

Preliminary notes on leaf-dwelling *Metagonia* spiders (Araneae: Pholcidae) in the Esquinas Rainforest near La Gamba, Costa Rica: leaf preference, mimesis, and web structure

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ABSTRACT

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Leaf-dwelling pholcids have evolved several times independently on different continents. They are pale greenish in life and are therefore barely visible on the undersides of leaves where they rest during the day. Apart from that, very little is known about their biology. Here we give some preliminary data on the biology of two species of the New World genus *Metagonia*. Both species occur on a variety of plant species, but there is evidence that certain plants are preferred, and this preference seems to be species-specific. We find no evidence that prey availability and leaf surface ultrastructure are responsible for these preferences, but additional factors, like thermal conditions and macroscopic leaf morphology remain unstudied. The web of *M. uvita* consists of a single layer of silk close to the leaf surface, while that of *M. osa* has an additional tarpaulin-like sheet of silk suspended above the other sheet. *Metagonia osa* specimens preferably orient their bodies in agreement with the nearest leaf veins, but this may result from space and shelter availability rather than from selection for mimesis. Males were often found to accompany females, but never females with egg-sacs.

Keywords: Pholcidae, *Metagonia*, leaf-dwelling, habitat selection, mimesis, web structure, cohabitation

Introduction

Even though there are only few studies demonstrating specific relationships between spiders and particular plant species (e.g. Young & Lockley 1989, Romero & Vasconcellos-Neto 2004, 2005, Romero 2006), it is clear that many spiders depend on specific habitat features ensuring an optimal thermal environment, proper construction of their webs, prey availability, protection from

predators, and conduction of vibratory signals (e.g. Billaudelle 1957, Greenstone 1984, Janetos 1986, Riechert & Gillespie 1986, Morse 1990, Henschel & al. 1992, Halaj & al. 1998, 2000, Kotiaho & al. 2000, Barth 2001, Souza & Souza Módena 2004, Souza & Martins 2005). Due to the combination of multiple factors influencing the spider's decision, the causal mechanisms explaining some overriding phenomena (e.g. the impact of plant structural complexity on plant-dwelling spider abundance and diversity) are difficult to disentangle.

Pholcid spiders occur in a variety of habitats, ranging from leaf-litter to tree canopies (Huber 2005). Some species live on the underside of leaves, well camouflaged by their morphology and behavior (Fig. 1; see below). Such leaf-dwelling pholcids are diverse in the tropics, and have obviously originated several times independently. For Indonesia alone, Deeleman-Reinhold (1986a) listed seven genera, but their phylogenetic relationships remain obscure. In the New World, at least two genera contain typical leaf-dwellers: *Leptopholcus* SIMON (Huber & Pérez 1998, Huber & Wunderlich 2006), and *Metagonia* SIMON (Huber 1997a, b). Most *Metagonia* species are leaf-dwelling, but some live in caves (Gertsch 1986, Huber 1998a), and a few are known from the leaf-litter (Gertsch 1986, Huber & al. 2005). Little is known about the biology of these spiders: what do their webs (if any) look like? Which animals share the microhabitat and which is the spiders' prey? Do males cohabituate with females as has been observed in other pholcids? Do these spiders prefer certain plant species?

It has been noted that in most reports of strict associations between spiders and certain plant groups, the plants are monocotyledons (Romero 2006 and references therein). This may also apply for leaf-dwelling pholcids [Deeleman-Reinhold (1986a) lists Liliaceae and Araceae as examples, Huber (2004) gives *Musa domestica* as preferred plant of *Metagonia mariguitarensis* GONZÁLEZ-SPONGA, 1998 in Northern Venezuela], but apart from this vague assumption, the only recurring statement is that the spiders are preferably found on large leaves (Brignoli 1980, p. 649 on *Leptopholcus*: "sur la face inférieure des grandes feuilles"; Deeleman-Reinhold 1986a, b; Huber 1997a, b, 1998a). No quantitative analysis of such an alleged preference has been published, nor have any potential explanations been proposed.

