Research Note

HOWARDULA *SP., A NEMATODE NEW FOR PUERTO RICO, PARASITIZING A PARTHENOGENETIC SWEET POTATO-ASSOCIATED FLEA BEETLE,* CHAETOCNEMA PERPLEXA *BLAKE*[1]

In 1941, Blake[2] described *Chaetocnema elachia* as a bisexual flea beetle species from Vieques and Puerto Rico, mentioning *Ipomoea* sp. as its host plant. Wolcott[3] believed that the small *Chaetocnema* found on sweet potato leaves was this same species, and Martorell[4] (p. 145) agreed, reporting it to be "destructive when abundant on foliage of the host plant."

An experimental sweet potato plot of 11 x 42 m was found infested by a species of *Chaetocnema* at the Isabela Substation November 1987. Dr. Shawn M. Clark (Montana State University, Bozeman) identified it as *Chaetocnema perplexa* Blake. The plot was shared in equal proportions by two cultivars: "Mina" (lobulated leaves) and "Miguela" (non-lobulated leaves). Both were similarly attacked. The adults do not perforate the leaves, but produce essentially curved feeding tracks on both the upper and lower surface of the leaves.

There had been no prior record of *C. perplexa* infesting any convolvulacean plant in Puerto Rico before it was encountered on an introduced ornamental, *Ipomoea crassicaulis*, at Guánica Lagoon, January 1987, and on *Ipomoea pes-caprae* near the lighthouse of Cabo Rojo, December 1988 (Virkki and Santiago-Blay, unpublished). Twenty individuals of both samples were dissected and all were found to be females. Blake[2] described *C. perplexa* as a bisexual species present in several West Indian islands, complaining, however, on the rarity of males in the collections. Clark (personal communication, 1988) has received only females from the West Indies.

These findings render somewhat doubtful the former Puerto Rican records on the association of *C. elachia* with sweet potato. It seems possible that it always was *Ch. perplexa*.

We visually determined the sex of some 500 specimens sampled from the *C. perplexa* deme of Isabela, and all were females. For 178 of them, we confirmed the sex by dissecting the abdomen. At the same time, we encountered a very frequent and heavy abdominal infestation by a small nematode, which proved to belong to a genus new for Puerto Rico: *Howardula* (Allantonematidae: Tilenchida), as was tentatively determined by Dr. George Poinar, University of California at Berkeley. For the present communication, presence vs. absence of ovarial eggs were used as a criterion of oogenesis suppression. Most moderately or

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[2]Blake, D. H., 1941. New species of *Chaetocnema* and other chrysomnelids (Coleoptera) from the West Indies. *Proc. Entomol. Soc. Wash.* 43 (8): 171-80.

[3]Wolcott, G. N., 1948. The Insects of Puerto Rico: Coleoptera. *J. Agric. Univ. P. R.* 32: 225-416.

[4]Martorell, L. F., 1976. Annotated Food Plant Catalog of the Insects of Puerto Rico, Río Piedras, 1976.

TABLE 1.—*Infestation of the flea beetle* Chaetocnema elachia *by the oogenesis-suppressing nematode* Howardula *sp., from November 1987 to March 1988*

	Degree of infestation						
	Heavy		Little to Moderate		None		
Date	Normal oogenesis	Suppressed oogenesis	Normal oogenesis	Supressed oogenesis	Normal oogenesis	Suppressed oogenesis	Totals
3-11-87	1	8	0	6	15	4	34
24-11-87	0	11	1	1	18	3	34
29-12-87	0	2	1	1	24	3	31
17-2-88	0	2	0	7	34	5	48[1]
17-3-88	0	0	0	0	15	16	31[2]
Totals	1	23	2	15	106	31	178
Mean % of females with suppressed oogenesis[3]	76.6 ± 15.1 a		59.2 ± 18.6 ab		22.13 ± 7.5 b		

[1]Young females. Only young *Howardula* seen.
[2]Young females. No *Howardula* seen.
[3]Mean values bearing the same letter do not differ significantly (P>.05) with LSD method.

heavily infested females had their oogenesis affected (table 1). The negative association between the presence of *Howardula* and the ovarial eggs is statistically significant (Yule's Q = -9549; SE = .2795 E-01).

Many flea beetles and other chrysomelids are attacked by Allantonematidae[5]. Elsey[6] reports *Chaetocnema confini* and *C. pulicaria* being infested by *Howardula* sp. in North Carolina. Females of *Epitrix hirtipennis* were sterilized and larvae killed by *Howardula dominicki*[7]. In *Phyllotreta* flea beetles of Great Britain, the gonads of both sexes were somewhat less dramatically affected by *Howardula phyllotretae*, although reports on full female sterility in Germany and the USA were cited in the same paper[8]. Body size and female fertility were reduced in *Diabrotica* spp. (Galerucinae) infested by *Howardula benigna* in the United States[9]. No attempts to evaluate male sterility in the *Howardula*-infested chrysomelids were made. Infertility, prevention of ovarial development, and destruction of existing gonads have been reported in *Drosophila* spp. infested by *Howardula aoronymphium*[10,11] *Howardula* spp. seem to be capable of a heavy infestation of beetle and fly demes, and of high numbers of parasites per individual host. Cobb[9], who established the genus, had already considered it for biological control purposes.

