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Insect Visitors to Two Forms of *Aristolochia pilosa* in Las Cumbres, Panama[1]

Henk Wolda

Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Republic of Panama

Curtis W. Sabrosky

Systematic Entomology Laboratory, Agricultural Research Service, United States Department of Agriculture, c/o National Museum of Natural History, Washington, DC, 20560, U.S.A.

ABSTRACT

During two seasons insects that visited flowers of *Aristolochia pilosa* were studied in Las Cumbres, Republic of Panama. The vast majority of visitors were Diptera, notably Milichiidae (942 individuals, 18 species in 7 genera) and Chloropidae (97 individuals, 7 species in 5 genera). Occasional visitors, probably nonpollinators, included several other kinds of Diptera, a few wasps, an ant, a few Homoptera, and a spider. No significant differences in relative abundance of the visiting insect species were observed between two very different forms of *A. pilosa* growing side by side. The fimbriae on the flag of the flowers are important for long-distance attraction of flies, but the conspicuous purple markings seem to be irrelevant. At shorter range attraction to the floral tube overrides that of the flag, and the flies struggle their way down the tube among a dense mat of trichomes. All Milichiidae and Chloropidae captured were females. It is not clear what, if any, benefit accrues to the flies from being incarcerated repeatedly in *Aristolochia* flowers, but if they obtain some nutrient or other substance, it may be needed for the development of the ovaries.

Members of the family Aristolochiaceae share a peculiar mode of pollination. Insects, mostly Diptera, many of them covered with pollen from previous entrapment, enter the tube of the flower, which often has trichomes (permitting only one-way traffic), and become trapped in the inflated flowerbase (utricle), where they pollinate the then pistillate flowers. The insects remain trapped until the stamens ripen and cover the insects with pollen and the trichomes in the floral tube have wilted (Müller 1883, Pfeiffer 1960, Daumann 1971, pers. obs.). Insects are attracted to *Aristolochia* flowers by their odor (Daumann 1971, Brantjes 1980). Visitors reported for *Aristolochia clematitis* consist mostly of Diptera of the families Chironomidae, Ceratopogonidae, and Bibionidae (Müller 1883; Daumann 1971; Havelka 1978, 1983). Brantjes (1980) reports Lauxanidae and Phoridae as pollinators of *Aristolochia melanostoma* and Chloropidae and Milichiidae as pollinators of *Aristolochia arcuata,* both in Brazil. The present paper reports visitors to flowers of *A. pilosa* in Panama.

MATERIALS AND METHODS

The species of *Aristolochia*.—Vines from Las Cumbres, Panama key out to *A. pilosa* (Pfeiffer 1960, 1966; Croat 1978), but there is a problem. Both flowers and leaves can be distinguished easily from *A. pilosa* as found on Barro Colorado Island (BCI), Panama (*cf.* Croat 1978, pp. 373–374). Pfeiffer (1966) refers to variability within what he considers to be *A. pilosa,* incuding what had previously been named *Aristolochia costaricensis* (*cf.* Pfeiffer 1960).

In early 1981 a small vine from Barro Colorado Island was transported to Las Cumbres and planted next to a Las Cumbres vine (referred to hereafter as "BCI" and "LC," respectively). It grew rapidly into a typical BCI vine, so that the differences between the two forms are not caused by edaphic or climatic differences between the two sites.

The two forms are illustrated in Figures 1–4. The LC form is less hirsute than the BCI vine. The LC leaves are more elongate, shinier, and darker green than the BCI ones, and its flowers are slightly smaller. The tube is rather short, and the throat lacks the conspicuous purple coloration. The limb, which stands straight up and at a right angle to the tube, consists of two parts, a slender stalk and a rounded terminal flag. Purple fimbria and purple markings are all concentrated on the flag; the tube and stalk have only some vague purple coloration on the outside. The BCI form, on the other hand, has a longer tube with a conspicuous, wide throat and an elongate limb, which is almost all flag and is bent over to cover the throat. As with the LC form, the fimbriae are confined to the flag. However, they are green, not purple, and the conspicuous purple markings are found only on the inside and outside of the throat. The green fimbriae are only half as long as the purple fimbriae of the LC flag.