As indicated above, predation pressure may be an important factor for habitat selection in spiders. Leaf-dwelling pholcids appear well adapted to avoid predation by visually hunting predators like birds and insects: their cryptic coloration (pale greenish in life) makes them very difficult to spot unless the leaf is turned around and viewed against the dark forest floor. Some species seem to spend most of the time with the body pressed against the leaf surface, possibly avoiding shadows and imitating leaf veins. The similarity with



Fig. 1. Female of a leaf-dwelling *Metagonia* species, carrying an egg-sac. The species shown here was photographed on the Caribbean side of Costa Rica (near Cahuita) and is probably *M. delicata*, but the habitus is indistinguishable from that of *M. uvita* studied herein (photo courtesy M. Schmitt).

leaf veins is usually aided by long and thin abdomens and extremely thin legs, sometimes even by elongate rather than round egg-sacs (Deeleman-Reinhold 1986a, b, Huber & Wunderlich 2006). Whether or not they adjust their position relative to the leaf-veins has never been tested quantitatively.

The aim of our study is to present some preliminary observations on two congeneric and sympatric leaf-dwelling pholcid spiders, as a basis for future experimental studies. Our main questions were: do the two *Metagonia* species prefer certain plants, and do both prefer the same plants? Is there a difference between preferred and avoided plants in (a) prey availability, (b) leaf surface ultrastructure? Are these *Metagonia* species restricted to a few plants or do they occur on many? Do they align their bodies with the nearest leaf

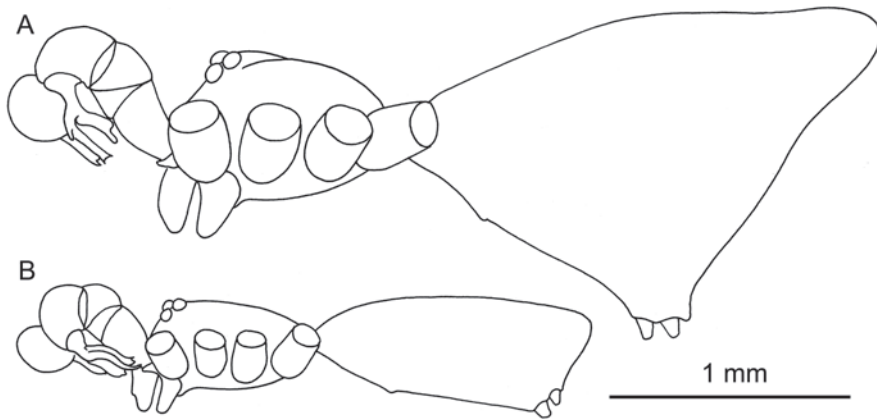


Fig. 2. *Metagonia osa* (A) and *M. uvita* (B) males, drawn to the same scale to show size and shape differences allowing easy identification in the field.

veins? What do their webs, if any, look like? And finally, do males cohabit with females?

Materials and Methods

Observations in the field were conducted from August 17–20, 2006 in the "Rainforest of the Austrians" within the Piedras Blancas National Park, Costa Rica. The quantitative analyses were restricted to a small area of forest along the "Waterfall Trail" near the Esquinas Rainforest Lodge (8° 41.7' N, 83° 12.3' W, 120 m a.s.l.). The more general documentation of plant species hosting *Metagonia* spiders included further trails around the lodge (Fila Trail, Ocelot Trail, Riverbed Trail). Voucher specimens of the two spider species studied (*Metagonia osa* GERTSCH, 1986, *Metagonia uvita* HUBER, 1997) are deposited at the ZFMK (Zoologisches Forschungsmuseum Alexander Koenig, Bonn). The two species are easily distinguished in the field (Fig. 2): *M. osa* is larger (about 2.5 mm body length, versus <2.0 mm in *M. uvita*) and has a posteriorly pointed abdomen (rounded in *M. uvita*). The latter character also serves to identify most juveniles.

For the quantitative analysis of leaf preference we chose five species of large-leaved plants (Fig. 3): *Anthurium ravenii* (Araceae), *Carludovica drudei* (Cyclanthaceae), *Calathea crotalifera* (Marantaceae), *Heliconia imbricata* and *H. latispatha* (Heliconiaceae). Even though leaf length differed among species

