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Observations on Host Plant and Biogeographical Differences in Bruchid Beetles in Southern Ecuador[1]

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ABSTRACT

An abrupt change of bruchid taxa, distribution, and host range is evident in central and southwestern Ecuador. There are several hypotheses supported by data. One is expanded host range of the genus *Sennius*, which is very specific to *Cassia* (s.l.) north of Colombia, but feeds in seeds of other genera and subfamilies of Leguminosae in South America. *Stator testudinarius* was found also to feed in *Pithecellobium saman*. *Acanthoscelides isla* has a disjunct distribution due to past geologic changes. It feeds in seeds of *Rhynchosia* spp. only in Panama, Costa Rica, and Ecuador. Endemism in a biogeographically isolated area is exemplified by *Acanthoscelides siemensi* which feeds only in seeds of *Duranta dombeyana* in one locality in Ecuador. Guilds of bruchids are discussed because *Stator testudinarius* and *Pseudopachymerina spinipes* replace other bruchids in the same seed guilds there. Based on our data, we hypothesize that the distribution of bruchids in Ecuador is due to geologic events and present floral composition.

Key words: *biogeography; Bruchidae; competition; disjunct distribution; Ecuador; guild; host plants; seed predation.*

CAMPBELL (1982), GENTRY (1982), and Humphries and Parenti (1986) all have indicated that Ecuador is biogeographically different from Panama and Amazonia in various ways. Results of our studies agree with these authors. We collected bruchid beetles and their hosts in northern South America from 1982 until 1989, during all seasons of the year, for studies of the systematics and bruchid-plant interactions of the genera *Acanthoscelides* (Johnson 1990), *Sennius*, and *Stator* (Johnson *et al.* 1989). Seeds were collected intensively and extensively to find hosts for bruchids. Based on field experience in Mexico and Central America it was apparent that the bruchid fauna in arid areas of central and southwestern Ecuador was very different from Colombia, Venezuela, Central and North America in host relationships and distribution. Our observations on these differences in distribution, host plants, bruchid guilds, and endemism are related below.

METHODS

We spent more than a year on collecting trips to northern South America from 1982 until 1989, collecting bruchid beetles. To associate bruchid beetles and their hosts for studies of bruchid systematics, bruchid-plant interactions, *etc.*, random samples of seeds and the bruchids that feed in them were made in Ecuador during September 1983 and June 1984. From January to March 1989 we collected numerous seeds in the southwestern and southern lowlands of Ecuador and in northern Venezuela. Seeds and pods were collected directly from the plant or from beneath the parent plant and placed in paper bags in the field. Voucher plant specimens were also collected for plant identification. In the laboratory the seeds were stored in jars with ring top lids and Kelthane-impregnated paper towels to prevent depredations by pyemotid mites. The seeds were examined on a regular schedule for the presence of adult bruchids. Adult bruchids that emerged from seeds were then mounted and labeled. Voucher specimens of insects, seeds, and duplicate plant specimens are deposited in the C. D. Johnson collection. Voucher plant specimens are deposited in the Missouri Botanical Garden.

RESULTS AND DISCUSSION

EXPANDED HOST RANGE.—For convenience and the very prevalent use of *Cassia* (Leguminosae: Caesalpinioideae) in the literature, we will use *Cassia* (s.l.) in this paper. In other papers we usually follow the classification of Irwin and Barneby (1982) who consider *Cassia* (s.l.) to consist of the genera *Cassia, Chamaecrista,* and *Senna.*

Sennius is a genus that is very host specific, feeding only in seeds of *Senna* and to a lesser extent *Chamaecrista* (Leguminosae: Caesalpinioideae) from Panama northward (Johnson & Kingsolver 1973,

