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THE BRUCHIDAE (COLEOPTERA) ASSOCIATED TO SEEDS OF *DESMODIUM* (LEGUMINOSAE: PAPILIONOIDEAE)

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Abstract: A study was conducted to determine the bruchid (Coleoptera: Bruchidae) species that feed on *Desmodium* Desv. (Leguminosae: Papilionoideae) seeds worldwide. Dichotomous keys to determine the genera and species of bruchids from the New and Old World were prepared. Seeds infested by insects in *Desmodium* plants from 23 herbaria were reviewed in Mexico and Belize, the seeds were removed and the reference samples were determined. There were seven bruchid genera associated with *Desmodium* seeds: *Acanthoscelides* (14 species), *Amblycerus* (1), *Bruchidius* (8), *Bruchus* (1), *Callosobruchus* (1), *Conicobruchus* (1), and *Meibomeus* (12); a total of 38 species were identified. In total 47 species of *Desmodium* were susceptible (17.09%) to be attacked by bruchids. *Desmodium tortuosum* (10 species) and *Desmodium caum* (9) were the two most vulnerable species to be attacked; while *Acanthoscelides biustulus* (14) and *A. desmoditus* (17) were the two most prominent polyphagous species feeding on *Desmodium*.
Key words: Coleoptera, Bruchidae, taxonomy, dichotomous keys, host plant, Leguminosae.

Los brúquidos (Coleoptera: Bruchidae) asociados a las semillas de *Desmodium* (Leguminosae: Papilionoideae)
Resumen: Se realizó la presente investigación con el propósito de determinar las especies de brúquidos (Coleoptera: Bruchidae) que se alimentan de semillas de plantas del género *Desmodium* Desv. (Leguminosae: Papilionoideae) en el mundo. Se prepararon claves dicotómicas para determinar géneros y especies de brúquidos del Nuevo y Viejo Mundo. Se revisaron semillas de *Desmodium* infestadas por insectos en 23 herbarios de México y Belice, se extrajeron las semillas y se determinaron los ejemplares de referencia. Se encontraron siete géneros de brúquidos relacionados con semillas de *Desmodium*: *Acanthoscelides* (14 especies), *Amblycerus* (1), *Bruchidius* (8), *Bruchus* (1), *Callosobruchus* (1), *Conicobruchus* (1) y *Meibomeus* (12); en total se identificaron 38 especies. Un total de 47 especies de *Desmodium* fueron suceptibles (17.09%) al ataque por brúquidos. *Desmodium tortuosum* (10 especies) y *Desmodium caum* (9) fueron las más vulnerables al ataque por brúquidos; mientras tanto, *Acanthoscelides biustulus* (14) y *A. desmoditus* (17) fueron las especies polífagas prominentes de *Desmodium*.
Palabras clave: Coleoptera, Bruchidae, taxonomía, claves dicotómicas, planta hospedera, Leguminosae.

Introduction

The Bruchidae family commonly known as bruchids, or seed-eating beetles are widely spread intemperate and warm regions of the world. A high number of species are found in tropical and subtropical regions (Romero, 2002). Most of the bruchids are specialists feeding on a given number of host plants that belong to the same genus or tribe; host selection is successfully accomplished by females ovipositing on pods or fruits that are only available during a short period of the year (Huignard *et al*., 1990). The larval stage of these insects feed on seeds of approximately 34 families of plants, mainly in Leguminosae; however, the adults may feed on pollen, which is important for mating and oviposition, and are often found feeding on flowers of different plants, distinct from their immature forms (Johnson, 1977; Romero, 2002).

Bruchids frequently lay eggs attached to pods or seeds of a suitable larval food plant; and seldom deposit them into pods after the female cuts a hole in the pod wall or insert them into crevices or old emergence cavities (Kingsolver, 2004; Johnson & Romero, 2004).

During the first instar bruchids possess a thoracic toothed plate, which disappear during the first molt (Pfaffenberger & Johnson, 1976). The neonate larva uses this special adaptation to penetrate the pods or the seed testa, and eventually the cotyledons. All larval instars develop in the excavated cavity, due to the nature of its feeding habit. Subsequently, in the majority of cases, the cavity made by the fourth larval instar serves as a pupation chamber.