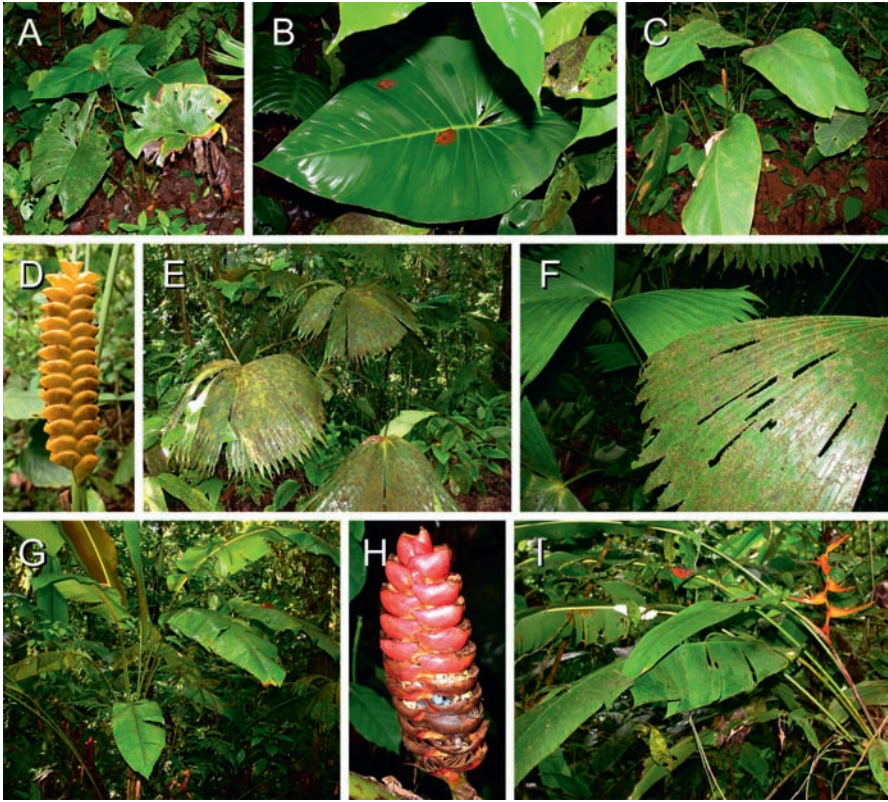


Fig. 3. Plants used for the quantitative analysis of leaf preference. – A–B: *Anthurium ravenii*; – C–D: *Calathea crotalifera*; – E–F: *Carludovica drudei*; – G–H: *Heliconia imbricata*; – I: *Heliconia latispatha*.

(Tab. 2), leaf surface area was roughly similar due to different leaf shapes. The sample size was limited by the fact that all species had to occur in sufficient numbers within a relatively small area of roughly homogeneous forest. We gently turned the underside upwards and took notes of all animals encountered of the leaf surface. All available leaves up to a certain number (about 60–70) were studied, with the exception of entirely brown leaves.

For SEM photos of leaf surfaces, pieces of leaves preserved in ethanol were cleaned ultrasonically, dried in HMDS (Brown 1993), and photographed with a Hitachi S–2460 scanning electron microscope.

For the analysis of web structure we blew a cloud of maize powder over the leaf surface using a plastic pipette. This method covers the silk threads with a fine layer of powder, making the otherwise virtually invisible threads fairly well visible. Many webs were observed, but twelve were studied in detail (2 ♂ 5 ♀ *M. osa*, 1 ♂ 4 ♀ *M. uvita*), including photographs and sketches.

Taxon	N leaves	Leaves with <i>Metagonia</i>		N specimens <i>Metagonia</i>	N specimens <i>M. osa</i>	N specimens <i>M. uvita</i>	N specimens indet.
		Total	%				
<i>Anthurium r.</i>	59	14	24%	18	15	3	0
<i>Calathea c.</i>	71	7	10%	8	6	0	2
<i>Carludovica d.</i>	61	15	25%	26	5	21	0
<i>Heliconia i.</i>	62	13	21%	17	4	13	0
<i>Heliconia l.</i>	63	4	6%	4	2	2	0

Tab. 1. Summary of quantitative results on leaf preference of *Metagonia* for five selected species of plants.