The final sample, taken March 17, 1988, contained a higher number of females with underdeveloped ovaries than did earlier samples. *Howardula* was not encountered. We regard these beetles as the last most recently-emerged females not more inoculated by the declining nematode deme. Within two weeks, by April 4, the beetle population disappeared from the area. These population declines, despite an abundance of hosts (*Chaetocnema* for the nematodes, sweet potato for *Chaetocnema*) concur with our experience that most of the Puerto Rican flea beetle populations are drastically reduced during the annual spring dry season. Because the dry period is irregular, resulting in frequent rains in some years (as in 1988), our impression is that photoperiodism might be of more importance in controlling the populations than the actual precipitation and humidity.

The nematode does not reach an adult stage in the beetles. This apparently occurs in the soil following death of the hosts. Although the pre-adult stages of this *Chaetocnema* are unknown, we expect that at least the pupation takes place in the soil in typical flea beetle fashion[12]. In this context the inoculation of nematodes could proceed in the pupal earth chamber. The changes in frequency of infested females in 1987 suggest that environmental factors are

[5]Poinar, G. O., Jr., 1988. Nematode parasites of Chrysomelidae. Pp. 433-48 *in*: Jolivet, P., Petitpierre, E., and Hsiao, T. H. (Eds): Biology of Chrysomelidae. Kluwer Acad. Publishers, Dordrecht, The Netherlands.

[6]Elsey, K. D., 1977. Parasitism of some economically important species of Chrysomelidae by nematodes of the genus *Howardula*. *J. Invertebr. Pathol.* 29: 384-85.

[7]Elsey, K. D., 1977. *Howardula dominicki* n.sp. infesting the tobacco flea beetle in North Carolina. *J. Nematol.* 9: 338-42.

[8]Oldham, J. N., 1933. On *Howardula phyllotretae* n.sp.; a nematode parasite of flea beetles (Chrysomelidae:Coleoptera), with some observations on its incidence. *J. Helminthol.* 11: 119-36.

[9]Cobb, N. A., 1921. *Howardula benigna*: A nema parasite of the cucumber-beetle. *Science* 54: 667-70.

[10]Welch, H. E., 1959. Taxonomy, life cycle, development, and habits of two new species of Allantonematidae (Nematoda) parasitic in Drosophilid flies. *Parasitology* 49: 83-103.

[11]Jaenike, J., 1985. Parasite pressure and the evolution of amanitin tolerance in *Drosophila*. *Evolution* 39: 1295-301.

[12]Virkki, N. and I. Zambrana, 1983. Life history of *Alagoasa bicolor* (L.) (Coleoptera) in indoor rearing conditions. *Entomol. Arb. Mus. Frey* 31/32: 131-55.

capable of controlling the incipient infestation. Host/parasite incompatibility, or better-protected pre-adult stages, might account for *Cylas formicarius elegantulus* (Apionidae) and *Agroiconota propingua* (Chrysomelidae: Cassidinae) remaining unaffected by this nematode in the same field.

Absence of males is an indication of parthenogenesis. As we have seen in the present material, a heavy infestation by the nematode can suppress the oogenesis in over 50 percent of the females. This would appear to be a significant burden for any bisexual deme. Parthenogenesis of the deme might therefore be a response to the nematode. In view of the genetic difficulties that a recently-formed parthenote must encounter within the original bisexual deme[13], additional pressures towards parthenogenesis might have been present. In *Haploembia*[14], and even in Coleoptera (Saura 1988, personal communication), it is the male gametogenesis that suffers greatest of sterility under parasitism. Thus, we can visualize a preparthenogenetic situation in a deme where fertility of the males has been reduced to near zero by the parasites, and the only alternative for survival is parthenogenetization. A reduced competition by the bisexuals facilitates such a change. We think that this possibility should be kept in mind, even though the data up to now suggest that female chrysomelids are more frequently infested by *Howardula* and suffer more from the infestation than the males[6,7].

Another factor that might facilitate parthenogenetization in agricultural environments is the so-called survivor effect[15]. Very small invasions of outbreeding species suffer extensive homozygotization of recessive lethal genes through inbreeding. An incipient parthenogenesis is thereby offered an enhanced opportunity of survival, sheltered against competition by the bisexuals.

A genetic predisposition, which might already function in form of occasional gynogenesis, facilitates parthenogenetization in the above-mentioned situations. Generally, Chrysomelidae seem to be a family poorly predisposed for parthenogenesis. Suomalainen et al.[13] cite only eight cases, one of which is a flea beetle (*Altica lazulina*). The phylogenetic status of *Chaetocnema* is considerably above that of *Altica*[16]. Thus, the genetic allele combination supporting parthenogenesis is most probably not of common origin in these two flea beetles.

More investigation is needed to clarify biological aspects of the Puerto Rican *Howardula* sp. together with potential use in the biological control of *Chaetocnema* and other beetles.

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[13]Suomalainen, E., A. Saura and J. Lokki, Cytology and Evolution in Parthenogenesis. CRC Press, Florida, 216 pp., 1987.

[14]Stefani, R., 1964. La telitochia. *Boll. Zool. Unione Ital.* 31: 119-45.

[15]Manning, J. T., 1981. The survivor effect and the evolution of parthenogenesis and self-fertilization. *J. Theor. Biol.* 93: 491-93.

[16]Seeno, T. N. and J. A. Wilson, 1982. Leaf beetle genera (Coleoptera: Chrysomelidae). *Entomography* 1: 1-122.