The adult bore an exit tunnel through the integument of the seed or in case of indehiscent legumes the pod is bored, in other cases the adult emerge through a gap created by the same larva. The operculum from where the bruchids emerge is typically circular, with a smooth cut; unlikely in other insects where the cavity is irregular with rough edges (Kingsolver and Decelle, 1979).

The terms bruchid-host or host plant in the association bruchid-*Desmodium* is referred to seeds of plants, which furnish food for the larvae, during the normal developmental stages from egg to adult (Bottimer, 1961). The main association known between bruchids and plants are with the Leguminosae family. A considerable number of bruchids have specific host plant; nevertheless, the most common relationship is the association of a bruchid with one or more species

of a plant genus. Few bruchids are less discriminative and can be related with different genus of plants or various families (Kingsolver & Decelle, 1979). According to Romero *et al*. (2002) *Amblycerus spondiae* is one of the most polyphagous bruchids; based on records, they feed on species of four different families of plants. Likewise, *Acanthoscelides obtectus*, the Mexican bean seed-eating beetle is another polyphagous species reported on approximately 35 species of Leguminosae (Romero & Johnson, 2004).

The genus *Desmodium* A. N. Desvaux belongs to the tribe Desmodieae (Benth.) Hutch. (Leguminosae: Papilionoideae) extensively distributed in the tropic, subtropic and temperate regions of the world (Africa, Madagascar, Southeastern and Eastern Asia, Australia and the American Continent). Ohashi (2005) calculated more than 275 species of *Desmodium* in the world, distributed in two main geographical centers of diversity: Mexico and Southeastern Asia. In Mexico close to 100 species are registered (31.00%) (Sousa & Delgado, 1998; Torres-Colín, personal communication 2011).

Desmodium spp. possesses an allelopathic weed control mechanism that can effectively eradicate the most destructive weeds. This unique quality discovered in *Desmodium* Desv., is a call for potential exploration in plant breeding programs for creating transgenic plants, for both, subsistence farming systems, and agriculture systems for developed countries (Khan *et al*., 2008). In Africa, when *Desmodium intortum* was intercropped with finger millet, and sorghum, it resulted in a drastic suppression of African witchweed, known as one of the most aggressive parasitic weed, and accounted for a reduction effect on the damage caused by the cereal stem-borer, simultaneously; also increased soil fertility (Khan *et al*., 2006; Midega *et al*., 2010).

Desmodium gangeticum and *Premna tomentosa* contained antioxidants (alkaloids, flavonoids, steroids, tannins and phenols), identified as common phytochemical constituents, providing some biochemical basis for ethanopharmacological treatment and for the prevention of various diseases and disorders (Suriyavathana *et al*., 2010). *Desmodium intortum* is also used as fodder for livestock production in Africa (Midega *et al*., 2010). In addition, to its numerous benefits, in central-western part of Brazil *D. tortuosum* is reported as a common weed (Bianco *et al*., 2004).

Presently, there is no integral work of this genus; nonetheless, Ohashi (1973) delimitates near 60 Asiatic *Desmodium* species and grouped them in seven subgenus and 15 sections; this author also discusses their phylogenetic relationships within them and allied genus. In the New World Vanni (2001) did a revision for the genus in Argentina, the author report 21 species for the later country. In Mexico, only few revisions have been carried out on regional flora, like for instance, Flora de Yucatán (Standley, 1930), Flora de Baja California (Wiggins, 1980), Flora Fanerogámica del Valle de México (Rzedowski *et al*., 2005), Flora Novo-Galiciana (McVaugh, 1987), Biodiversidad de Oaxaca (Torres-Colín, 2004), Biodiversidad del Estado de Tabasco (Torres-Colín, 2005), Tribu Desmodieae, *Desmodium*: Flora del Valle de Tehuacán-Cuicatlán (Torres-Colín & Delgado, 2008), Diversidad Biológica de Sonora (Van Devender *et al*., 2010), Los Géneros *Alysicarpus* y *Desmodium* (Fabaceae) en la península de Yucatán (México) (Torres-Colín *et al*., in press), as well as the inclusion of species in different floristic checklists.