There is a taxonomic problem here, but we defer possible taxonomic decisions on these populations of *Aristolochia* for experts in that genus. An example of each "form" has been deposited in the U.S. National Mu-

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Milichiidae Blütenbesuch Sexualverhalten Aristolochia

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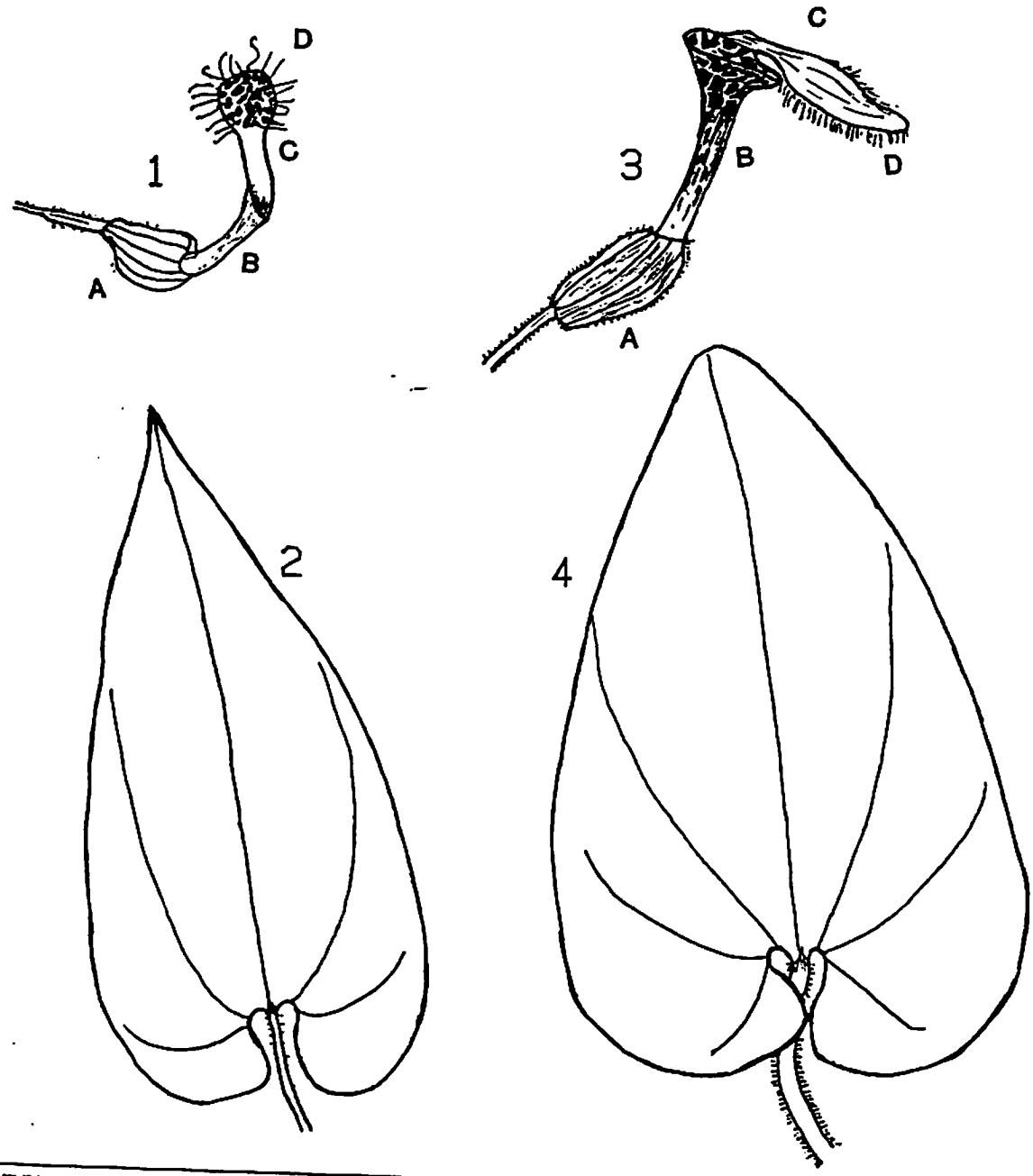

FIGURES 1–4. A flower and a leaf of each of two forms of *A. pilosa*. 1. Flower of the LC (=Las Cumbres) form. 2. Leaf of the LC form. 3. Flower of the BCI (=Barro Colorado Island) form. 4. Leaf of the BCI form. A = Utricle, B = Floral tube, C = Flag, D = Fimbriae.

seum. The differences between the forms are not only morphological: the LC vines flower from late October to February, whereas the BCI form, growing in the same locality, flowers through most of the year.

COLLECTIONS.—The *A. pilosa* flowers were collected from vines behind residence #999, Via de los Caobos, Las Cumbres, Panama (HW's residence) during the 1980–1981 and 1981–1982 seasons. That backyard is wooded,

TABLE 1. *The number of flower-visiting flies (Chloropidae and Milichiidae) found in individual flowers of* A. pilosa *in Las Cumbres, Republic of Panama. "Few" means approx. 2–4, ">10" may go as high as 30.*

Visitors:	0	1	2	Few	3	4	5	6	7	8	9	>10
A. pilosa LC	34	4	0	3	3	2	6	6	3	2	1	28
A. pilosa BCI	26	2	4	4	4	4	4	0	1	0	1	1

with a mixture of natural, fruit, and ornamental trees, and adjoins an area with young second-growth forest (Wolda 1980). During preliminary observations newly opened flowers were located and marked around 8 A.M., then collected the next morning. Insects were rarely found in these flowers, and the trichomes in the tube, where insects had been observed struggling their way in, had wilted, so that any trapped insects could have left. Flowers collected in the evening of the same day on which they were marked, on the other hand, usually had flies in them, so the latter procedure was adopted through parts of the 1980–1981 and 1981–1982 flowering seasons.

