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Surface structures of *Cecropia* plants as landmarks for orientation of ant foundress queens?

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Myrmecophytes are plants which provide nesting space and food for ants. *Cecropia* plants (Urticaceae) from South and Central America are such myrmecophytes. They have a mutualistic relationship with *Azteca* ants (Formicidae, Dolichodorinae), which defend their host plant against herbivores. For this service, *Cecropia* plants offer food to their resident ants (Mullerian bodies) at the base of the petioles and nesting space in the hollow stem (= domatia). To enter the hollow stem, young *Azteca* foundress queens bite a hole into a zone where the domatium wall is thinner (the so-called prostoma), enter the cavity and close the hole. It is not yet clear how *Azteca* ants locate the prostoma zone. The study presented here indicates that surface structures on prostoma and stem could be the clue. We found a significant difference between stem and prostoma zone in three ant-associated *Cecropia* species (*C. insignis, C. obtusifolia, C. peltata*), regarding the number of trichomes and papillae. Additionally, we found an influence of internode age on the number and distribution of trichomes and papillae. The differences are interpreted as landmarks to signal to the young queens the position of the prostomata, and the age and the size of the internode. All three are important to find an internode suitable for successful colony founding.

Busch J.S. & Mayer V.E., 2019: Sind die Oberflächenstrukturen auf den Stämmen von *Cecropia* Pflanzen eine Orientierungshilfe für junge, koloniegründende Ameisenköniginnen?
Ameisenpflanzen stellen Nahrung und Nistraum für symbiotische Ameisen zur Verfügung. Die in Mittel- und Südamerika sehr häufigen *Cecropia*-Arten (Urticaceae) sind solche Ameisenpflanzen. Sie gehen eine Symbiose mit *Azteca* (Formicidae, Dolichodorinae) Ameisen ein, die ihre Wirtspflanze gegen Fressfeinde verteidigen. *Cecropia* bietet seinen „Untermietern" dafür Futterkörperchen an der Basis der Blattstiele und Wohnraum im hohlen Stamm an (= Domatium). Um ins Innere des hohlen Stammes zu gelangen, untersuchen die jungen Königinnen die Oberfläche junger *Cecropia* Stämme und beißen sich schließlich durch das sogenannte „Prostoma", eine Stelle, an der die Wand des Stamms dünner ist als das umliegende Gewebe. Bis jetzt war nicht klar, wie *Azteca* das Prostoma lokalisieren. Unsere Studie bei drei mit Ameisen vergesellschafteten *Cecropia* Arten (*C. insignis, C. obtusifolia, C. peltata*) zeigt, dass Oberflächenstrukturen der Schlüssel sein könnten. Wir fanden erstens signifikante Unterschiede bei der Anzahl und Verteilung von Trichomen und Papillen je nachdem, ob es sich um die Oberfläche des Prostomas oder der umliegenden Stängeloberfläche handelt. Zweitens wurden Unterschiede in der Anzahl der Oberflächenstrukturen bei Internodien unterschiedlichen Alters festgestellt. Unsere Ergebnisse legen den Schluss nahe, dass die Oberflächenstrukturen den jungen Koloniegründerinnen die Position als auch das Alter der Internodien signalisiert. Sie sind daher eine wichtige Voraussetzung für die erfolgreiche Koloniegründung.

Keywords: *Cecropia*, *Azteca*, surface structures, trichomes, papillae, internode age, symbiosis, ant-plant interaction, orientation cues.