Actually there are not a complete work about the association between bruchids and its host plants, the information is spread in different papers, and there is a lot of information unpublished. The objectives of this research is to determine the bruchid species that feed on *Desmodium* Desv. seeds worldwide, and to develop dichotomous keys for their prompt taxonomic identification.

Materials and Methods

There were checked the following 23 herbariums in search of *Desmodium* species with damaged seeds by bruchids:

ANSM Departamento de Botánica, Universidad Autónoma Agraria Antonio Narro, Saltillo, México.
BRH The Forest Department Herbarium, Belize.
CFNL Facultad de Ciencias Forestales, Universidad Autónoma de Nuevo León, México.
CHAP División de Ciencias Forestales, Universidad Autónoma Chapingo, Chapingo, Edo. de México, México.
CHAPA Herbario-Hortorio, Centro de Botánica, Colegio de Postgraduados, Montecillo, Edo. de México, México.
CICY Departamento de Recursos Naturales, Centro de Investigación Científica de Yucatán, A. C., Mérida, Yucatán, México.
CIIDIR Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Instituto Politécnico Nacional, Durango, México.
EBUM Escuela de Biología, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, México.
ECO-SC-H Colegio de la Frontera Sur, San Cristóbal de Las Casas, Chiapas, México.
ECO-CH-H Colegio de la Frontera Sur, Chetumal, Quintana Roo, México.
ENCB Departamento de Botánica, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, México D. F., México.
HGOM Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, México.
HUMO Facultad de Ciencias Biológicas, Universidad Autónoma del Estado de Morelos, Cuernavaca, Morelos, México.
IBUG Instituto de Botánica, Universidad de Guadalajara, México.
IEB Centro Regional del Bajío, Instituto de Ecología, A. C., Pátzcuaro, Michoacán, México.
MEXU Herbario Nacional, Departamento de Botánica, Instituto de Biología, U.N.A.M., México.
QMEX Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro, Juriquilla, Querétaro, México.
SLPM Instituto de Investigación de Zonas Desérticas, Universidad Autónoma de San Luis Potosí, México.
UAT Instituto de Ecología y Alimentos, Universidad Autónoma de Tamaulipas, México.
UNL Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León, México.
UAMIZ Departamento de Biología, División de Ciencias Biológicas y de la Salud, Universidad Autónoma Metropolitana- Iztapalapa, México D. F., México.
XAL Instituto de Ecología A. C., Xalapa, México.
XALU Facultad de Ciencias Biológicas, Universidad Veracruzana, Xalapa, Veracruz, México.

The infested seeds were collected utilizing an entomological tweezers; individual samples were placed inside an envelope and labeled. The collection data of the specimens were recorded in a research logbook. The botanical material was transferred and processed in the Laboratory of Insect Taxonomy, Colegio de Postgraduados, México.

The insect extraction method entailed the introduction of damaged seeds into a 15 ml beaker containing 10 ml 70% alcohol, subsequently, set on hot plate and heated to 75 °C, during an average time of 30 minutes, to facilitate softening and removal the male genitalia from bruchids. Once the separation was achieved, the bruchids were preserved in 2 ml eppendorf filled with 1.5 ml 70% alcohol, and further stored, until ready for their taxonomic identification.

The species were determined using the technique of the male genitalia described by Kingslover (1970) and Romero & Johnson (1999). All bruchid identified specimens were deposited in the Colección Entomológica del Instituto de Fitosanidad (CEAM), Colegio de Postgraduados, México. Finally, the taxonomic data were entered in the BRUCOL database.

The information obtained from the inspection of herbarium plants was complemented with information from the BRUCOL database of Romero and Johnson (2004).

