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Genic and color polymorphism in Puerto Rican phyllobiine weevils *Diaprepes abbreviatus* (L.) and *Compsus maricaco* Wolcott¹

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ABSTRACT

Diaprepes abbreviatus is an important pest of cultivated plants of the West Indies east from Hispaniola. It displays a distinctive variation in the vittae and background color of the elytra, ranging from white through yellow to intense ochre and brown. It is extremely polyphagous, occurring also on numerous wild plants. *Compsus maricaco*, endemic in the Cordillera Central of Puerto Rico, does not display a similar color variation and is oligophagous, living on a few wild plants. Genic variation in these species was studied with starch gel electrophoresis. The amount of variability was low and there was no apparent correlation to the color variants within *D. abbreviatus*. The genetic distance between the two species is great.

INTRODUCTION

Diaprepes abbreviatus (L.), "la vaquita," is a most serious pest insect of agriculture, horticulture, and silviculture in Puerto Rico. It is extremely polyphagous, attacking severely at least 70 different species of plants, including such cultivated species as avocado, *Citrus* spp., corn, mahogany, mango, papaya, sugarcane (1). The adults feed on foliage, the larvae on roots. It has proven to be difficult to control because of its versatility.

D. abbreviatus displays a distinctive color variation. The western lowland populations tend to have individuals with whitish elytra. This background color turns to brownish in the southern and eastern lowlands. This may be combined with a lighter or grayer area around the *scutellum*: the "periscutellar spot." Specimens found on Culebra and Vieques islands are of the eastern lowland type. Cordillera Central, west from Barrio Hayales (Aibonito), is inhabited by a larger vaquita, sometimes

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of uniformly yellow, blackstriped elytra, as in the back mountains of Peñuelas (road 378) or, more commonly, of a background color varying from white to yellow to brownish, with additional red or yellow stripes at the sides, and one additional vitta per elytron. These large colorful variants are not seen in the corresponding elevations of the eastern mountains of El Yunque, where a smaller, grayish, sometimes greenish, variety prevails.

The aim of the present study is to establish whether the color variation of the elytra is connected with some electrically detectable variation and also whether the species would show any detectable genetic variation between populations of different origin within Puerto Rico. Samples of different populations were subjected to starch gel electrophoresis and assayed for different enzymes thereafter to establish the extent of genetic variation. The results are compared to data obtained on related *Compsus maricao* Wolcott, another oligophagous and less variable weevil of the same tribe, Phyllobini.

MATERIALS AND METHODS

Seven samples of about 30 specimens of *Diaprepes abbreviatus* and two of *Compsus maricao* were collected during the summers of 1983 and 1984 (figs. 1 and 2; table 1). The samples were shipped alive by air to Helsinki, Finland, where they were deep-frozen at -80°C , and later assayed for the following enzymes: adenylate kinase, acid phosphatase, esterase, glutamate-oxaloacetate transaminase, alpha-glycerophosphate dehydrogenase, hexokinase, isocitrate dehydrogenase, leucine aminopeptidase, malate dehydrogenase, malic enzyme, phosphoglucose isomerase, 6-phosphogluconate dehydrogenase, phosphoglucomutase, superoxide dismutase, and triosephosphate isomerase.

Because of poor resolution, data for adenylate kinase, hexokinase, and phosphoglucomutase are not included.

Ordinary starch gel electrophoresis (in two buffer systems, Poulik and tris-citric acid, pH 7.1) was used. The methods were essentially similar to the ones used in our previous weevil studies (4, 7).

RESULTS AND DISCUSSION

The following loci were polymorphic in *Diaprepes abbreviatus*: *Isocitrate dehydrogenase* (IDH-1), *Malate dehydrogenase-2* (MDH-2), *Malate enzyme* (MEN-1), *Phosphoglucose isomerase* (PGI-1), and *Triosephosphate isomerase* (TPI-1), i.e., loci commonly polymorphic in weevils (7).