Introduction

Myrmecophytes are plants which provide nesting space and food for ants. From the tropics all over the world, about 650 vascular plants living in symbiosis with ants are known (Chomicki & Renner 2015). There are two kinds of ant-plant interactions, facultative and obligate associations. In facultative associations, ants visit the plant to look for food. In obligate ant-plant interactions, the host plants provide specialised food as well as nesting space (domatia) to their symbionts (Jürgens et al. 2006). One of the oldest reported mutualistic interactions between ants and plants is the association of *Cecropia* sp. Loefl. plants (Urticaceae) with *Azteca* Forel ants (Dolichoderinae, Formicidae) (Müller 1880, Belt 1874). The ants nest in the internodes of the hollow trunk and branches. The ants harvest phytoglycogen-rich multicellular bodies (Müllerian bodies)

Fig. 1: (A) *Cecropia obtusifolia* tree. The arrows indicate the position of the prostomata; (B) Foundress queen of *Azteca alfari* biting an entrance hole into the prostoma tissue of a young *C. peltata* stem; (C) SEM detail of a *C. insignis* prostoma. Bar: 200 µm. – Abb. 1: A) *Cecropia obtusifolia* Stamm. Die Pfeile zeigen die Position der Prostomata; (B) Eine Azteca alfari Koloniegründerin beisst ein Eingangsloch in das Prostomagewebe eines jungen Stängels von *C. peltata*; (C) REM Detail eines *C. insignis* Prostomas. Maßstab: 200 µm.

produced on pads of trichome-covered tissue (trichilia) at the petiole base interface (Rickson 1971, Bischof et al. 2013) to feed their larvae.

To colonize the hollow stem of myrmecophytic *Cecropia* plants, foundress queens and later the workers must bite entrance holes into the domatia wall to enter the domatia (Fig. 1B). There are zones in many myrmecophytes where the domatium wall tissue is thinner and weaker, a so-called prostoma (Ihering 1907, Bailey 1922, Brouat et al. 2001, Sanchez 2016). The prostomata are elliptical or round areas and longitudinal structures running all over the internode (Fig. 1A, C). They consist of unvascularized tissue, lack latex vessels and have a delayed cambium formation (Bailey 1922, Davidson & Fisher 1991, Brouat et al. 2001; Federle et al. 2001). Brouat et al. (2001) showed that prostomata can act as a morphological and behavioural filter to exclude generalist ants and favor colonization with the symbiont ants. This is because, first, ants must be able to chew entrance holes, and second, the size and shape of the prostoma must match the queen's body size and shape. It is not yet known how ants find the position of the prostomata once they have landed on their host plant.

A first indication of how ants can perceive the prostoma zone was found in *Macaranga*, where ant workers use incident daylight to recognize the prostomata from inside (Federle et al. 2001). Light as an orientation cue does not work outside and is thus unsuitable for colony-founding queens. Therefore, it is suggested that prostomata have orientation cues on their outer surface to facilitate an ant queen's colony foundation.

In the present study we analysed, in three *Cecropia* species (*C. insignis, C. obtusifolia, C. peltata*) which are obligately associated with *Azteca* plant-ants, whether the surface structure of the prostoma and regular stem provides mechanical orientation cues for *Azteca* foundress queens. We show that the presence of bigger trichomes and smaller papillae exist, and that the number and density clearly differs between prostoma sites and the surrounding stem surface and between younger and older internodes.

Material and Methods

The fieldwork was conducted at the La Gamba Field Station, a research facility of the University of Vienna (Austria). The station is situated in the Golfo Dulce region in Costa Rica near the Pacific coast (N 8°42.61′, W 83°12.97′), next to the Parque Nacional Piedras Blancas and 70 m above sea level. Plants and ants were collected on plantations, along roads and in the secondary rainforest around the field station.

Three young saplings each of *Cecropia insignis*, *C. obtusifolia* and *C. peltata*, between 50–150 cm, were collected in the field, and one additional *C. peltata* was taken from the Botanical Garden in Vienna (Austria) and was unoccupied. Previous studies revealed that the foundress queens are predominantly found between the second youngest and the eighth internode (I2–I8, counted from the apex downward) (Fig. 2), therefore we investigated only the 10 youngest internodes. The collected stems were cut into c. 15 cm long stem pieces and fixated in FAA (Formaldehyde, acetic acid, 70 % ethanol – 5:5:95).