Results

According with the information got directly to the *Desmodium* seeds and from the records previously recorded from literature and unpublished data of the database, there were seven registered bruchid genera associated with *Desmodium* seeds as follows: *Acanthoscelides* (14 species), *Amblycerus* (1), *Bruchidius* (8), *Bruchus* (1), *Callosobruchus* (1), *Conicobruchus* (1), and *Meibomeu*s (12); a total number of 38 species. A high amount of bruchids were found associated to genera from the New World (*Acanthoscelides, Amblycerus*, and *Meibomeu*s) with 27 species, while the genera from the Old World were represented by *Bruchidius*, *Bruchus*, *Callosobruchus*, and *Conicobruchus*, with 11 plant species (Table I). Apparently, the best adapted bruchid species to feed on *Desmodium* seeds were in the genera *Acanthoscelides* and *Meibomeu*s. In the original record of host plant (*Desmodium cinereum* # 770-79) collected by C.D. Johnson, three species of bruchids emerged: *Acanthoscelides desmoditus* (n= 432 specimens), *A. mazatlan* (n= 6) and *Amblycerus perfectus* (n= 1); however, the captured specie of *A. perfectus* is ambiguous, due to the small seed size as compared to the larger body size of the insect; therefore, the information on host plant needs to be verified, with more collections, to prove host plant-insect relationship.

De Luca (1961) recorded *Paleoacanthoscelides gilvus* from Algeria, associating it to *Hedysarum capitatum*, a species considered synonymous then of *Desmodium styracifolium*. However, as we proved (Yus Ramos, 2009), that species of seed beetle is associated with the tribe Hedysereae, not Desmodieae, the subject of this analysis, so we excluded this record because probably is a misidentification.

At the present time, the following bruchid specimens: *Acanthoscelides cuernavaca*, *A. desmodicola*, *A. howdenorum*, *Meibomeus rodneyi* and *M. serraticulus* appeared to be endemic to Mexico; *Acanthoscelides mazatlan* to Mexico and Nicaragua; *A. desmodicola* to Mexico and the United States of America (U.S.A.); *Acanthoscelides longistilus* to U.S.A. and *Meibomeus musculus* to U.S.A. and Canada, respectively; *Meibomeus dirli* to Panama in the New World (Table II). Species endemism is also detected in the Old World (Asia), specifically in Sri Lanka and Vietnam: *Bruchidius anderssoni* and *B. brincki*; in Vietnam: *Bruchidius mendosus*, *B. nebulatus*, *B. vinhanensis* and *B. alacer*; *Callosobruchus anjaliae* and *Conicobruchus caeruleus* in India (Table II).

The most cosmopolitan species of the New World were: *Acanthoscelides megacornis*, *A. desmoditus*, *A. modestus*, *A. pertinax*, *Meibomeus apicicornis*, *M. panamensis*, and *M. surrubresus*; in the Old World, *Bruchidius diversimembris*, *B. ivorensis*, and *Bruchus multivariegatus* (Table II).

A total of 47 species of the genus *Desmodium* that were recorded resulted susceptible to attack by bruchids. Actually, this plant genus summed up to approximately 275 species in the world (Ohashi 2005) and from that amount, 47 species are related to bruchids; it is calculated that 17.09% are host plants of this spermophagous group of insects. In Mexico from the 100 species of *Desmodium* officially recorded (Sousa & Delgado, 1998; Torres-Colín, personal communication 2011), only 31 resulted susceptible to bruchids, accounting for 31.00%. In the New World, *Meibomeus musculus* feeds on five additional *Desmodium* species (Table I).

Desmodium tortuosum resulted, the most vulnerable specie to be attacked by bruchids, seven species of *Acanthoscelides* and three of genus *Meibomeus*, followed by *Desmodium caum* with four species of *Acanthoscelides* and five of *Meibomeus*, respectively. The two most prominent polyphagous species of bruchids, in this plant genus were *Acanthoscelides biustulus* and *A. desmoditus*, which were documented feeding on 14 and 17 species, respectively in the New World (Table I). In general, the majority of the bruchid species feeding on *Desmodium* demonstrated to be specialists or monophagy feeding behavior and a minority ranged from stenophagy or oligophagy to polyphagy from both, the New and Old World (Table I).