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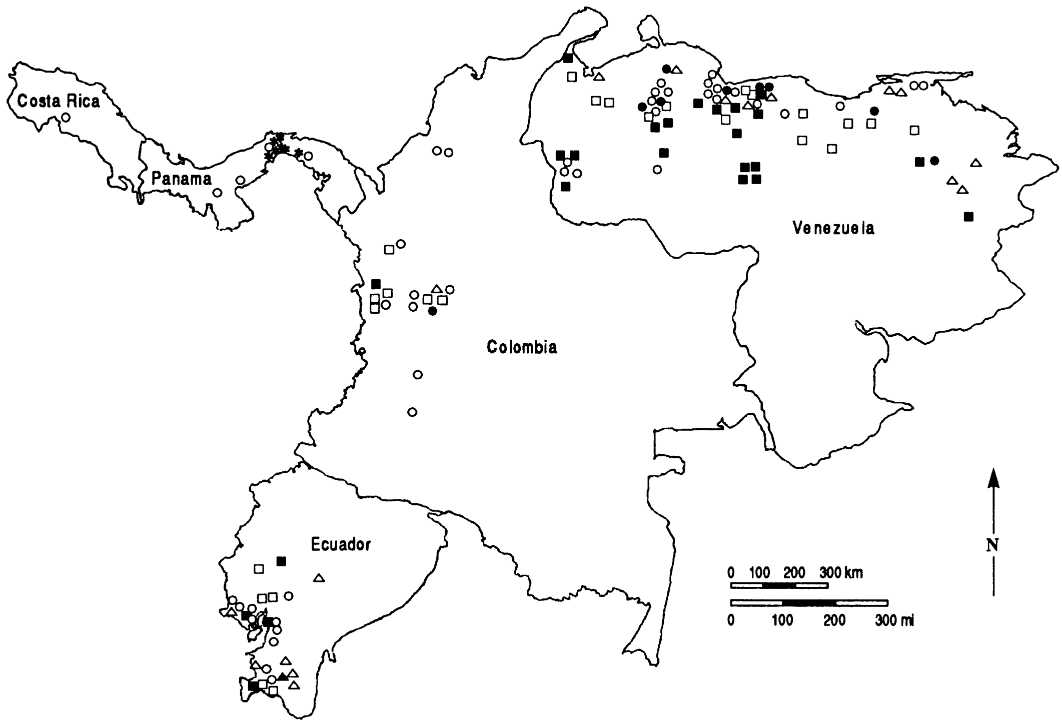

FIGURE 1. Map of collecting sites in Costa Rica, Panama, Colombia, Venezuela, and Ecuador. All collections were made by one or both authors except for those in Costa Rica. This shows the amount of sampling effort in the various countries. See text for bruchids reared from these plants. Symbols: Dark squares = *Pithecellobium saman;* empty squares = *Acacia farnesiana;* empty triangles = *A. macracantha;* solid circles = *A. flexuosa;* solid triangle = *Duranta dombeyana;* open circle = *Rhynchosia minima;* * = *R. calycosa.*

Johnson 1980). In Colombia and Venezuela, however, on several occasions we have collected an unidentified species of *Sennius* that feeds in the seeds of *Indigofera suffruticosa* (Leguminosae: Papilionoideae) (pers. obs.). Another unidentified species of *Sennius* feeds in the seeds of *Desmanthus virgatus* (Leguminosae: Mimosoideae) in Ecuador (pers. comm.). These are the first records of species of *Sennius* feeding in seeds other than *Cassia* (s.l.). This is an example of expanded host range for *Sennius* and is indeed remarkable because species of the genus are now known to feed in seeds of three subfamilies of Leguminosae. *Desmanthus* and *Indigofera* are hosts for other genera of bruchids (Johnson & Kingsolver 1976, Johnson 1990). Thus, our misconception that all species of *Sennius* feed in species of *Cassia* (s.l.) has been revised. The general tendency in Bruchidae is that small genera are usually restricted to one or a few host genera in the same subfamily, while large genera (*e.g., Acanthoscelides, Amblycerus*) have many host genera.

In *Stator* it appears that the host ranges of *Stator vachelliae* and *S. testudinarius,* both of which feed primarily in seeds of acacias, have expanded their host ranges into *Pithecellobium saman.* Apparently their success in these seeds has been limited. Several hundred seeds of *P. saman* were collected on different occasions in Ecuador and especially Venezuela, but the two species of *Stator* were only reared from seeds from one location in each country, southwest of Calabozo, Venezuela, and 43 km west of Guayaquil, Ecuador (Appendix, Fig. 1). Campbell (1982), Gentry (1982), and Humphries and Parenti (1986) all have stated that Ecuador is isolated from Panama and Amazonia in various ways. Thus, the best explanation for new, and in some cases, very different hosts is that during a long period of isolation bruchids have moved into (or evolved into) new hosts.

