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REASSESSING COMMENSAL-ENABLED CARNIVORY IN
PROBOSCIDEA AND *IBICELLA*?

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In 1999 I conducted experiments to look for enzymatic activity on the glandular leaves of *Ibicella lutea* (Pedaliaceae), also known as the devil's claw or unicorn plant. I saw no evidence for enzymes, inferred the plants were not carnivorous, and wrote that "These are interesting plants, but I have no room for them in my carnivorous garden. The seeds I will send to the ICPS seed bank will be my last" (Meyers-Rice 1999). Furthermore, on my web site I wrote that "...on the whole, I have lost interest in this non-carnivore" (Rice 2004). Ah, how presumptuous I was.

As the years passed, I started second-guessing my conclusions. Was it possible I was hasty in discounting carnivory in *Ibicella lutea*? Is enzyme production an absolute requirement for carnivory? *Darlingtonia californica* does not produce enzymes—it achieves digestion of captured prey via arthropods and microorganisms that live inside its pitcher. I find it unreasonable to remove *Darlingtonia* from the ranks of carnivorous plants, for it is a highly effective hunter that incorporates both attributes of a pitfall trap and a lobster pot trap (Rice 2007). And if I maintained that *Darlingtonia* was carnivorous, what about the two plants in the genus *Roridula*? These plants capture prey, but like *Darlingtonia*, they achieve digestion through accomplices. In *Roridula*, these accomplices are capsids—bugs in the Miridae family. The capsid species are *Pameridea marlothii* (for the species that lives on *R. dentata*) and *Pameridea roridulae* (for the species on *R. gorgonias*). These bugs live on the leaves of the plants and consume prey captured on the leaves. Their feces are apparently absorbed through special cracks in the leaf cuticles and thus complete the carnivorous pathway of nutrients from prey to plant (Ellis & Midgley 1996, Anderson 2005). Of course, *Roridula* is not the only sticky plant that provides home for ravenous insects—many field workers such as Robert Gibson, Allen Lowrie, and Siegfried Hartmeyer have documented other Miridae-family insects such as *Setocoris* sp. living on *Drosera* and *Byblis* (Hartmeyer 1998, Lowrie 1998; and others), plants in which carnivory is not questioned.

In mid-2006 I decided to treat the two species of *Roridula* as full-fledged carnivores in my book (Rice 2006) for the reasons outlined above. Shortly after I had finished reviewing the last set of proofs for that book, travel took me to Tucson in southern Arizona. I took some time to look for *Proboscidea parviflora*, a native desert plant so similar to *Ibicella lutea* that the two are often confused. *Proboscidea parviflora* likes disturbed soils, so finding specimens along roads was relatively easy. While studying these plants, I looked for evidence of commensal organisms such as capsid bugs but found none. However, I was impressed by the heavily glandular nature of every above-ground part of the plant (see Figure 1), and the large numbers of tiny bugs captured on the leaves (see Figure 2).

A few months later, back in northern California, I was speaking with two faculty members (Art Shapiro and Tom Lanini) at the University of California, Davis, and they told me of two nearby sites in Yolo county where I could see *Ibicella lutea*. I visited the sites in November 2006. At both locations the plants occurred in weedy areas between agricultural fields. The muddy ground was littered with woody fruit, and gauging by the conditions they were in—they ranged from fresh through tattered to nearly disintegrated—it was clear that *Ibicella* had been growing at the site for many years. *Ibicella* is an annual, and at this time of the year the plants were dying, but there was still plenty of green foliage and ripening fruit on sprawling stems. The largest plants were over a few meters across (see Figure 3). The plants were extremely glandular, and had captured many insects (see Figures 4, 5).

The plants at both sites were being fed upon by larval lepidopterans, an interesting observation because it was the first time insect herbivory of *Ibicella* had ever been documented (Shapiro & Rice 2008). I was particularly fascinated to see two types of insects crawling on the glandular leaves,



Figure 1: Glands on *Proboscidea parviflora* petiole and leaf in Arizona.



Figure 2: Numerous insects trapped on the leaves and petioles of *Proboscidea parviflora*.



Figure 3: Sprawling *Ibicella lutea* plants in northern California.



Figure 4: *Ibicella lutea* inflorescence covered with insect-retaining glands.



Figure 5: A small fly trapped on an *Ibicella lutea* leaf.



Figure 6: Insects observed on *Ibicella lutea*. Left: Juvenile (top) and mature (bottom) capsids, probably *Cyrtopeltis modesta*; right: Berytidae stilt bug.

stems, and flowers without being impeded by the plant's glands (see Figure 6). Specimens of these bugs were identified by staff at the Bohart Museum (Davis), as members of the Berytidae (stilt bug) and Miridae families. The latter species of course is a capsid, and while its species identification is uncertain, it is probably *Cyrtopeltis modestus*. This species is omnivorous, and uses its piercing mouthparts to suck juices from plants but also insects and their eggs. This is one of the species that fulfilled China's (1953) description of a possible evolutionary pathway from a phytophagous capsid to a carnivorous one that might enable commensal-enabled carnivory by a plant.

My interest in the bugs was growing, so I contacted Sigg Hartmeyer; there are few carnivorous plant naturalists who have thought more about capsid bugs than Sigg and his wife Irmgard. Sigg informed me that he had conducted extensive literature searches on the topic of insects that live on sticky plants, and while he had found many papers describing such relationships, none involved *Proboscidea* or *Ibicella* (Hartmeyer, pers. comm., 2006).

So what conclusions can be drawn from these new observations of capsids on *Ibicella*? With *Ibicella* and *Proboscidea* we have two genera of highly glandular plants that trap and kill arthropods. There is no evidence for enzyme production by either set of plants, but for the first time *Ibicella* has been seen hosting carnivorous capsids. This is far from proof that *Ibicella* is carnivorous, but it is suggestive of possibilities. The interactions between *Cyrtopeltis modestus* (?) and *Ibicella* are probably complex, as *C. modestus* is both carnivorous as well as a sap-sucking insect. However, Anderson & Midgley (2007) have noted that *Pameridea* species have similar diets, and apparently become sap-sucking when no prey are available.

A caveat that must be explicitly noted is that these observations were made of escaped plants in California, far outside of the native range of *Ibicella*. However, the Miridae family has a global distribution, and it is likely there are capsids in the native South American range of *Ibicella* that are well-suited to perform a commensal function. But only field observations within the native range of *Ibicella* can prove this. And even if *Ibicella* plants swarm with carnivorous capsids in its native range, do they absorb the fecal nutrients expelled by the capsids? This also must be demonstrated.

So in the final assessment, carnivory in *Ibicella* has not been proven. Perhaps the plant is non-carnivorous, perhaps it is a commensal-enabled carnivore (i.e. a mutualist), or perhaps it is somewhere between. I just don't know! But I think it would be presumptuous to relegate the plant to the "not carnivorous" category just yet.

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