Leaf length (cm)	N leaves	Leaves with <i>Metagonia</i>	Specimen details
<i>Anthurium ravenii</i>			
35–40	12	2	1 ♂ + 1 ♀ <i>osa</i> , 1 ♀ <i>osa</i>
40–45	20	6	2 x 1 ♂ + 1 ♀ <i>osa</i> , 2 ♀ <i>osa</i> , 1 ♀ <i>osa</i> , 1 ♂ <i>osa</i> , 1 j <i>uvita</i>
45–50	19	6	1 ♂ <i>osa</i> , 2 x 1 ♀ <i>osa</i> , 1 j <i>osa</i> , 2 x 1 ♀ <i>uvita</i>
50–55	8	0	
<i>Calathea crotalifera</i>			
40–60	71	7	1 ♂ + 1 ♀ <i>osa</i> , 1 ♀ <i>osa</i> (with eggsac), 1 ♀ <i>osa</i> , 2 x 1 j <i>osa</i> , 2 x 1 j indet.
<i>Carludovica drudei</i>			
10–30	22	1	4 j <i>uvita</i>
30–50	25	7	1 ♂ + 1 ♀ <i>osa</i> , 1 ♂ <i>osa</i> , 1 j <i>osa</i> , 1 ♂ + 1 ♀ + 1 j <i>uvita</i> , 1 ♂ <i>uvita</i> , 1 ♀ <i>uvita</i> , 1 ♀ <i>uvita</i> (with eggsac)
50–70	14	7	1 ♀ <i>osa</i> , 2 x 1 ♂ <i>uvita</i> , 1 ♀ + 1 j <i>uvita</i> , 1 ♀ <i>uvita</i> (with eggsac), 2 x 1 ♀ <i>uvita</i> (with eggsac) + 2 j <i>uvita</i>
<i>Heliconia imbricata</i>			
40–60	7	0	
60–80	10	1	1 ♂ <i>uvita</i>
80–100	5	1	1 ♀ <i>uvita</i>
100–120	12	7	1 ♀ <i>osa</i> , 2 x 1 j <i>osa</i> , 1 ♂ + 2 ♀ <i>uvita</i> , 2 x 1 ♀ <i>uvita</i> , 1 j <i>uvita</i>
120–140	23	4	1 ♀ + 1 j <i>uvita</i> + 1 ♀ <i>osa</i> , 3 x 1 ♀ <i>uvita</i>
140–160	5	0	
<i>Heliconia latispatha</i>			
40–60	33	3	2 x 1 ♀ <i>osa</i> , 1 ♀ <i>uvita</i> (with eggsac)
60–80	4	0	
80–100	13	0	
100–120	13	1	1 ♀ <i>uvita</i>

Tab. 2. Leaf sizes of the plants studied in the quantitative analysis and specimen details of the *Metagonia* spiders found. j: juvenile.

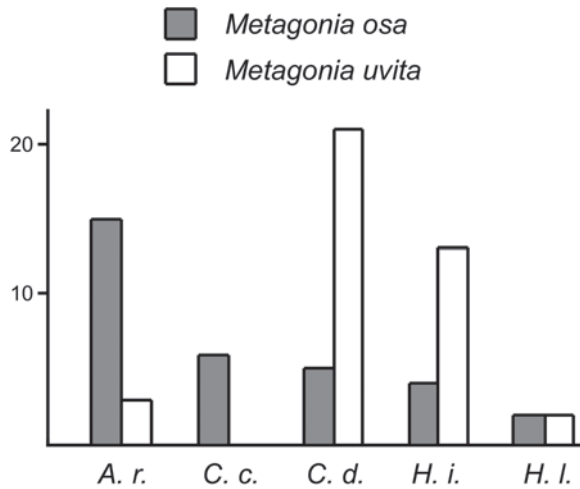


Fig. 4. Bar diagram showing absolute numbers of *Metagonia* spiders found on each of the five plant species in the quantitative analysis. For details see Tabs. 1 and 2.

To analyze the spider's orientation relative to the closest leaf veins we recorded the angle between the spider's longitudinal axis and the vein (0–90°, in 15° intervals). This analysis had to be restricted to *M. osa* because specimens of this species usually retain their resting position when the leaf is turned around, while *M. uvita* specimens often move or run away as soon as the leaf is turned.

Results

Leaf preference and morphology

We found *Metagonia* specimens on all plants studied quantitatively, though in very different numbers (Tabs. 1, 2, Fig. 4). The percentages of leaves occupied by a *Metagonia* spider ranged from 6% (*Heliconia latispatha*) to 25% (*Carludovica drudei*). Interestingly, the second *Heliconia* species studied (*H. imbricata*) had a relatively high percentage of leaves occupied by *Metagonia* (21%). The two species of *Metagonia* appear to prefer different plants: *M. osa* was more common on *Anthurium r.* and *Calathea c.*, *M. uvita* was more common on *Carludovica d.* and *Heliconia imbricata*. We found no evidence that leaves of certain sizes were preferred.