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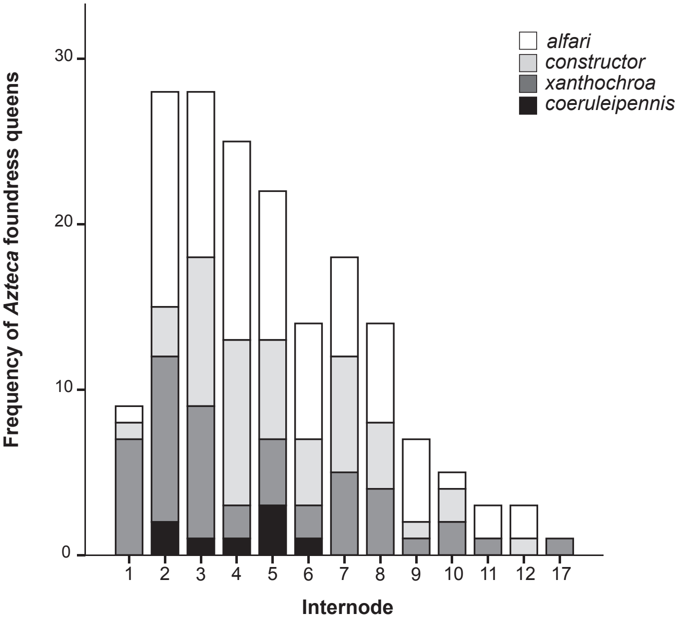

Fig. 2: Distribution of *Azteca*-foundress queens. Bars give the frequency of the azteca foundress queens found (*A. alfari, A. constructor, A. xanthochora, A. coeruleipennis*) in the internodes (n=56 *Cecropia* saplings from Monteverde and La Gamba, Costa Rica). – Abb. 2:Verteilung von *Azteca*-Jungköniginnen. Die Balken zeigen die Häufigkeit von Jungköniginnen aufgeschlüsselt nach *Azteca*-Art (*A. alfari, A. constructor, A. xanthochora, A. coeruleipennis*) in Internodien von 56 *Cecropia* Jungpflanzen (aus Monteverde und La Gamba, Costa Rica).

Electron-microscopical investigation

We investigated the stems of three *Cecropia insignis*, four *C. peltata* and three *C. obtusifolia* plants. The respective stems were fixated in the field FAA (Formaldehyde, acetic acid and Ethanol 70 %) and transported to Vienna. From each internode, the prostoma area as well as a representative area of the surrounding stem surface was cut out, dehydrated in an increasing ethanol series (70 %, 85 %, 96 %) with acetone as final step and critical point dried with a tousimis Autosamdri 815 critical point dryer and acetone as exchange medium. Sputter coating with gold was applied for 5 min at 10 kV in an Argon-atmosphere (Scd 050, Balzers Ag). After 5 min, the gold layer on the specimens is approximately 60 nm thick. Samples were then investigated with a Jeol Jsm-6390 electron microscope. It was not possible to investigate all internodes of one stem, because partly the internodes were already colonised by foundress queens and the prostoma modified, and sometimes they were destroyed by woodpeckers looking for ant larvae to feed on.

SEM pictures were taken from the center of the prostoma area and the surrounding stem surface. Then, a square of 0.5 mm × 0.5 mm was drawn into the SEM picture with ImageJ (Rueden et al. 2017) and the length of all surface structures was measured. Due to the considerable length differences of surface structures (Fig. 3A), we looked at the length distribution and distinguished two classes: the ones from maximal length to the average length were defined as “trichomes”, and the ones from average to minimal length were defined as “papillae”. With the same software, all trichomes and papillae that were inside the square with at least 50 % of their base were then counted, and their length as well as their base width was measured.

The youngest internode, which is normally enclosed by the caducous spathe, was not regarded. The first internode free of the caducous spathe was classified as internode I1.

