Heteroptera: Thaumastocoridae) originally restricted to Australia, is an important emerging pest of Eucalyptus plantations in the Southern Hemisphere. It feeds on mature leaves, causing the loss of photosynthetic surface area and defoliation and, according to some studies, even tree death. In this work, feeding activities of *T. peregrinus* on *Eucalyptus camaldulensis Dehn* leaves and its primary food resources were identified. In cross sections of leaves, solid salivary deposits on epidermal cells and in the vicinity of stomata cells were detected. In subepidermal cells of the palisade parenchyma near the stylet penetration point, disorganization and removal of chloroplasts were also observed. The presence of chlorophyll in guts of adults and nymphs was analyzed using spectrophotometry and confocal laser scanning to obtain in situ fluorescent spectra. Both spectra showed chlorophyll absorbance peaks. In addition, the presence of chlorophyll in guts of *T. peregrinus* using fluorescence microscopy was identified. These results provide the first evidence that *T. peregrinus* feeds from the palisade parenchyma (chlorenchyma) of Eucalyptus leaves.

Key words: Bronze bug, feeding behavior, mesophyll, salivary deposit, chlorophyll

The bronze bug, *Thaumastocoris peregrinus* Carpintero & Dellapé, 2006 (Heteroptera: Thaumastocoridae), is an important emerging pest of Eucalyptus plantations worldwide (Martínez and Bianchi 2010; González et al. 2012; Nadel and Noack 2012; Soliman et al. 2012; Martínez et al. 2014). This species, originally restricted to Australia, was first recorded outside its natural range in South Africa in 2003 (mistakenly identified as *Thaumastocoris australicus* at first [Jacobs and Nesser 2005]). It was first recorded in Argentina in 2005 (Noack and Coviella 2006), and it was later recognized as the new species *T. peregrinus* (Carpintero and Dellapé 2006). Besides its native range in Australia, this species is now well established in New Zealand, South America, Africa, and Europe (Wilcken et al. 2010, Ide et al. 2011, Laudonia and Sasso 2012, Nadel and Noack 2012, Sopow and Bader 2012, and Garcia et al. 2013). Currently, *T. peregrinus* is one of the most important emerging pests of Eucalyptus plantations worldwide (Martínez et al. 2014).

Thaumastocoris peregrinus is a piercing–sucking feeder that feeds, develops, and reproduces on mature Eucalyptus leaves (Nadel et al. 2009, Ramanagouda et al. 2010). It is a small flattened bug (2–4 mm in length) with a gregarious behavior; both nymphs and adults live together on the same leaves (Bouvet and Vaccaro 2007). *Thaumastocoris peregrinus* feeding causes the loss of photosynthetic surface area and defoliation, and sometimes even tree death (Jacobs and Nesser 2005). Infested trees show leaf silvering, ranging from chlorosis to bronzing when heavily infested, whereas leaves become reddish-brown when defoliation occurs (Laudonia and Sasso 2012).

The study of the feeding behavior is an important step for understanding the biology of heteropteran species and to describe the damages produced on their host plants. The family Thaumastocoridae belongs to the suborder Heteroptera and the infraorder Cimicomorpha, which also includes phytophagous species belonging to the families Tyngidae and Miridae. It has been reported that cimicomorpha, such as these families, use the lacerate-and-flush feeding strategy (Miles 1968, 1972; Backus 1988), which has been more recently renamed cell rupture feeding (Backus et al. 2005).