The average degree of heterozygosity based on a direct count of heterozygotes is 0.039 per locus per individual. The observed genotype frequencies did not deviate from Hardy-Weinberg expectations. The low level of enzyme gene heterozygosity in *D. abbreviatus* is interesting. As the species is a major pest, one would, on the basis of its large population

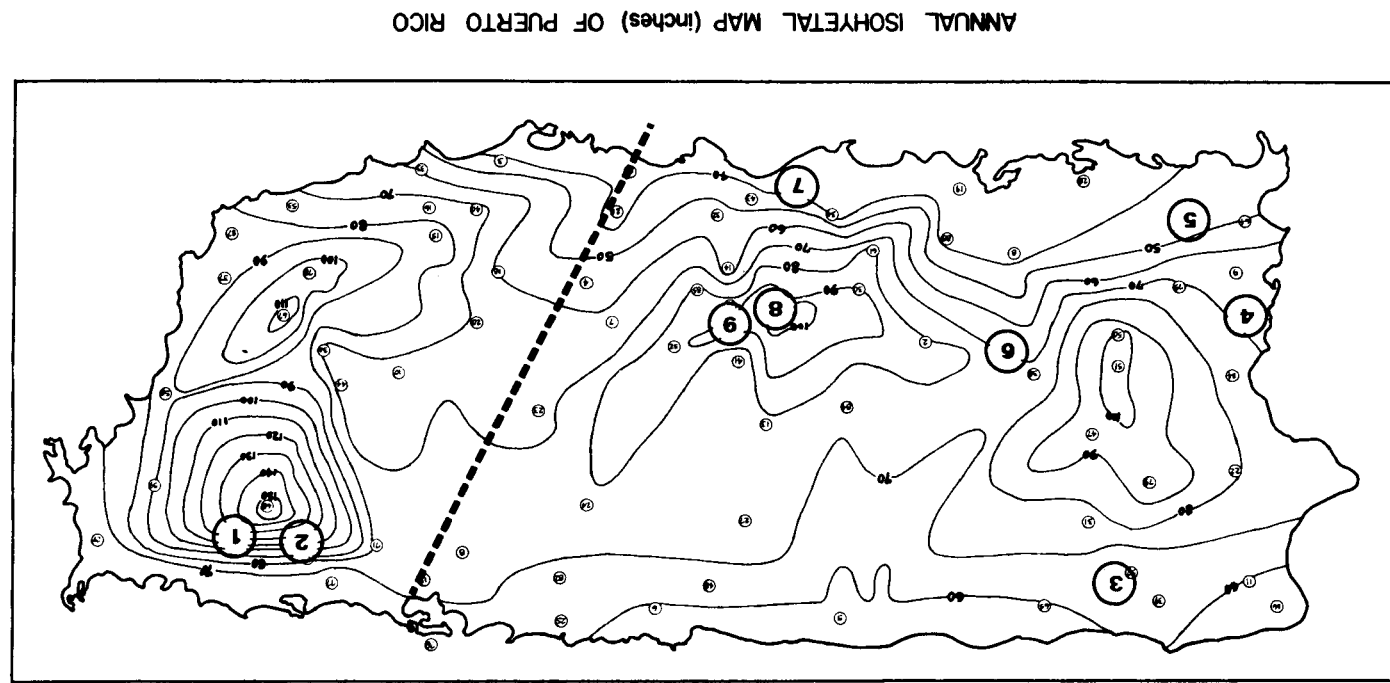


FIG. 1.—Isohyetal map of Puerto Rico, showing annual rainfall in inches. Large encircled numbers give sites of Phyllobini samples studied in this paper, as follows (numbers in parentheses indicate altitude from sea level in meters): — 1. El Yunque, Catalina (210). — 2. El Yunque, Jiménez (90). — 3. Isabela (130). — 4. Cabo Rojo (40). — 5. Lajas (30). — 6. Adjuntas (660). — 7. Fortuna (22). — 8. Toro Negro, Road 143, km 18 to 20 (1150). — 9. Doña Juana (900). Dotted line gives the approximate course of the expressway San Juan to Salinas. — Modified from Ravalo et al. (3), with permission.