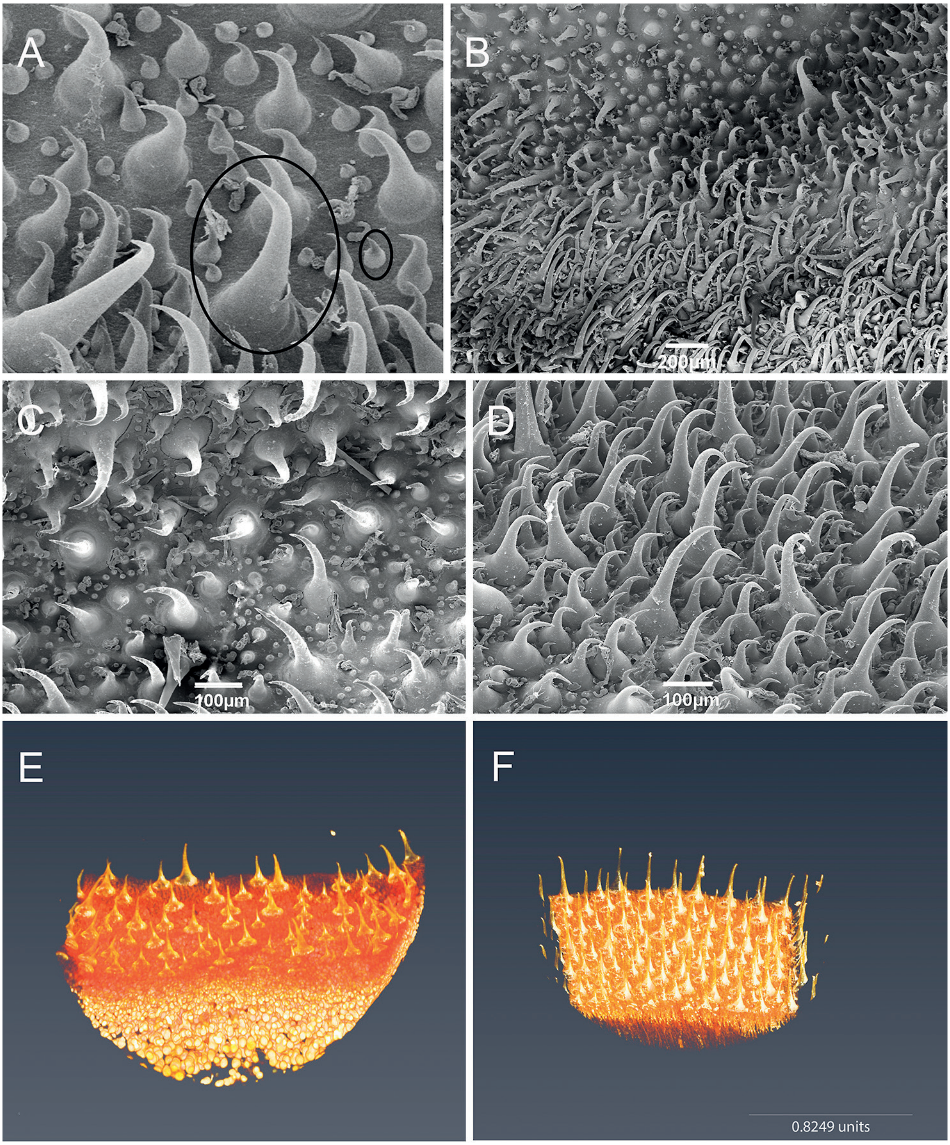

Fig. 3: (A) Trichomes (big circle) and papillae (small circle) on a *Cecropia insignis* stem; (B) transition zone between stem and prostoma of *C. peltata*; (C) prostoma surface of the second youngest internode of *C. obtusifolia*; (D) the corresponding stem surface; (E) CT-scan of the prostoma surface; (F) CT-scan of the corresponding stem surface (both from *C. peltata*). – Abb. 3: (A) das große schwarze Oval markiert ein Trichom, das kleine eine Papille; (B) Übersicht über das Prostoma; (B) Übergangszone zwischen Stängel- und der Prostomaoberfläche bei *C. peltata*; (C) Prostoma-Oberfläche des zweitjüngsten Internodiums von *C. obtusifolia*; (D) die zugehörige Stängeloberfläche; (E) CT-Scan der Prostoma-Oberfläche; (F) CT-Scan der zugehörigen Stängeloberfläche (beides von *C. peltata*).