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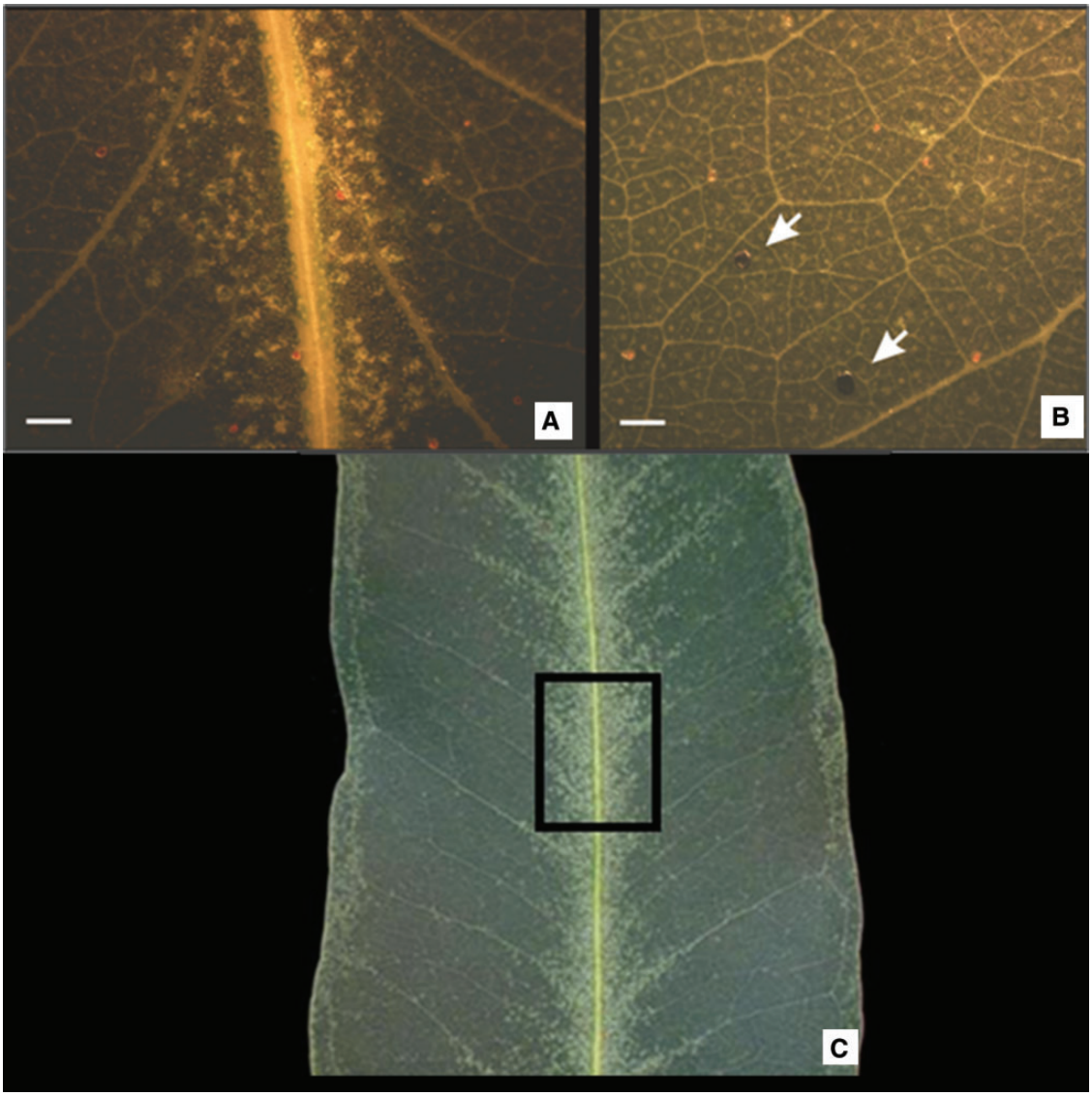

Fig. 1. (**A**) Chlorotic spots observed after 2 d of *T. peregrinus* feeding on *E. camaldulensis* leaves. The damage was visualized near the main leaf vein. (**B**) Arrows show dark excretion droplets. Scale bar: 1 cm. **C**: Context for image a.

These insects use the stylets to vigorously lacerate plant cells in a small area, simultaneously secreting watery saliva into the ruptured cellular layers, and then ingest the resulting lacerated/macerated "soup" (Backus et al. 2007). Insects that exhibit this cell rupture feeding behavior were referred to primarily as mesophyll-feeders (Miles 1968); however, it has also been reported that they may also ingest from secondary sites, such as the cells of the vascular bundles (Backus 1988, Wheeler 2001). These feeding habits have been well documented elsewhere (Pollard 1959, Mathen et al. 1988, Johnson and Lyon 1994, Buntin et al. 1996, Castañé et al. 2011). Among the Thaumastocoridae, the studies about feeding behavior are scarce, and they are particularly related to the feeding habits and macroscopic damage produced on their host plants (i.e., damages produced by the royal palm bug, *Xylastodoris luteolus* Barber (Schuh and Slater 1995, Hill and Schaefer 2000). Reports regarding feeding habits of *T. peregrinus* are conflicting. Although some studies report that it employs a lacerate-and-flush feeding strategy (González et al. 2012), others have reported that it is a sap-sucking insect (Laudonia and Sasso 2012, Oumar and Mutanga 2014, Nadel et al. 2015). To the best of our knowledge, there is no evidence about the food resources exploited by this insect.

