PROBOSCIDEA AND DICYPHINI: AN EXAMPLE OF SPONTANEOUS MUTUALISM BY A POPULATION OF PREDATORY BUGS INHABITING A STICKY PLANT

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Abstract: A population of the mirid-bug Dicyphus errans (Miridae) a species occurring in Europe, colonized a group of Devil's Claw (Proboscidea louisianica subsp. fragrans (Martyniaceae)) native to the USA and cultivated in a garden in Germany. More than 20 individuals of these predatory bugs have been found living and moving freely on these sticky plants, feeding on stuck victims, while garden ants (Lasius spp. (Hymenoptera)) trying to place aphids for "sugar farming" became captured together with their "productive livestock", as do small flies and bees. The observations on this spontaneous mutualism between the American Devil's Claw and a small mosquito-like European mirid-bug has been recorded on video (Hartmeyer 2022). This constitutes an additional example for the adaptation of these ubiquitous predatory bugs to feed on the prey of sticky plants that would usually capture small-sized insects. The American Frank Obregon (2017), who found native mirid-bugs on his cultivated Roridula (Roridulaceae) in California, called the phenomenon assisted carnivory, which fits quite nicely. Proboscidea as well as Roridula do not produce digestive enzymes, so they cannot benefit directly from their diverse captured prey. But as soon as predatory bugs colonize the plants and feed on the sticking prey, their droppings provide a suitable fertilizer to be absorbed by the stomata of the leaf. A perfect mutualism. In addition, some historic facts on bug-plant interaction are provided.

A short history on Miridae and the designation "assassin bugs"

The Assassins (also called Hashashins), were notorious for attacks and murder with dirks and poisoning during the 11th to 13th century in Persia and Syria. The terms "assassin" and "assassination" go back to this group as a synonym for killer or murderer and murder, respectively. They were first introduced to the Italian and later to the English language. The trivial names assassin bug or heath assassin bug have been assigned to the predatory true bug *Coranus subapterus* (Reduviidae) (De Geer 1773). Furthermore, "assassin bugs" became a common name for the family Reduviidae, because these large predators use their pronounced proboscis very violently to stab prey to death, as the Assassins were said to do.

In the same manner as it became usual in the English language to call all insects "bugs", "assassin bug" became an umbrella term for all predatory true bugs. This is only marginal if used colloquially; it is, however, not fit to scientific standards in publications. Let us take a glance at the history. In the early 20th century, Francis E. Lloyd learned from A. G. Hamilton, that *Byblis gigantea* harbors a small insect which he called a "buttner". Later, H. Stedman provided the same information and guided Lloyd to the natural habitat. In his book "The Carnivorous Plants", Lloyd (1942) reported for

the first time about the Australian mutualistic bugs, using the term "capsid" derived from the family name Capsidae (Hemiptera): "At some distance north of Perth we found a lot of plants ... infested with a small wingless capsid which turns out to be a new genus and will be described by Dr. W. R. China of the British Museum". Furthermore "Similar insects, also capsids move freely without difficulty over the surface of *Drosera* leaves in Australia, and of the African genus *Roridula*". Indeed, Dr. China described the mentioned capsid bugs found in the surroundings of the town Perth (China & Carvalho 1951; China 1953). However, in those days it was a rather exotic issue.

In the 1980s, the public interest in carnivorous plants increased significantly and subsequently also the availability of artificially propagated CPs. Particularly in Western Europe, *Roridula* plants became available, including their mutualistic *Pameridea* bugs (Miridae). In the 1990s, the authors travelled over months through Australia to study and film carnivorous plants. Already experienced for several years in the cultivation of *Roridula* and *Pameridea* in Germany, in 1995 we stumbled coincidentally upon several new *Setocoris* (Miridae) and *Cyrtopeltis* species (Miridae) living on *Byblis filifolia* (Byblidaceae) and various sundew species (*Drosera*). It was the first documentation far away from the former known records in the Southwest, on widespread plants in remote tropical regions of Western Australia and in the Northern Territory (Hartmeyer 1996 and videos Hartmeyer & Hartmeyer 1995; Hartmeyer 2016).