Higher numbers mean older internodes, and they were numbered from the apex downwards to the stem base. For better handling, we made four groups comprising the first free internode as group 1, internode 2–4 as group 2, internode 5–7 as group 3, and internode 8–10 as group 4.

In total 84 prostomata and 86 stem areas (both from internode 1 to internode 17) were investigated.

Statistics

The statistical analyses were performed with IBM SPSS Statistics 23 (IBM 2015). To test whether the density of papillae and trichomes differed in general, whether the surface structure of the prostomata differed from the surface structure of the surrounding stem surface, and whether the age of the internode resulted in differences of the surface structures, a non-parametric Wilcoxon signed rank test for paired samples was used.

CT Analysis

For X-ray micro-CT scans, the FAA-fixated stem pieces were cut into smaller, 5 cm long parts and the tissue stained with a solution of 1 % (w/v) PTA (Phosphotungstic acid) in 70 % FAA (Gamisch et al. 2013; Staedler et al. 2013). The FAA/PTA solution was changed every second week.

After four months, the stained stem pieces were put into a test tube, fixed with synthetic cotton wool which was placed around the stem, and the tubes closed with parafilm. The stems were imaged with a MicroXCT-200 X-ray tomography system from Zeiss Microscopy (Jena, Germany). This system uses a 90 kV microfocus X-ray source (L9421-02 from Hamamatsu, Hamamatsu City, Japan), a cooled 2k CD camera, and switchable scintillator objective lens units. The three-dimensional reconstruction of the scans was made with the XM Reconstructor 8.1.6599 software (Zeiss Microscopy) and the scans subsequently rendered with the software Amira 5.5.0.

Results

The counts of surface structures in *Cecropia insignis*, *C. peltata*, and *C. obtusifolia* resulted in a considerable difference. The total number of all surface structures was significantly different between prostoma and stem in *C. peltata* and *C. obtusifolia*, but not in *C. insignis.* In *C. peltata* and *C. obtusifolia* the stem surface had a considerably higher number of surface structures than the prostoma site (Wilcoxon signed rank test, $P<0.05$; see also Tab. 1 and 2, Fig. 3). The CT scans additionally reinforced the difference between prostoma and stem surface (Fig. 3E, F). In *C. insignis* the average number of surface structures was more or less equal between stem and prostoma surface (Wilcoxon signed rank test, $P=0.13$).

If the total number is separated into the average number of papillae and trichomes, the prostoma site of *C. peltata* ($n=25$) and *C. obtusifolia* ($n=29$) had a significantly higher number of trichomes than of papillae, especially in the stem area (Wilcoxon signed rank test, $P=0.000$). Both had many more long trichomes than short papillae, the proportion is, however, similar with 82.9 % (*C. peltata*, $n=27$) and 85.9 % (*C. obtusifolia*, $n=27$) trichomes and

17.1 % (*C. peltata*) and 14.2 % (*C. obtusifolia*) papillae on the stem, and on the prostoma 66.5 % and 64.5 % trichomes and 33.3 % and 35.5 % papillae, respectively.

In contrast, *C. insignis* had a much higher number of papillae (70.9 % of the surface structures) and less trichomes (29.1 %) in the prostoma site. On the stem surface, 52.0 % were papillae and 47.96 % were trichomes and the average amount was more or less equal (Table 1).

Tab. 1: Average number of all surface structures per 0.25 mm², and trichomes and papillae, respectively. N gives the number of investigated internodes from 10 different plants. – Tab. 1: Durchschnittliche Anzahl aller Oberflächenstrukturen pro 0,25mm^2 und der jeweilige Anteil von Trichomen und Papillen. N entspricht der Anzahl der untersuchten Internodien von 10 verschiedenen Pflanzen.