To provide more information about the biology of this important pest, the aim of this study was to identify the feeding site of *T. peregrinus*, feeding in Eucalyptus leaves.

Materials and Methods

Plants and Insects

Eucalyptus camaldulensis leaves were used for this work. Leaves were obtained from 10-yr-old trees, grown in the arboretum of the experimental field of the Universidad Nacional de Luján, Luján, Buenos Aires, Argentina (34° 34′41″ S 59° 05′14″ W). For the experiments, we used mature leaves that were collected on the same day of the trials. We selected this species because it is the most preferred species for the bronze bug and is also one of the most widely cultivated species in Argentina (Invernoz 2011).

The insects were reared on *E. camaldulensis* plants in a JEIO Tech (JEIO Tech Co., Ltd., South Korea) GC-300/1000 growth chamber under 24 ± 2 °C, 60 ± 2% RH, and a photoperiod of 16:8 (L:D) h. We used fourth and fifth instar nymphs and females (3-d-old) of *T. peregrinus*.

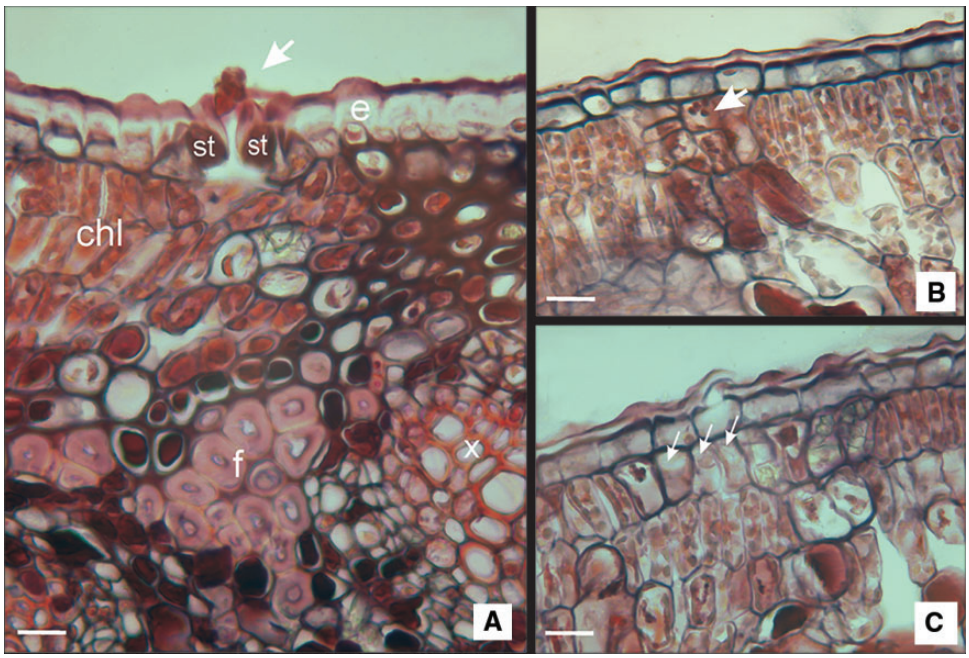

Fig. 2. Cross sections of *E. camaldulensis* leaves after *T. peregrinus* feeding (**A**) Salivary-flange (arrow) in relation to stomatal cells; (**B**) Degenerate chloroplasts in the subepidermal cells (chlorenchyma) (arrows); and (**C**) Chloroplast removal (arrows) in chlorenchyma cells. e: epidermal cell; st: stomata cell; chl: chlorenchyma cells; f: fiber (sclerenchyma cells); x: xylem (vascular tissue). Scale bar: 25 μm.