In 1995, when translating the documentary into English, the authors realized that the general use of the umbrella term "assassin bugs" for capsids leads to misinterpretations. As a result, the problem was first discussed in the Bulletin of the Australian Carnivorous Plant Society (Hartmeyer 1996) with regard to the newly found tropical mutualisms: "The comprehensive term assassin bugs – up to now current – should however not be used since this name is already given to the bug *Coranus subapterus*." In the comprehensive book Carnivorous Plants of Australia Magnum Opus (Lowrie 2014), the author who found even more plant-bug associations in tropical Australia in the late 1990s, quoted Hartmeyer's sentence and suggested to replace the misleading term "assassin bugs" by "sundew bugs". This sounds good and is probably less misleading. But as these bugs are found on *Byblis* as well, the term would be inappropriately exclusive. Therefore, it is recommended to use simply the family names Miridae, mirids or mirid bugs, respectively the synonym Capsidae, capsids or capsid bugs. In recent literature, Miridae is used predominantly.

Garden ants and domestic mirid bugs find a cultivated Proboscidea louisianica.

In late March 2022, the sown seeds of *Proboscidea louisianica* subsp. *fragrans* (Lindl.) P.K. Bretting (syn. *P. fragrans* (Lindl.) Decne.) germinated inside our greenhouse and developed nicely. At the end of April, it was warm enough to move the now already flowering plants into our garden. It needed only a day and the sweet aromatic scent of the pretty flowers attracted garden ants, which immediately tried to place aphids on the sticky plants. But they were unlucky! The ants, as well as the aphids, stuck to the numerous sticky hairs of the plant (Fig. 1), no longer able to free themselves. After the first week the *Proboscidea* looked typical: Particularly the lower leaves were covered with dead ants, aphids as well as small flies and bees. On a first glance, also mosquitos seemed to stick on the leaves; however, a closer look showed that they walked freely over the plant. That seemed very unusual and a macro-shot brought to light that they were mosquito-like domestic mirids of the genus *Dicyphus* (Fig. 2). What a nice surprise! There are several closely related species, only distinguished by the shape of their penis, which we did not examine. However, most likely a population of the predatory bug *Dicyphus errans*, specialized to hunt on sticky plants and mulleins, had settled on all six of our *Proboscidea* plants. An ideal set to record the mutualism on video.

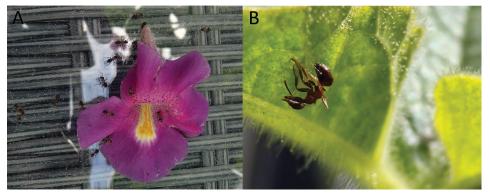


Figure 1: Lasius ants: A) Attracted by a fallen flower; B) Captured by the sticky plant.

Four weeks later, more than 20 bugs lived on four flowering plants inside a 34 cm pot (Fig. 3), placed on a garden table, providing a good view around. When one approached the plants, the mirids hid on the lower leaf side but did not fly away. After growing *Roridula* with *Pameridea* bugs for many years, the scenery looks now very similar, and regarding the mutualism, we observed just another example of assisted carnivory. Frank Obregon (2017) had a similar experience when domestic mirids settled on his cultivated *Roridula*. If sticky plants, unable to produce their own digestive enzymes, capture diverse prey, they cannot make use of it directly. But as soon as mirid bugs assist in digesting the prey and leave their droppings on the leaves, the prey nutrients may become available for the plant too. A clear win-win situation, which is obviously more widespread in nature than generally known.

Such assisted carnivory is at least a part of the digestion in almost all known plants acknowledged as truly carnivorous (Hartmeyer 1997). Different organisms even build complex food webs in pitchers of many truly carnivorous *Nepenthes* species (Clarke 1997). In this regard, it is important that most of the commensal mirids are associated with non-carnivorous plants: *Pinalitus parvulus* is connected to *Salvia canariensis*, *Apolygus lucorum* to *Passiflora* species, and *Dicyphus agilis* and *Nesidiocoris tenuis* to *Nicotiana tabacum* (tobacco) and *Solanum* (tomatoes and potatoes). Recently Miridae even became interesting as biological pest control for associated plants (Martinez *et al.* 2014). Associated bugs feed on parasites and victims that stick coincidentally to the defensive glands and they leave their droppings on the host plants.