	<i>Anthurium</i> <i>r.</i> (59)	<i>Calathea</i> <i>c.</i> (71)	<i>Carludovica</i> <i>d.</i> (61)	<i>Heliconia</i> <i>i.</i> (62)	<i>Heliconia</i> <i>l.</i> (63)
Ants *	1	6	-	3	4
Ant nests	-	1	1	11	2
Blattodea	1	-	1	-	1
Coleoptera	5	24	3	10	1
Diptera	3	-	3	1	-
Heteroptera	-	34	5	14	1
Homoptera	6	1	3	4	3
Lepidoptera larvae	-	1	-	-	-
Orthoptera	6	36	6	9	19
Psocoptera	-	1	-	-	-
Araneae indet.	1	-	4	1	5
Salticidae	5	1	13	3	1
Scytodidae	-	1	-	-	-
Theridiidae	1	2	7	13	4
Thomisidae	1	-	-	-	-
Opiliones	-	-	1	1	-
Chilopoda	-	-	1	-	-
Plathelminthes	-	-	-	1	-
Gastropoda	-	1	-	-	-

Tab. 3. Animals found on the leaves of the five plant species of the quantitative study, apart from *Metagonia* spiders. Numbers of leaves studied in parentheses.

* only the presence of ants was recorded, not the number of specimens.

Leaf ultrastructure varies considerably among the five plant species, but there is no obvious correlation between leaf morphology at this level and spider preference (Fig. 5). *Heliconia latispatha* (which had the fewest *Metagonia* specimens) has relatively smooth leaves, but so does *Calathea crotalifera*. Considering the prominence of leaf veins, there is equally no obvious correlation. *Anthurium* and *Carludovica* have prominent veins, *Calathea* and the two *Heliconia* species have less prominent veins.

Other animals observed on the undersides of leaves

We observed high numbers of other animals on the undersides of leaves (Tab. 3), mostly ants, beetles, true bugs, homopterans (mostly leafhoppers), orthopterans (mostly crickets), and spiders (mostly jumping spiders and cobweb-weavers). On only two occasions we observed *Metagonia* spiders feeding on prey. In one case, a *M. osa* female fed on an ant, in the other case a *M. osa* male fed on a cobweb-spider. In both cases, the prey was approximately the same size or slightly smaller than the predator.

Taxon	Leaf length (cm)	Leaf height above ground (cm)	N leaves checked	<i>Metagonia</i> found
magnoliids				
Piperaceae: <i>Piper</i> sp.	20	30–60	5	1 ♀ <i>osa</i> (with eggsac), 1 j <i>osa</i>
monocots				
Araceae: <i>Dieffenbachia</i> sp.?	10	20–30	15	1 ♀ <i>osa</i>
Araceae: <i>Dieffenbachia</i> sp. (<i>daguensis</i> ?)	30	30–50	10	1 ♀ <i>osa</i>
Araceae: <i>Philodendron</i> sp.1	25	50–200	8	1 ♀ <i>uvita</i>
Araceae: <i>Philodendron</i> sp.2	20	up to 50	8	2 ♂ <i>osa</i>
Araceae: <i>Syngonium</i> sp.	25	100–200	25	2 ♂ <i>uvita</i> , 1 j <i>uvita</i>
Cyclanthaceae: <i>Asplundia</i> sp.	20–30	30–60	40	1 ♂ <i>osa</i> , 5 ♀ <i>osa</i> , 1 ♀ <i>uvita</i>
Cyclanthaceae: <i>Cyclanthus bipartitus</i>	50	100	6	1 ♀ <i>osa</i> (with eggsac), 1 ♀ <i>osa</i> , 1 ♀ <i>uvita</i> (with eggsac)
Arecaceae: <i>Geonoma</i> sp.	40–120	100–150	20	1 ♀ <i>osa</i> , 1 ♀ <i>uvita</i>
Costaceae: <i>Costus</i> sp.	15	40	11	1 ♀ <i>osa</i> , 1 ♀ <i>osa</i> (with eggsac)
eudicots				
Moraceae: <i>Ficus</i> sp.	20	100	10	1 ♂ <i>osa</i>
Malvales, gen. sp. indet.	20–25	70–180	12	1 ♂ <i>uvita</i>
Theophrastaceae: <i>Clavija</i> sp.	40–50	50–100	?	1 ♀ <i>osa</i>
Gesneriaceae: <i>Besleria</i> sp.	30	150	12	1 ♀ <i>osa</i>

Tab. 4. Additional plants on which *Metagonia* spiders were found. Taxa are arranged according to the classification in APG II (2003). j: juvenile.