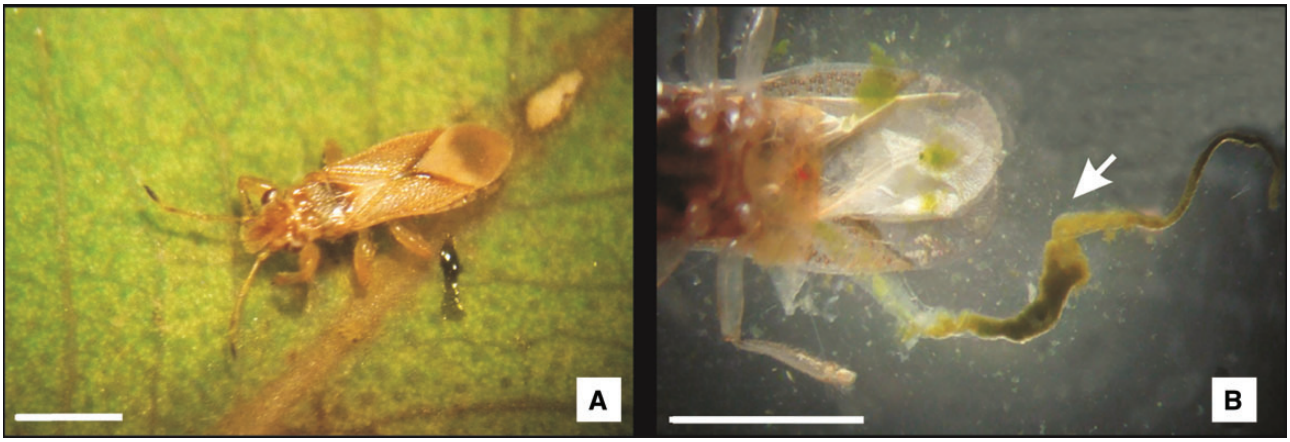

Fig. 3. Dissected gut of an adult *T. peregrinus* showing chlorophyll inside the midgut (arrow). Scale bar: 1 mm. Image taken using a stereoscopic microscope (LEICA EZ5) equipped with a digital camera (RRID 18 HD).

Feeding Behavior

In total, 20 *T. peregrinus* females (0- to 5-d-old) were starved for 1 d and were individually exposed for 2 d on *E. camaldulensis* leaves for feeding. The experimental area was limited using feeding chambers, with a 3-cm exposure diameter. Other leaves were used as controls. Control and damage leaves were photographed using a stereoscopic microscope LEICA EZ5 (Leica AG, Wetzlar, Germany) equipped with a digital camera RRID 18 HD.

To detect evidence of feeding activities, small blocks of the exposed leaves were cut, fixed in a formaldehyde–acetic acid–alcohol solution (90 ml of 70% ethanol; 5 ml of glacial acetic acid, and 5 ml of 38% formaldehyde for 12 h at room temperature, dehydrated in a standard ethanol series, embedded in Paraplast, and serial-sectioned at 10 μm). Sections were then stained with 0.5% aqueous red safranin and 0.1% ethanolic fast green, and then coverslipped with Eukkit. Cross sections of leaves were examined with a light microscope (Nikon YS2-H, Tokyo, Japan) equipped with a digital camera (Nikon D40).

Chlorophyll Detection

Spectrophotometry

To detect the presence of chlorophyll, entire abdomens ($n = 10$) and guts ($n = 10$) of *T. peregrinus* adults and nymphs were used. Guts were obtained from dissections using thin needles under a stereoscopic microscope (LEICA EZ5). Abdomens and guts of each developmental stage were separately macerated in 0.5 ml of 80% acetone (Porra et al. 1989), and a spectrophotometer (Shimadzu UV-160A, Kyoto, Japan) was used to determine the chlorophyll spectra.