If the term assisted carnivory were accepted to turn *Roridula* and *Proboscidea* into true carnivores, it would – if no clear limitations were defined – also turn tobacco, tomatoes, and potatoes into true carnivores. Generally, it does not matter if the bugs are present for a lifetime or temporarily after plants used volatiles to "announce" parasite-attacks (observed in *Nicotiana*) to their "partners". Without any limiting definition for the term assisted carnivory, all those herbs would become at least temporary true carnivores. Even worse, is it true carnivory when herbs benefit from nutrients broken down by maggots that fed on dead animals on a meadow? Carnivorous grass? Discussion opened! To provide a sufficient answer now would certainly exceed the scope of this article.

Pleasant feedback on the first go

Only one day after uploading our video recordings on YouTube on 16 June 2022 (Hartmeyer 2022), combined with the request to report bug colonization on own Martyniaceae, we received several reports with photos via Facebook and e-mail. These confirmed the described mutualism

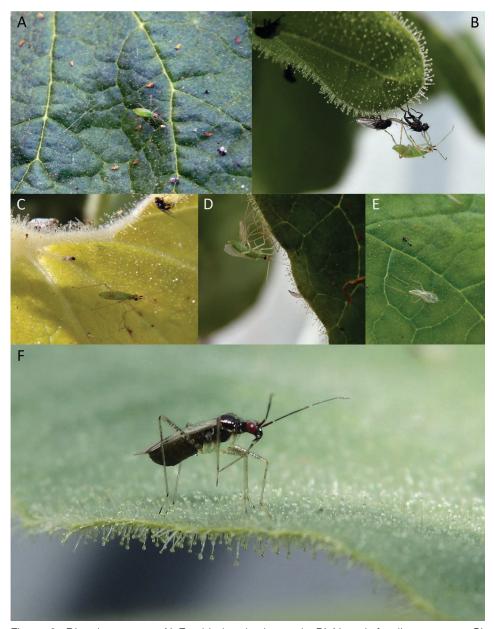


Figure 2: *Dicyphus errans:* A) Freshly hatched nymph; B) Nymph feeding on prey; C) Unwinged nymph after 1st moult; D) Winged nymph moulting; E) Empty exoskeleton after moult; F) Adult.

at the first go for two more European countries. *Dicyphus errans* on *Proboscidea* or *Ibicella* was found by Nils Klare (West Germany), Constantin Dormann (West Germany), Mathias Maier (South Germany, already for five years), Stéphane Joly (North France), and Jure Slatner in Slovenia. Jure had the bugs on his *Proboscidea* determined as *Dicyphus errans* by a Slovenian expert and reported



Figure 3: Proboscidea louisianica subsp. fragrans with Dicyphus errans population.

about it in a Slovenian book he wrote (Slatner 2019). In fact, he posted photos of the settlement in a Slovenian CP-forum as early as December 2008. Unfortunately, it was probably due to the language barrier that these early observations were not further examined. Remarkably, all photos sent to us, from northern France through Germany to Slovenia show identical bugs.

From the U.S., Matt Paddock mentioned a natural site in California with wild growing *Proboscidea louisianica* that seem to host a few different species of Miridae, very similar to our photos. Many of the mirids are not host specific, he wrote. That is certainly true. We also find *D. errans* on mullein in our garden; however, with fewer individuals than on the *Proboscidea*. Although an American plant is colonized by European bugs here, the wide distribution of this spontaneous mutualism confirms both partners are obviously well matched.

Dr. Barry Rice (2008) reported in CPN a mutualism in California. He found (probably) *Cyrtopeltis modesta* (Miridae) on *Ibicella lutea* (Martyniaceae). So, it doesn't matter where these Martyniaceae grow, they turn out to be typical bug plants and usually find partners. Their choice is quite impressive, as in Europe alone >1,200 species of Miridae are known. Some more papers (Anderson & Midgley 2002; Ellis & Midgley 1996; Heslopp-Harrison 1976; Penn State New Kensington 2014; Lloyd 1934; Voigt & Gorb 2008) add to the topic.

Finally, a look at the scene in our garden in the far southwest of Germany. The plants have developed well during a hot summer until early August and bear fruit abundantly by now (Fig. 3). On 25 June 2022, I found the first newly hatched nymphs of *D. errans* (Fig. 2), moving over sticky leaves and stems as easily as the adults. They found plenty of food and moulted after about 1-2 weeks. Only after the 2nd or 3rd moult, around mid July, the bright green nymphs with their striking red eyes formed wings for the first time. So far plants and bugs are doing well.

Methods: Photography and videography were done using an Olympus SH2 for photos and a Sony HXR-NX 80 with Zeiss Vario-Sonnar lens for 4K-video.

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