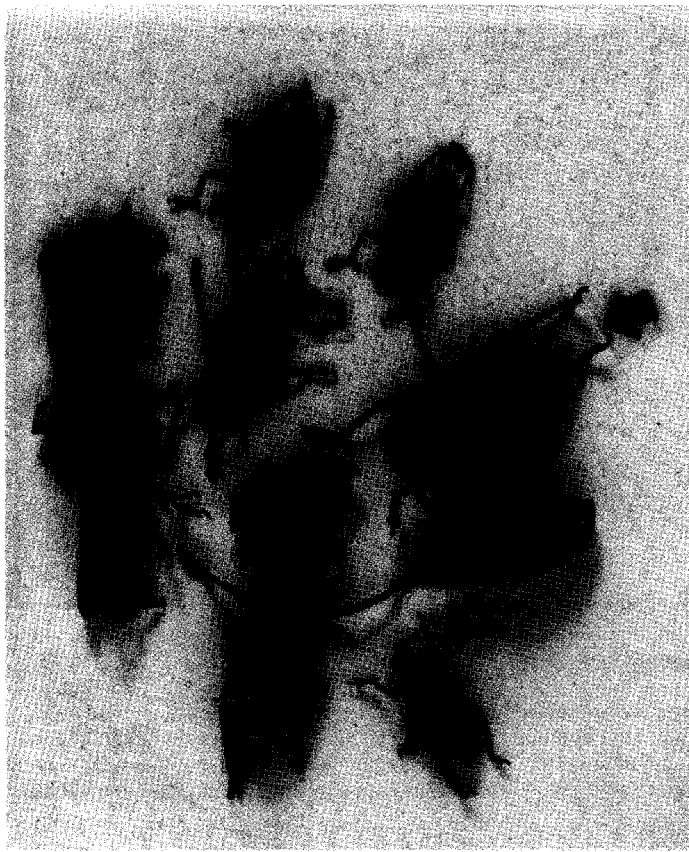


FIG. 2.—*Diaprepes abbreviatus*. Size and color variation in a sample from Adjuntas substation. Note red or yellow side strips in specimens shown laterally, and two full-length vittae in the middle of each elytron in all but the specimen pointed with a hollow arrow. This specimen is an invader from northern lowlands, probably from Rio Piedras, with which a regular transportation is maintained. The filled arrow shows a bicolored (yellow and black) morph similar to the monomorphic, *Erythrina poeppigiana*-associated vaquita of Road 378 (Penuelas). No golden brown specimens were encountered when this sample was taken Oct. 20, 1986. — Magnification 1.3 ×.

sizes, expect much higher heterozygosity values. The relative uniformity might make the species susceptible to control.

In *Compsus maricao*, only two loci, PGI-1 and MDH-2, were polymorphic. The average degree of heterozygosity in the two populations was 0.047 per locus per individual.

To establish differentiation between populations, unbiased genetic distances (2) were calculated between them. Populations of *D. abbreviatus* formed a homogeneous group, with values of D ranging from zero to 0.029. Unexpectedly, the greatest value was found between the two El Yunque populations, so the population on *Sweetenia* (Catalina) differed from all the other populations, which never had pairwise D's higher than 0.003. The color morphs were not found to be associated with anything detectable on the electrophoretic level. As expressed in a

TABLE 1.—Origin, foodplant association, and prevailing color morph of the nine samples studied

Sample	Origin	Foodplant(s)	Color
1. <i>Diaprepes abbreviatus</i>	El Yunque, Catalina Forest Tree Nursery	<i>Sweetenia macrophylla</i> and <i>Persea americana</i>	Grayish, sometimes greenish
2. <i>Diaprepes abbreviatus</i>	El Yunque, Jiménez	<i>Citrus sinensis</i>	Ochre to brown
3. <i>Diaprepes abbreviatus</i>	Isabela	<i>Mangifera indica</i>	Whitish, sometimes greenish ¹
4. <i>Diaprepes abbreviatus</i>	Cabo Rojo	<i>Mangifera indica</i>	Whitish, sometimes greenish ¹
5. <i>Diaprepes abbreviatus</i>	Lajas	<i>Mangifera indica</i>	Whitish, sometimes greenish ¹
6. <i>Diaprepes abbreviatus</i>	Adjuntas	<i>Citrus</i> spp.	White to yellow ^{1,2}
7. <i>Diaprepes abbreviatus</i>	Fortuna	<i>Mangifera indica</i>	Ochre to brown ³
8. <i>Compsus maricao</i>	Toro Negro, Rd. 143, Km 18 to 20	<i>Miconia pycnanura</i>	Green iridescent
9. <i>Compsus maricao</i>	Toro Negro, Doña Juana	<i>Miconia racemosa</i>	Green

¹Yellow or red side stripe common.
²One extra vitta per elytron.
³Pertscutellar spot common.

is not a sufficient barrier to isolate contemporary eastern and western Phyllobiini populations. It might have been so in the Pleistocene, when drying up of northern South America resulted in humid forest isolates involved in speciation (6, 8). The El Yunque/Jiménez population is presumably of coastal origin.