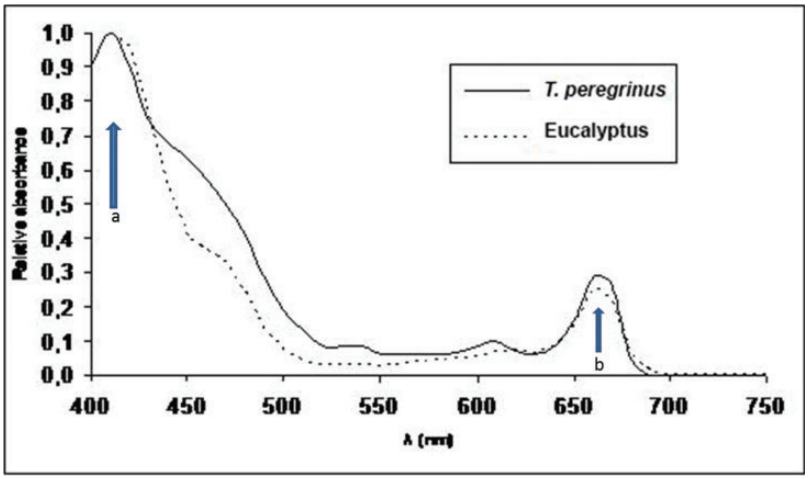

Fig. 4. Absorbance spectra obtained from 80% acetone macerates of *E. camaldulensis* leaves (dotted line) and *T. peregrinus* guts (full line) ($R^2 = 0.97$). Relative absorbance values were calculated relative to the maximum intensity obtained for each sample. Arrows show: a. absorption peak at 410 nm and b. absorption peak at 664 nm.

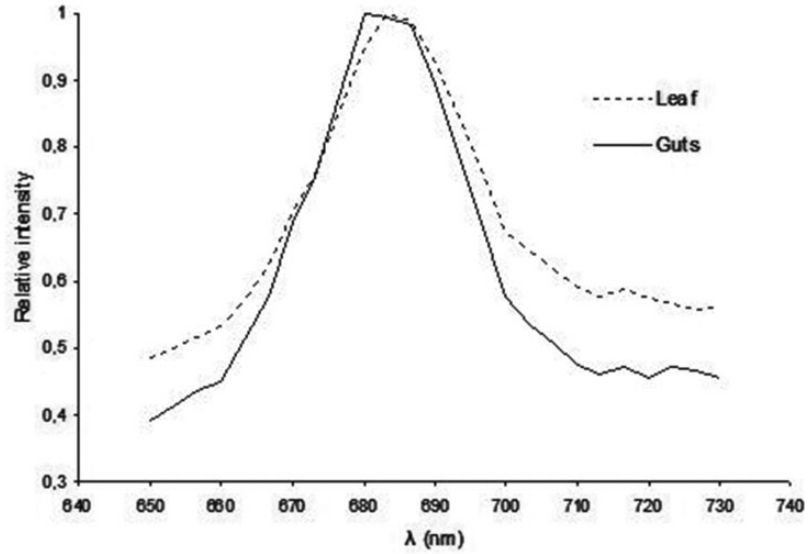

Fig. 5. In situ fluorescent spectra of *E. camaldulensis* leaves (dotted line) and *T. peregrinus* guts (full line) obtained from confocal images ($R^2 = 0.99$). Excitation/emission settings were 633/650–730 nm, and the resulting peaks were 683 nm for leaves and 680 nm for guts. Relative intensity values were calculated relative to the maximum intensity obtained for each image.

Confocal Laser Scanning and Fluorescence Microscopy

Pieces of *E. camaldulensis* leaves ($n = 5$) and *T. peregrinus* adults ($n = 5$) and nymphs ($n = 5$) were observed under a LEICA TCS SP5 laser scanning confocal microscope. Excitation/emission settings for chlorophyll were 633/650–730 nm (Carrión et al. 2013) and in situ chlorophyll spectra were determined for each sample. In addition, nymphs ($n = 5$) and adults ($n = 5$) were observed under an epifluorescence Olympus BX-51 (Olympus Corp. Tokyo, Japan) microscope with a longpass dichroic mirror (wavelength cutoff of 505 nm).

Results

Feeding Behavior

After 2 d of *T. peregrinus* feeding on *E. camaldulensis* leaves, chlorotic spots on abaxial leaf surfaces near the main vein were visualized (Fig. 1a). In addition, several excretion droplets (dark-green color) were detected in the feeding area (Fig. 1b).

In histological sections, salivary deposits (solid saliva) were detected in relation to epidermal or stomata cells (Fig. 2a), indicating that the stylet penetration can occur through them. Feeding activity was also detected in some subepidermal cells (chlorenchyma); some cells showed an atypical chloroplast disposition and appearance (Fig. 2b) or their complete removal (Fig. 2c).