DISJUNCT DISTRIBUTIONS.—*Acanthoscelides isla* breeds extensively in seeds of *Rhynchosia minima* primarily west of Guayaquil on the Santa Elena Peninsula but also north and south of Guayaquil.

The only other areas where this species is known to occur are in Panama and Costa Rica, where it also breeds in seeds of *Rhynchosia* (Johnson 1983, 1990). Thus the species has a disjunct distribution (Fig. 1). Campbell (1982) discussed evidence that during the Pleistocene there was a dry corridor between Panama and southern Ecuador and Peru. This would have allowed species adapted to savanna and dry forest types to move between these two areas. The disappearance of this corridor apparently has resulted in disjunct populations of *A. isla*.

ENDEMISM.—Campbell (1982) indicates that southern Ecuador is arid and is part of a desert that extends to Chile. Gentry (1982) has phytogeographic evidence that the Andes effectively isolate the Pacific coast of South America from Amazonia. This should result in a high incidence of endemism in this area and apparently does.

Acanthoscelides siemensi Johnson feeds in seeds of *Duranta dombeyana* (Verbenaceae) near Catamayo, Ecuador (Fig. 1) (Johnson & Siemens 1991a). This is remarkable because this is the first substantiated record of a bruchid feeding in the seeds of Verbenaceae, and is probably due, in part, to endemism. Johnson and Siemens interpreted their data that the ancestors of *Acanthoscelides siemensi* probably moved from the Leguminosae and adapted to this host. The bruchids bred freely in the seeds of the host which indicated that there are few protective mechanisms in the seeds or fruits. Because this species is only known from one locality in Ecuador, we believe that the species is endemic.

GUILDS.—Johnson (1981) described three guilds of bruchids, each containing different species. One guild (mature pod guild) oviposits on intact pods on the plant and the larvae enter through the pod valve, feed in seeds, and emerge through the pod valve. A second guild (mature seed guild) enters the pods through exit holes or dehiscent pod valves, also while they are still on the plant. A third guild (scattered seed guild) oviposits only on seeds once they have become exposed on the substrate, usually beneath the parent plant. This is of extreme importance to host plants because some have their seeds attacked in succession by all three guilds. The effects of these insects may be profound on dispersal of seeds and insect-plant coevolution.

From January to March 1989 we collected numerous seeds in the southwestern and southern lowlands of Ecuador and in northern Venezuela in an attempt to associate bruchid beetles and their hosts. The principal discovery relevant here was that *Stator testudinarius,* which had no previously recorded hosts (Johnson *et al.* 1989), was a member of the "scattered seed guild" (Johnson 1981). It has several hosts in different genera (Appendix). The obvious importance of this discovery is that many other species of bruchids are in this guild.

Although seeds of *Pithecellobium saman* exposed on the substrate beneath the tree were collected on numerous occasions in Ecuador and especially Venezuela (Fig. 1), bruchids were only reared from seeds from one location in each country, southwest of Calabozo, Venezuela, and 43 km west of Guayaquil, Ecuador (Fig. 1). *Stator testudinarius* is in guild three. It oviposited on and adults emerged from exposed seeds of *Pithecellobium saman* (#4177), *Acacia farnesiana* (#4156, 4252, 4328) on the ground, and on seeds of *A. macracantha* in horse or burro dung (#4316, 4324) and in cow dung (#4317) under the parent plant (Appendix, Fig. 1). Apparently *S. testudinarius* is the ecological equivalent of *S. vachelliae* as a member of guild three in Ecuador. *Stator vachelliae* is not known to live in Ecuador but feeds in acacias from Mexico to Venezuela and in *P. saman* in Venezuela (Appendix).

Assuming that the original hosts for these guild three bruchids were species of acacia, the habit of feeding on seeds of *P. saman* by *S. testudinarius* and *S. vachelliae* could have evolved by the close proximity of exposed seeds of species of acacia. Expansion of host range then could have occurred by bruchids ovipositing onto susceptible hosts. This has been documented in Venezuela where *S. vachelliae* has expanded its host range and occasionally is able to complete development in seeds of *Parkinsonia aculeata* L. that are intermixed with seeds of *Acacia flexuosa* (Fig. 1), their normal host (Johnson 1988, Johnson & Siemens 1991b). Contrary to the ability of *S. vachelliae* to only occasionally complete its development in seeds of *P. aculeata* (Johnson 1988), it apparently is able to feed freely in the seeds of *Pithecellobium saman,* but only in localized areas.