RESULTS

The vast majority of the insects visiting *A. pilosa* were Diptera of the families Milichiidae and Chloropidae. Ignoring for the moment other rare visitors (see below and Table 4), the number of these regular visitors observed per flower is listed in Table 1. Without exception, these flies were females; males have not been observed at the flowers. In a number of cases, the number of flies was only roughly scored as "few" (approx. 2–4 flies) or "several" (more than 10). The largest number counted in a LC flower was 30; the largest number counted in a BCI flower was 9. The large number of flowers with no visitors was probably due to weather conditions: after a rainy day few if any flies were observed. On average, the number of flies observed in LC flowers was much larger, in spite of the fact that LC flowers tend to be smaller than flowers of BCI vines. If the ">10" of Table 1 is assumed to average 15 (probably correct for LC and probably too large for BCI), the average number of Diptera per flower, with standard error, from the data of Table 1, is 6.0 ± 0.7 in LC and 2.1 ± 0.4 in BCI.

On a number of occasions flies were observed struggling their way into LC flowers. It usually took several minutes to make their way among the trichomes and disappear from sight. Sometimes they came out after the first few minutes of struggling, then tried again. The attraction of the tube must be very powerful. The nature of the attractant(s) was not determined; it may be chemical, although we could not detect any conspicuous odor. However, we attempted to assess the possible attractive effects of the flag and of the fimbriae on that flag. On a number of occasions some flowers were left intact, whereas on others the flag was clipped off or the fimbriae were trimmed off the otherwise intact flag. The results are presented in Table 2. If, again, the class >10 is taken as 15, intact LC flowers averaged 6.6 flies, whereas flowers with the flag clipped off averaged only 0.4, and those with only the fimbriae trimmed averaged 1.3 flies. This demonstrates that the flag, and especially the fimbriae on the flag, are necessary to attract flies. A possible explanation for the presence of some flies in the mutilated flowers is that the clipping and trimming was usually done at 8 A.M., by which time the first flies may have already entered the flowers.

The common Dipteran species found in the flowers of *A. pilosa* are listed in Table 3. A total of 942 individuals of Milichiidae, 18 species belonging to 7 genera, and 97 individuals of Chloropidae, 7 species in 5 genera, were found. Tropical insects, like temperate zone species, vary in abundance from year to year (Wolda 1983), so it is not surprising that the two years differ in relative abundance of visiting Diptera species. The NESS similarity

TABLE 2. *The number of flies (Chloropidae and Milichiidae) visiting flowers of two forms of* A. pilosa *in three treatment classes: "intact" flowers, flag clipped off, and flag trimmed of fimbriae. ">10" may go as high as 30.*

Visitors:	0	1	2	3	4	5	6	7	8	9	10	>10
A. pilosa LC												
Intact	29	2	—	4	4	5	6	3	1	—	—	30
Flag-clipped	23	7	1	—	1	—	—	—	—	—	—	—
Fimbriae-trimmed	5	3	1	1	1	1	—	—	—	—	—	—
A. pilosa BCI												
Intact	2	—	1	1	1	3	—	—	—	—	—	1
Flag-clipped	8	—	1	—	—	—	—	—	—	—	—	—

TABLE 3. *List of common visitors to flowers of two forms of* A. pilosa *in Las Cumbres, Republic of Panama.*

	LC		BCI
	1980–1981	1981–1982	1981–1982
Milichiidae Total	453	424	65
Milichiella sp. "a"	7	4	—
sp. "b"	2	—	—
sp. "c"	—	1	—
Pholeomyia sp.	1	—	—
sp. nr. leucozona Bk.	74	15	24
Paramyia sp. "a"	2	8	—
sp. "b"	3	7	2
Neophyllomyza sp. "a"	42	77	5
sp. "b"	6	24	1
sp. "c"	3	7	2
Desmometopa evanescens Sabr.	9	—	—
tarsalis Loew	73	141	27
atypica Sabr.	7	6	—
woldai Sabr.	151	29	2
obscurifrons Sabr.	2	6	—
glauconota Sabr.	69	89	1
New genus nr. *Litometopa* sp.	1	4	—
New genus sp.	1	6	1
Chloropidae Total	12	81	4
• *Chaetochlorops scutellaris* (Beck.)	1	—	—
• *Goniaspis* sp.	—	2	—
• *Olcella trilineata* (Duda)	—	—	1
• sp.	9	76	1
• *Apallates* sp. "a"	—	1	1
• sp. "b"	—	1	—
• Unknown genus	2	1	1