Chlorophyll Detection

Spectrophotometry

Dissected guts of both *T. peregrinus* adults and nymphs showed a green color (Fig. 3).

Macerated guts and entire abdomens, as well as *E. camaldulensis* leaves, showed an almost identical spectrum ($R^2 = 0.97$), with peaks at 411 and 665 nm (Fig. 4). The difference between our results and the typical 430-nm chlorophyll *a* peak could be due to interference from other pigments and internal tissues of *T. peregrinus*, but the 665-nm peak clearly corresponds to chlorophyll *a*.

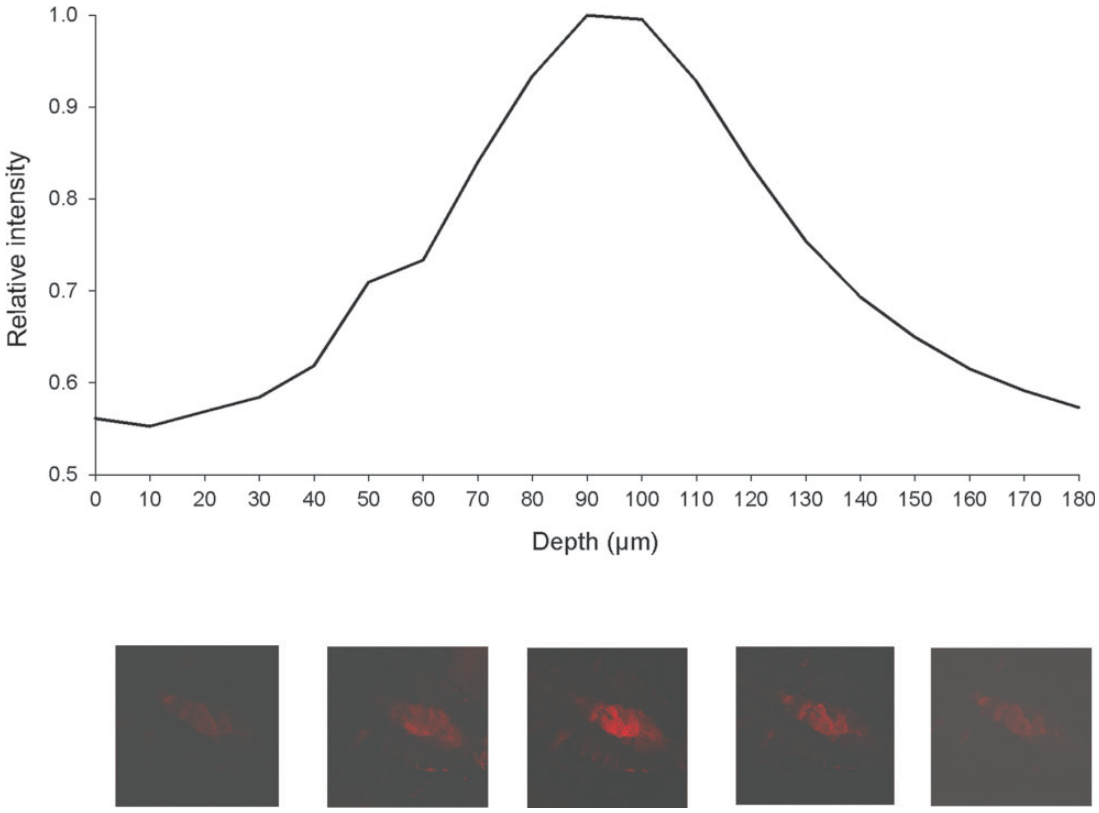

Fig. 6. Chlorophyll location in *T. peregrinus* midgut cross section, through confocal microscopy. Readings were taken at 10-μm-depth intervals through the abdomen, and the relative intensity was measured as shown in the pictures below. Excitation/emission settings were 633/650–730 nm. Images below show chlorophyll excitation at 30-μm-depth intervals through the abdomen.