Other plants on which *Metagonia* was observed

We found *Metagonia* specimens on a variety of additional plant species (Tab. 4), including a wide range of leaf sizes (10–120 cm leaf length), glabrous and hairy leaves, leaves with or without prominent leaf veins, and leaves from close to the ground up to about 2 m. Most of these additional plants (as well as all five plant species from the quantitative study) were monocots.

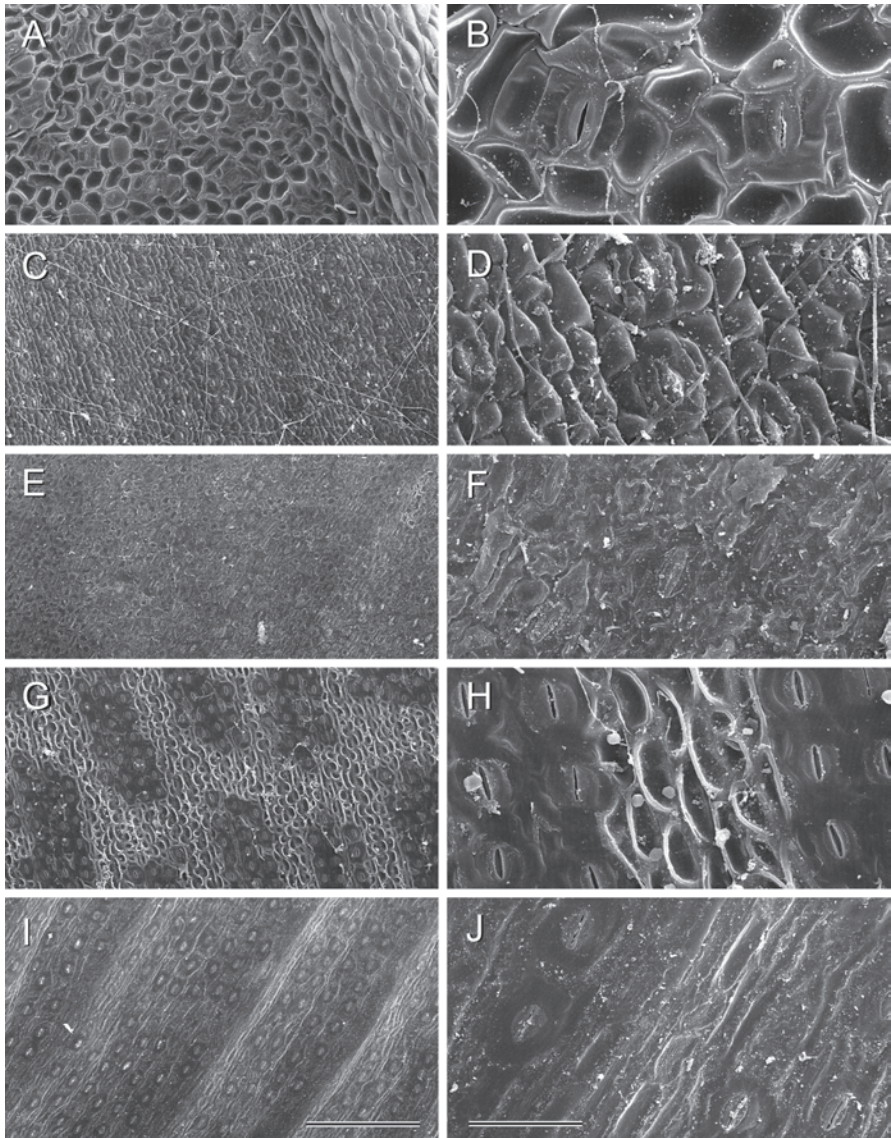


Fig. 5. Surface structure of the undersides of leaves of the plants used for the quantitative analysis of leaf preference. – A–B: *Anthurium ravenii*; – C–D: *Calathea crotalifera*; – E–F: *Carludovica drudei*; – G–H: *Heliconia imbricata*; – I–J: *Heliconia latispatha*. Scale lines identical for each column: 300 μm (left column), 60 μm (right column).

Angle between spider and leaf vein	N specimens
0°	23
15°	4
30°	5
45°	5
60°	2
75°	0
90°	4

Tab. 5. Orientation of *M. osa* specimens towards the nearest leaf veins.

Orientation relative to leaf veins

Of the 43 *M. osa* specimens for which we noted the deviation from perfect alignment with the underlying leaf veins, 23 (53%) were perfectly aligned. Misalignments of various degrees occurred at about equal frequencies (Tab. 5).