RESUMEN

Polimorfismo génico y de color en dos escarabajos picudos de Puerto Rico

Diaprepes abbreviatus causa daños serios en las plantas cultivadas al este de La Española. La especie muestra una variación notable en las vitas y en el color del fondo de los élitros, extendiéndose del blanco via amarillo hasta ocre y pardo intensos. Es extremadamente polífago y ataca también numerosas plantas silvestres. *Compsus maricao*, endémica para la Cordillera Central de Puerto Rico, no muestra tanta variación de color y es oligófago; como unas pocas plantas silvestres. La variación génica de algunas poblaciones de estas dos especies se estudió mediante la electróforesis de almidón. La extensión de la variación fue limitada; no se detectó correlación alguna con la variabilidad de la coloración en *Diaprepes abbreviatus*. La distancia genética entre las dos especies es grande.

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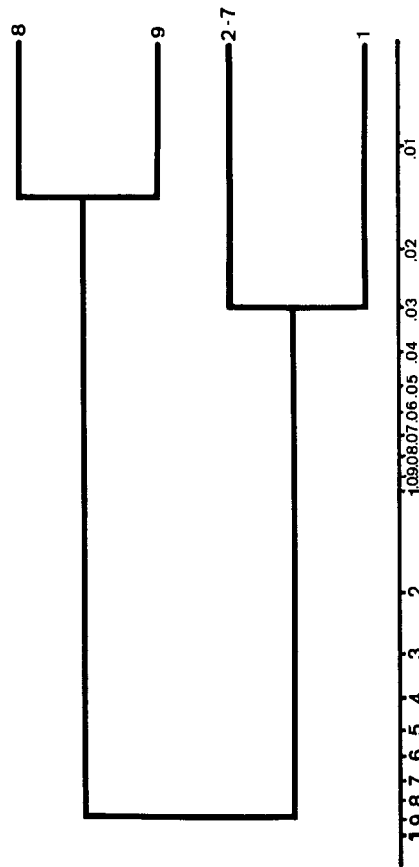


FIG. 3.—Dendrogram of the phylogenetic relationships among Puerto Rican populations of *Diaprepes abbreviatus* (populations 1 through 7; see fig. 1), and *Compsus maricao* (populations 8 and 9), based on a UPGMA cluster analysis. The figures below the graph refer to Nei's genetic distance values (logarithmic scale). Note that the El Yunque/Catalina population differs from the others, which have very short genetic distances, and that the two *C. maricao* populations are relatively far apart.

UPGMA dendrogram (5), the *Diaprepes* populations consisted of two branches, one the El Yunque-Catalina (*Swietenia*) branch, and the other consisting of all the other populations (fig. 3).

Compsus maricao turned out to be a rather distant relative of *D. abbreviatus*. Genetic distance values between the two taxa ranged from 0.9 to 1.01. This range indicates that in many loci different alleles were established as fixed monomorphic ones. The distance between the two *Compsus* populations was 0.014.

The data on *Diaprepes abbreviatus* indicate that most populations of the species show an undifferentiated pattern of allele frequencies, as might be expected of a widespread pest. The color morphs or variants do not show evidence of being more than just that; the genetic basis and eventual adaptive nature of this variation remain unexplained. The differentiation of the El Yunque *Swietenia*-associated population is interesting. It is firmly established in a nursery of the big-leaf mahogany, *Sw. macrophylla*, an introduced forest tree. The host is of little significance, because the same type of vaquita has been seen in the same nursery and in higher elevations of the same mountain infesting avocado and mango. The differentiation might be age-old, paralleling the splitting of *Compsus* into two species, the eastern *luquillo* Wolcott, and the western *maricao* Wolcott. The divisory between them coincides more or less with the modern San Juan to Salinas expressway and a dry zone extending north from the south coast (fig. 1). Thus Carite-Guavate and El Yunque belong together, despite the deep Gurabo valley separating them. The dry zone