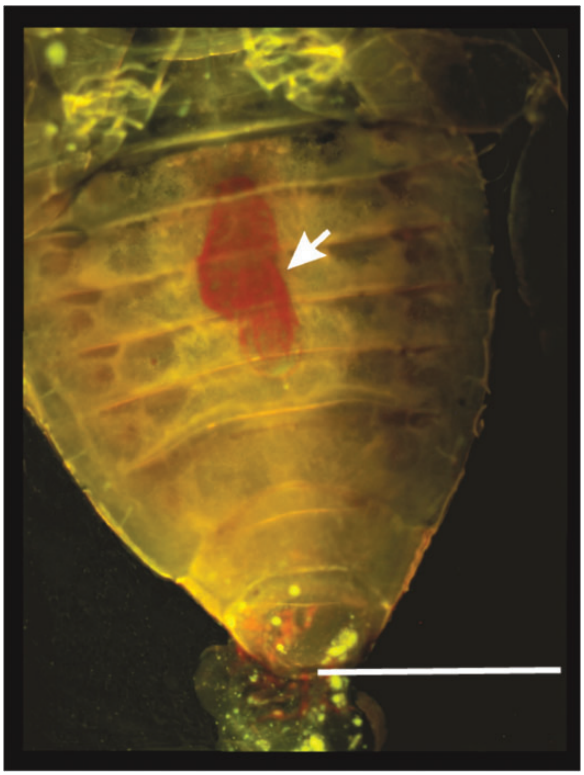

Fig. 7. Presence of chlorophyll (arrow) inside the guts of *T. peregrinus* through epifluorescence microscopy. Scale bar: 0.5 mm.

Confocal Laser Scanning and Fluorescence Microscopy

In situ fluorescent spectrum obtained through confocal microscopy showed almost identical peaks of absorbance ($R^2 = 0.99$) for *E. camaldulensis* leaves and *T. peregrinus* guts (Fig. 5). Chlorophyll location in *T. peregrinus* individuals ($n = 10$) through confocal microscopy is shown in Fig. 6. Staking images showed a higher relative intensity inside the abdomen (~90–100 nm in depth) clearly related to gut contents. The observations with epifluorescence microscopy also showed the presence of chlorophyll inside the *T. peregrinus* guts, which was visualized as a red color (Fig.7).

Discussion

This is the first study that shows strong evidence that *T. peregrinus* feeds from the mesophyll of Eucalyptus leaves and that this species produces salivary deposits during stylet penetration, which allows for a clear identification of the feeding spots.

The results show that after feeding, *T. peregrinus* produces chlorotic spots near the main vein of the leaves of *E. camaldulensis*. This macroscopic evidence is consistent with the removal of chloroplasts observed in cross sections of subepidermal cells (chlorenchyma palisade tissue) and with the loss of photosynthetic surface in leaves related to the feeding damage of *T. peregrinus* described by Jacobs and Nesser (2005). Similarly, studies by Buntin et al. (1996) showed that the physical damage of the palisade tissue produced by the tingid *Stephanitis pyrioides* (Scott) feeding would explain the observed leaf chlorosis on azalea (*Rhododendrum* sp.) leaves.