Web structure

Web structure differed substantially between the two species studied. *Metagonia uvita* builds a single layer of silk close to the leaf surface (Fig. 6a), while the web of *M. osa* consists of a similar layer close to the leaf surface plus a tarpaulin-like sheet of silk suspended about 5–20 mm above the other sheet (Fig. 6b). This detached sheet of silk is smaller than the surface layer, it is fastened unto prominent features of the leaf (veins, curved leaf borders, etc.), and the spider consistently rests between this cover and the surface layer of silk. We found no difference between webs of juvenile and adult specimens, nor between males and females. The webs of adult *M. osa* are slightly larger than those of *M. uvita* (about 10 x 15 cm vs. 8 x 12 cm).

Male-female cohabitation

Of the 14 males (8 *osa*, 6 *uvita*) found in the quantitative study, seven (5 *osa*, 2 *uvita*) were accompanying a female. A total of 38 females (18 *osa*, 20 *uvita*) were observed, of which 31 were singles. We found six females with egg-sacs (1 *osa*, 5 *uvita*), all of them singles. The present study thus agrees with previous data on pholcids indicating that adult females are guarded until egg-laying occurs (Huber 1998b on *Modisimus guatuso* HUBER, 1998). There was

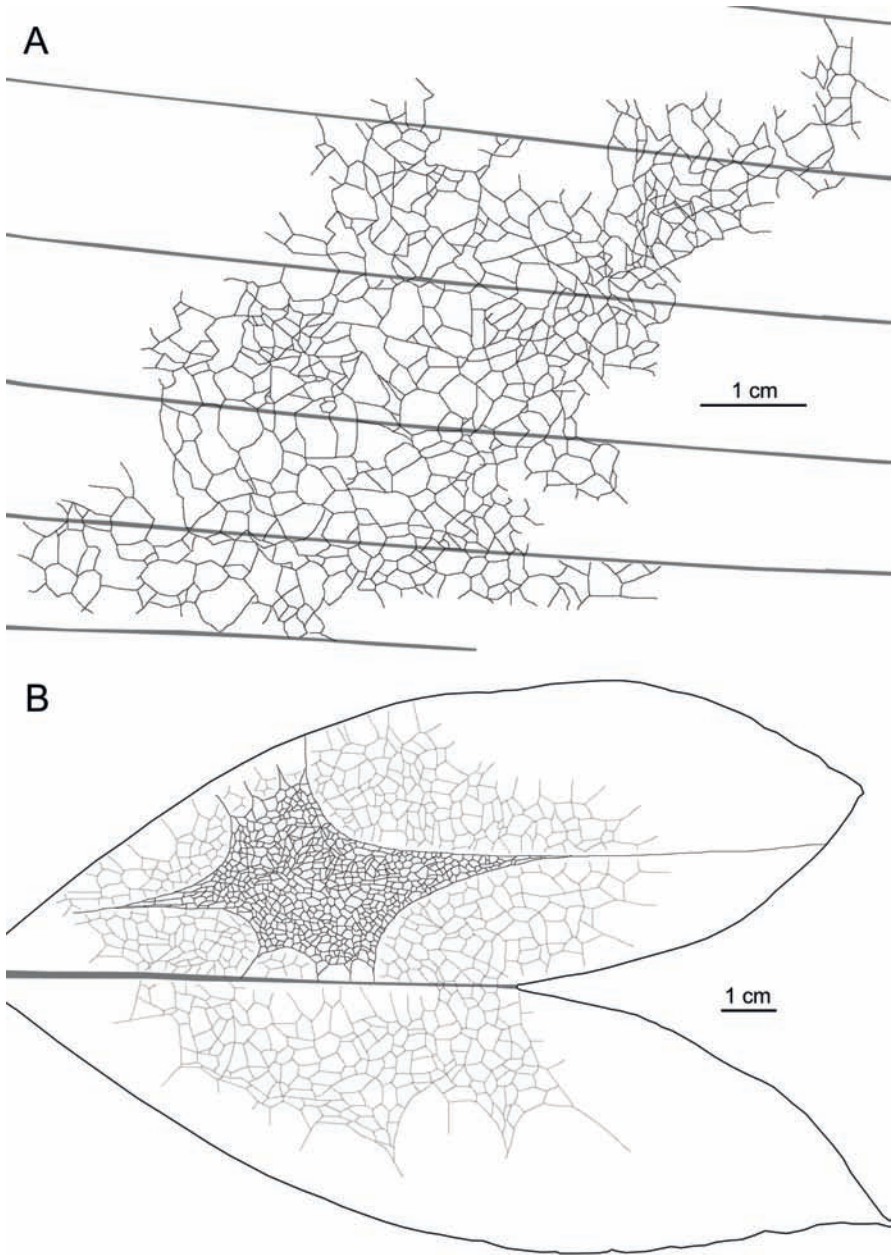


Fig. 6. Webs of *Megatonia uvita* on a *Carludovica drudei* leaf (A) and of *M. osa* on an *Asplundia* sp. leaf (B). The drawing of the *M. uvita* web follows closely the lines of a photograph of a web; only the main protruding leaf veins are shown in gray. The drawing of the *M. osa* web is more schematic, based partly on a photograph of a web, partly on a sketch drawn in the field; the tarpaulin-like sheet is graphically highlighted but the silks of the two sheets are not visibly different; only the main leaf vein is shown.

only one case where specimens of both species occupied the same leaf (two females).

Discussion

Leaf preference

Pervious studies have briefly mentioned that *Metagonia* is found on a variety of plant species (e.g. Huber 1997a on *M. rica* GERTSCH, 1986). The results of our study clearly demonstrate that none of the two spider species studied here is restricted to a specific species or even genus of plants. However, the quantitative analysis of five plant species suggests that there are preferences for certain species. Both species were rare on *Heliconia latispatha*; *M. osa* was more common on *Anthurium r.* and *Calathea c.*; *M. uvita* was more common on *Carludovica d.* and *Heliconia imbricata*. In addition, the qualitative analysis suggests that monocots are preferred; only four specimens were found on eudicots (Tab. 4).

The reasons for such preferences, if real, are far from clear. Our data suggest that differences in prey availability are not significant. Some of the insects observed (e.g. most crickets) probably were too large to be captured by *Metagonia* spiders, but we know almost nothing about these spiders' prey spectra. Future studies will have to concentrate on the actual prey of *Metagonia*, and on the abundance of these particular species on different plants.