	Prostoma					**Stem**		
Species	n	All	Trichomes	Papillae	n	All	Trichomes	Papillae
C. peltata	24	30.12	20.04	10.08	27	50.0	40.26	9.74
C. obtusifolia	29	49.35	31.83	17.52	27	61.30	52.67	8.63
C. insignis	30	38.96	11.33	27.63	32	36.76	17.63	19.13

Tab. 2: Comparison of trichome and papillae density, of stem and prostoma surface with respect to total number of surface structures, and the influence of the internode age on the surface structures. The significance was calculated with a non-parametric asymptotic Wilcoxon signed rang test for related data with the assumption (H_0) that surface structures are the same, independent of area and internode age. In most cases H_0 had to be rejected. – Tab. 2: Vergleich der Dichte von Trichomen und Papillen, der Gesamtanzahl der Oberflächenstrukturen im Prostomabereich und dem umliegenden Stängel, sowie der Einfluss des Internodienalters auf die Oberflächenstrukturen. Die Signifikanzwerte wurden mit einem nicht-parametrischen Wilcoxon-Vorzeichen-Rangtest für gepaarte Stichproben berechnet. Es wurde von der Nullhypothese ausgegangen, dass die Oberflächenstrukturen am Stamm gleich sind unabhängig von Prostoma und Internodienalter.

Species	**Trichome and papillae density**	**Surface structures on prostoma and stem**	**Internode age and surface structures**
C. peltata	Z=-3.21, **p=0.001**	Z=-3.824, **p=0.000**	Z=-3.824, **p=0.001**
C. obtusifolia	Z=-4.359, **p=0.000**	Z=-6.510, **p=0.000**	Z=-6.372, **p=0.000**
C. insignis	Z=-1.513, p=0.130	Z=-8.464, **p=0.000**	Z=-8412, **p=0.000**

Comparing internode age and surface structures, we found the highest trichome number on prostoma and stem of the youngest internode (Fig. 4). The papillae number is only significantly higher in the youngest internode in the prostoma site (Friedman ANOVA p=0.000). In older internodes (i2–4, i5–7 and older), the number of trichomes and papillae is the same on stem surface and prostoma area (Friedman ANOVA p=0.000) (Fig. 4).

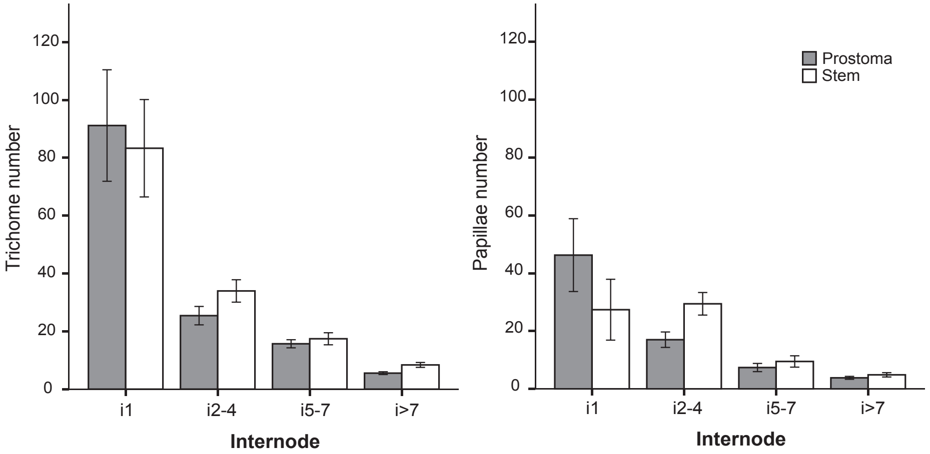

Fig. 4: Comparison of the average number of trichomes and papillae depending on internode age and surface area (prostoma or stem). The three *Cecropia* species are pooled. Bars represent the standard error. – Abb. 4: Vergleich der durchschnittlichen Anzahl von Trichomen und Papillen in Relation zu Internodienalter und Oberflächenbereich (Prostoma oder Stängel). Die drei *Cecropia* Arten wurden zusammengefasst. Die Fehlerbalken repräsentieren den Standardfehler.