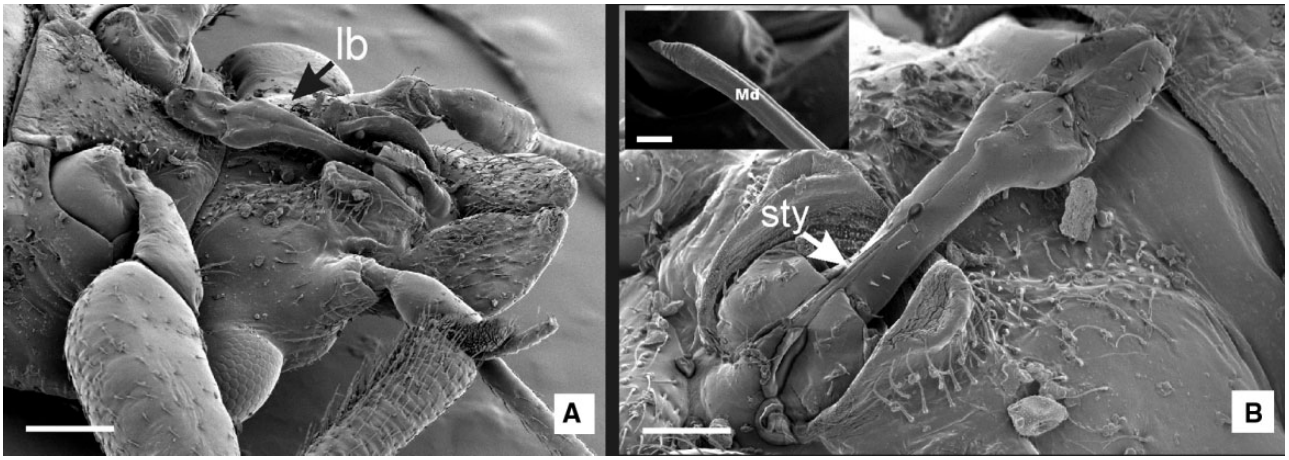

Fig. 8. *Thaumastocoris peregrinus* mouthparts' scanning electron micrographs. The gross morphology of the mouthparts resembles other plant-sucking hemipterans **A**) The labium (lb) extending to level of fore coxa; scale bar: 100 μm. **B**) Labium harboring mandibular and maxillary stylets (sty); scale bar: 50 μm. Detail of mandibular stylets (Md) showing serrations on its extreme apical region. Scale bar: 10 μm.

In cross sections of *E. camaldulensis* leaves, the presence of solid saliva on the epidermis indicated *T. peregrinus* feeding activity. This solid saliva has been termed "flange" by Miles (1972) and was related with the point where penetration of the stylets began (Fig. 8). The solid saliva in relation to epidermal cells and stomata indicates that stylet penetration can occur through them. Similarly, stylet penetration through stomata was reported for tingid species, such as the lace-bug *Urentius aegyptiacus* Bergevin feeding on *Solanum melongena* L. by Pollard (1959) and *Stephanitis yrioides* (Scott) feeding on azalea (*Rhododendrum* sp.) leaves by Buntin et al. (1996). The solid saliva produced by *T. peregrinus* was only detected on the leaf surface and it was not continued into the internal plant tissues. These observations agree with Miles (1972) who reported that phytophagous groups within the Cimicomorpha, such as Tingidae and many species of Miridae, do not produce a solidifying saliva of tubular appearance, known as stylet-sheath, that characterize the behavior of vascular feeders.

In cross sections, the results presented here also show that feeding activity occurs in subepidermal cells (palisade tissue). In agreement with these results, it was suggested by Miles (1972) that small tingids feed on individual cells or a small number of them near the epidermis, and Wheeler (2001) reported that injury produced by phytophagous mirids to palisade parenchyma is mostly confined to the cells actually penetrated.

One strong point of this work is the evidence of the presence of chlorophyll in the guts of adults and nymphs of *T. peregrinus*. The spectrum obtained using spectrophotometry showed coincidence between the absorbance spectrum of the macerated insects and that of the macerate *E. camaldulensis* leaves. In addition, the spectrum obtained using confocal laser scanning, showed peaks at 683 and 680 nm for Eucalyptus leaves and *T. peregrinus* guts, respectively. Fluorescence microscopy also evidenced the presence of chlorophyll in the guts of the bronze bug.

Furthermore, the dark-green excretion drops observed in this study on Eucalyptus leaf surface after *T. peregrinus* feeding was consistent with the typical dark excretion produced by mesophyll-feeders, such as phytophagous mirids among cimicomorphans (Wheeler, 2001) and by typhlocybine leafhoppers among auchenorrhynchans (Hunter and Backus 1989, Brentassi et al. 2010).

Wheeler (2001) suggested that despite phythopagous mirids being mainly lacerate and flush feeders on the mesophyll of leaves, they have been classified as phloem feeders apparently on the basis of casual field observations or perhaps just the assumption that this habit is common in mirids and others phytophagous heteropterans. This work shows that a similar assumption occurred with *T. peregrinus*, which was referred to as a sap-sucking species by several authors. The results presented in this work clearly show that *T. peregrinus* feeds from the palisade parenchyma (chlorenchyma) of Eucalyptus leaves. Further work through electrical penetration studies would be useful to shed more light on whether chlorenchyma is the only food source for this insect.

The knowledge of the food resource used by *T. peregrinus* is an important aspect of the biology of this species and it is important to better understand the possible mechanisms involved in the feeding injuries observed on Eucalyptus plantations.

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