We also see no evidence that leaf surface ultrastructure plays a major role in microhabitat choice in these spiders. In theory, since plant structural complexity is a major factor determining plant-dwelling spider abundance and diversity (Hatley & MacMahon 1980, Robinson 1981, Halaj & al. 1998, 2000, Raizer & Amaral 2001, Souza & Martins 2005), we might expect surface complexity to play a role too. This does not seem to be the case in the five plant species studied here: three of the four preferred species have relatively complex surfaces, but *Carludovica drudei*, which had the highest percentage of leaves with spiders, has a rather smooth and simple surface, similar to the only plant species that was largely avoided by both spider species. It is possible that complexity at this microscopic level is irrelevant for the spiders, and future studies should concentrate on macroscopic features of leaf complexity, like curvature, folding, and prominence of leaf veins.

Several additional factors may play a role in microhabitat choice, but our data are inappropriate to decide on their respective roles. Thermal conditions

may vary among plant species, and *M. uvita* with its larger surface area : volume ratio should be more susceptible to evaporative water loss. The leaves of all five plant species seem equally suited to protect the spiders from predators, but we know virtually nothing about these predators and about their strategies to capture *Metagonia* spiders. Finally, we see no evidence that leaf size per se is important because *Metagonia* was found on several species of plants with rather small leaves that just allow a web (see above) to be built.

Web structure and mimetic orientation

Previous data on the webs of *Metagonia* were very scarce and superficial (Huber 1997a on *M. delicata* O. P.-CAMBRIDGE, 1895 and *M. rica*). Our study shows that both males and females of the two species studied here construct very specific webs, and that these differ significantly between the two species. Since large spiders may in general be more vulnerable to bird predation (Waldorf 1976), we suggest that the tarpaulin-like sheet of silk built by *M. osa* might be related to the higher risk for this species to be attacked by predators. Alternatively, the two species may just have evolved different predator avoidance strategies: an additional sheet of silk versus running away (see Materials and Methods).

Our data show that *M. osa* is preferably aligned with the closest leaf veins while resting during the day. This is in agreement with previous observations on *M. rica* (Huber 1997a) and some Southeast-Asian leaf-dwelling pholcids (Deeleman-Reinhold 1986a). However, this need not necessarily result from selection on mimesis and predator avoidance. An alternative explanation is that the veins are oriented in the same way as certain leaf depressions and that the spider adjusts its orientation according to these shelters rather than to the veins. Future studies will have to distinguish between leaves that do and do not provide shelters along the leaf veins.

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