Discussion

After analyzing the surface structure of the prostoma site and the surrounding stem surface of three *Cecropia* species associated with *Azteca* ants, we found that the total number of trichomes and papillae differed significantly between prostoma site and stem surface in two *Cecropia* species. The number of trichomes and papillae was significantly lower on the prostoma surface and higher on the stem (see Tab. 1; Fig. 3B-F). The prostoma surface can, therefore, be clearly distinguished from the stem surface based on the number and density of trichomes and may be a kind of guiding system for the ant queen. Ant foundress queens once landed on a *Cecropia* stem were observed to antennate the stem thoroughly (J. Busch, personal observation), which indicates that ant queens are investigating the surface. The queens were observed to explore the plant from the apical end. It did not matter where the queen first landed, she first climbed to the top of the plant and worked her way down from there, constantly antennating (J. Busch, personal communication). Additionally, the length of the surface structures was smaller on the prostoma site than on the surrounding stem surface. The smaller size and lower trichome density probably facilitates chewing a hole, therefore the structural difference of the prostoma site might be important for the decision of the foundress ants where to bite in.

Survival rate of foundress queens in domatia seems to increase with increasing stem diameter (Nishi & Romero 2008). Also, *Azteca* foundress queens need an internode of a certain size and a big enough spongy parenchyma layer on the inner domatia wall to start their fungiculture on piles of scraped parenchyma, which seems to be important for a successful colony foundation (Mayer et al. 2018). Interestingly, the youngest internodes of a *Cecropia* stem were hardly colonized, though the internode wall is softer and it is certainly easier to chew a hole in a younger than in an older internode wall. The youngest internodes always had many more surface structures per square µm on the prostoma and stem surface than older ones.

Too many surface structures are a structural barrier which prevent the foundress queen from gnawing an entrance hole and investing energy in an internode which is not suitable for successful colony founding. A slight tendency can be seen that the overall number of surface structures decreases with internode age. Thus, the surface structures may not only indicate to the foundress queen the prostoma zone itself, but also the age of the internode and the degree of lignification of the internode wall.

Apart from *Cecropia*, surface structures also seem to be important in myrmecophytic *Macaranga* species for the final decision of a foundress queen to stay on a certain host plant (Jürgens et al. 2006). Federle et al. (2001) could show that *Crematogaster* sp. living in *Macaranga* stems use incident daylight to select the position of their entrance hole and use visual landmarks for decision making.

In summary, the density of surface structures seems to act as landmarks for (1) the position of the prostoma, and (2) for the age and size of an internode. Finding the right site for biting the entrance hole is important for the colony founding queen. First, because the stem tissue is much thinner at the prostoma site than in the surrounding stem, second the internode should be young enough to allow to gnaw an entrance hole. Both make it easier for the ant queens to gnaw the entrance hole and shortens the time considerably during which a foundress queen is unprotected and exposed to predators. Third, the internodes should be old enough to have a parenchyma layer on the inner domatia wall surface big enough to start the fungiculture. As young queens make parenchyma piles before laying eggs, they seem to be crucial for colony foundation (Mayer et al. 2018). In *Macaranga*, it was shown that chemical cues have an important impact on long distance attraction of *Crematogaster* foundress queens (Jürgens et al. 2006). Whether this is the case in the *Cecropia*/*Azteca* association is not yet known and requires further investigation.

Future work has to be done with broader sampling and, in addition to the surface structures, the anatomy of the stem wall should also be taken into account. Another important factor may be the diameter of the prostoma: as *Azteca* queens vary in size, diameter differences with increasing internode age could be important for the distribution of foundress queens in *Cecropia* saplings.

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