Of the species listed in the Appendix, *Pseudopachymerina spinipes* and *Mimosestes nubigens* are in guild one. *Stator limbatus* is in guild two, although Janzen (1977) and our studies with exposed seeds of *P. saman* indicate that *S. limbatus* may sometimes oviposit on seeds exposed on the ground.

COMPETITION OR DISJUNCT DISTRIBUTIONS?—Despite intensive collecting of seeds of species of acacias in northern South America, *Pseudopachymerina spinipes* has only been reared from seeds in Ecuador, not Colombia or Venezuela. Terán (1962) reported that this species has been found in South America in Argentina, Brazil, Chile, Peru, and Ecuador. It also has been introduced into North Africa, the Middle East, and Europe along with its hosts. It has evolved in and has an extensive distribution in western and southern South America. Because it has mutual hosts (*e.g., Acacia farnesiana,* Fig. 1) with *Mimosestes nubigens,* a very common and widely distributed species in North and Central America, we believe that there is probable competition between species in guild one that occurs in acacias in Ecuador and other localities where these species overlap; or, they may be geographically isolated by natural barriers. Isolation hardly seems likely, however, because of the widespread distribution and adaptability of both bruchids. Our data from collections indicate that the natural distributions of the two species terminate in northern South America.

Geologic changes and present floral composition probably account for profound differences in the bruchid fauna of central and southwestern Ecuador. Our data indicate that there is a great difference in host range, distribution, endemism, and species in bruchid feeding guilds. We suggest, based on the patterns described above, that continued research on bruchids and their hosts in South America will help to explain biogeographic patterns in the New World. Studies under way using cladistics indicate that there is an abrupt change in the bruchid fauna in central and southwestern Ecuador. Continued studies, especially on host relationships will help to resolve problems of present plant and animal distributions.

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Appendix *Some new host records of some Bruchidae from Ecuador and Venezuela.*

1. Hosts of *Stator testudinarius* (Erichson):

Acacia farnesiana (Linnaeus) Willdenow: Ecuador. 29 km S Babahoyo, 12-I-89 (CDJ#4156-89). El Oro: 9 km NW Arenillas, 19-I-89 (CDJ#4252-89).

Pithecellobioum saman (Jacquin) Bentham: Ecuador. Guayas: 43 km W Guayaquil, 14-I-89 (CDJ#4177-89).

Acacia cf. macracantha (Humb. & Bonpl.) Willdenow: Ecuador. *ca* 4400', 15 km S Catamayo, 24-I-89 (CDJ#4316-89 & 4317-89). *ca* 6300', 16 km W Catamayo, 24-I-89 (CDJ#4324-89). 5900', 84 km SW Cumbe, 25-I-89 (CDJ#4328-89).

2. Hosts of *Pseudopachymerina spinipes* (Erichson):

Acacia farnesiana: Ecuador. El Oro: 9 km NW Arenillas, 19-I-89 (CDJ#4252-89).

Acacia sp.: Ecuador. Guayas: Salinas, 16-I-89 (CDJ#4205-89).

Acacia cf. macracantha: Ecuador. *ca* 4400', 15 km S Catamayo (CDJ#4315-89). 5900', 84 km SW Cumbe, 25-I-89 (CDJ#4329-89).

3. Hosts of *Mimosestes nubigens* (Motschulsky):

Acacia farnesiana: Ecuador. 29 km S Babahoyo, 12-I-89 (CDJ#4156-89).

4. Hosts of *Stator limbatus* (Horn):

Pithecellobium saman: Ecuador. Guayas: 43 km W Guayaquil, 14-I-89 (CDJ#4177-89). Venezuela. Guarico: 24 km SW Calabozo, 4-III-89 (CDJ#4603-89); 14 km SW Calabozo, 4-III-89 (CDJ#4607-89); 9 km SW Calabozo, 4-III-89 (CDJ#4609-89).

5. Hosts of *Stator vachelliae* Bottimer:

Pithecellobium saman: Venezuela. Guarico: 24 km SW Calabozo, 4-III-89 (CDJ#4603-89); 14 km SW Calabozo, 4-III-89 (CDJ#4607-89); 9 km SW Calabozo, 4-III-89 (CDJ#4609-89).