TABLE 4. *Occasional visitors to flowers of* A. pilosa *in Las Cumbres, Republic of Panama.*

Taxon	Individuals
Diptera	
Phoridae	
Megaselia sp.	2
"3–4 spp."	8
Psychodidae	2
Nematocera, 2 spp.	2
Drosophilidae, 2 spp.	2
Dolichopodidae	1
Cecidomyiidae	2
Lauxaniidae	1
Sciaridae	
Bradysia sp.	1
Hymenoptera	
Formicidae	1
Scelionidae	4
Homoptera	
Cicadellidae	
Agallia modesta	1
Agallia repleta	1
Cixiidae	
Bothriocera basalis	1
Derbidae	
Anotia sp.	1
Arachnida	1

index (Grassle and Smith 1976), here called "C20" (NESS with $m = 20$), is suitable for comparing the species composition of two samples (Wolda 1983). This index for the two years of LC visitors is 0.897 ± 0.021—close to, but significantly different from, unity; that is, the two sample years are significantly, but not very, different, as one might expect in samples taken in two successive years. The index for the LC-vs-BCI comparison in the 1981–1982 season is 0.876 ± 0.128, meaning that LC and BCI are not significantly different. The large standard error is caused by the small number of flies in the BCI sample. The raw data in Table 3 suggest the possibility of differences: the four most common species of LC in 1981–1982 comprise 75.8 percent of the individuals found; these same species in BCI make up only 49.3 percent of the individuals found. *Desmometopa tarsalis* is the most common species in both hosts, but is more common in BCI (39.1%) than in LC (27.9%).

The second most common species in BCI flowers is *Pholeomyia* sp. nr. *leucozona*, making up 34.8 percent of the flies caught; this species was relatively rare in LC at only 3 percent. The third and fourth most common species in LC, *Desmometopa glauconota* and *Olcella* sp., make up 17.6 and 15 percent, respectively, of the total, whereas in BCI each of these was represented by only a single individual (1.4%). However, as stated, these differences are not significant statistically.

Rare visitors to *A. pilosa* are listed in Table 4. They include various Diptera as well as some Hymenoptera and Homoptera. Even a small spider was once found inside the utricle of a flower.

DISCUSSION

The flag, especially the fimbriae on the flag, play a major role in attracting pollinators. Once the flies arrive at the flowers, however, they are apparently no longer interested in the flag: they do not walk on the flag, but immediately try to enter the tube. At short range the attractiveness of the fimbriae is overridden by the attraction of the tube. The latter may be chemical in nature, but we could not detect any strong odor.

The conspicuous purple markings may play no role at all in attracting flies. LC flowers with the fimbriae trimmed still had the purple markings on the flag, and BCI flowers with the flag clipped off still had their conspicuous purple markings left on the throat. Nevertheless, these flowers had lost almost all their attractiveness.

The regular pollinators of *A. pilosa* were Diptera of the families Milichiidae and Chloropidae, the same families which pollinate *A. arcuata* in Brazil (Brantjes 1980).

However, other visitors occasionally were observed making their way through the trichomes of the tube into the utricle. The diversity of these occasional visitors (Table 4) demonstrates that whatever the attractive agents of this plant are, they are quite general. Even insects which seem to have no reason to enter *Aristolochia* flowers, such as various Homoptera, Hymenoptera, and even a spider, were willing to struggle in.

Brantjes (1980) found a high pollinator specificity in Brazilian *Aristolochia* species. If this is also true for Panamanian species, then the high overlap in pollinator species between the two morphologically and phenologically different forms of *A. pilosa* suggests that they indeed belong to one species. No attempt has yet been made to cross-pollinate the two forms.

The benefit to the plants from pollen-laden flies entering the flowers is obvious. However, what, if any, benefit accrues to the insects is still unclear. Daumann (1971) mentions nectaries inside the flowers of *A. clematitis,* and possibly visitors to *A. pilosa* flowers also obtain nutrients, nectar, pollen, or stigmatic exudates from the utricle, but this also remains unclear. It seems unlikely that they would obtain no benefit, letting the plant heavily parasitize their pollinating ability. Some occasional visitors, such as the Homoptera, are almost certainly attracted without receiving a reward.

That all of the regular pollinators, Chloropidae as well as Milichiidae, are females suggests that either the nutrient-benefit hypothesis is wrong or that the nutrients offered by the plant are especially needed for egg maturation. Evidence of oviposition by the flies inside the flowers was completely lacking. The attractant chemicals may be related to male pheromones.

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