The species of *Acanthoscelides* found in *Desmodium arizonicum* needs to be cross checked with new collections of specimens on the same host plant; as well as the *Desmodium* species from where *Callosobruchus anjaliae* was recovered in the Old World (Table I), this is because females have been collected and males are required to identify the species.

In 2004, Romero collected *Meibomeus hidalgoi* in the State of Morelos infesting *Desmodium* sp.; however, the species of host plants need to be collected and be further verified by the specialist in this genus. Likewise, the host plant *Desmodium* sp. from where Johnson collected *M. mitchelli* in the State of Oaxaca in 1979 (Table I).

Key to bruchid genera associated with *Desmodium* in the World

1. Hind tibia with two long, sharp apical calcaria; with metepisternal sulcus; eyes emarginate at most to 1/3 length ..... *Ambycerus perfectus* (Sharp)
1'. Hind tibia without two long, sharp apical calcaria; without metepisternal sulcus; eyes emarginate at least to 1/2 length 2
2. Pronotum square or trapezial, usually with lateral denticle; hind femur with blunt or sharp spine on external ventral margin; mid tibia in male with apical spines or plates .... *Bruchus multivariegatus* Pic
2'. Pronotum usually campaniform or conical with distinctly concave sides, usually without lateral denticle; hind femur without, with one or more spines on internal ventral margin; mid tibia usually not sexually dimorphic 3
3. Old World genus 4
3'. New World genus 5

4. Hind femur without spines or with one very small subapical spine 6
4'. Hind femur bicarinate ventrally, both external and internal carina with subapical spine or only with ventral internal carina with one large and two minute subapical spines .. .. *Callosobruchus anjaliae* Singal & Pajni
5. Hind femur incrassate, with pecten having 4-8 large spines, one to three small teeth before pecten; hind tibia arcuate.....*Meibomeus* Bridwell
5'. Hind femur not so incrassate, without pecten, but with one large spines followed by one to three small spines; hind tibia usually straight ..... *Acanthoscelides* Schilsky
6. Pronotum conical with distinctly concave sides, hind tibia straight and slender, with carinae obsolete..... ..... *Conicobruchus caeruleus* Champion
6'. Pronotum capaniform, conical or transverse, without concave sides, hind tibia straight, with 2-4 carinae..... .....*Bruchidius* Schilsky

Key to *Acanthoscelides* species of the New World

1. Mucro at apex of hind tibia 0.16 or less as long as first tarsomere; without sinus at base of mucro 2
1'. Mucro at apex of hind tibia more than 0.16 as long as first tarsomere; with sinus at base of mucro 3
2. Width of eye 2 to 4 times width of frons, hind femur armed with subapical acuminate spine about 1.5 times as long as width of tibial base and 2 smaller spines ....*A. modestus* (Sharp)
2'. Width of eye up to 1.5 times width of frons, hind femur armed with subapical acuminate spine about 2 times as long as width of tibial base and 2 smaller spines ....*A. megacornis* Kingsolver
3. Mucro at apex of hind tibia up to 0.2 as long as first tarsomere ..... *A. bisignatus* (Horn)
3'. Mucro at apex of hind tibia 0.4 or more as long as first tarsomere..... 4
4. Deep sinus at base of mucro of hind tibia 5
4'. Sinus at base of mucro slight or lacking 7
5. First abdominal sternum of males with round patch of dense white short setae medially .... *A. longistilus* (Horn)
5'. First abdominal sternum of males without round patch of dense white short setae medially 6
6. Antennae extending to 0.5 length of elytra .... *A. desmodicola* Johnson
6. Antennae extending to base of elytra ....*A. biustulus* (Fall)
7. Antennae extending to 0.25 to 0.3 length of elytra 8
7'. Antennae extending to base of elytra or slightly beyond 12
8. First abdominal sternum of males with round patch of dense white setae medially or slightly concave medially with long setae at apex 9
8'. First abdominal sternum of males not as above, with uniform pubescence 11
9. First abdominal sternum of males with slightly concave medially, pubescence on cavity, with long setae at apex .....*A. schubertae* Johnson
9'. First abdominal sternum of males with round patch of dense white pubescence medially 10
10. Body usually black, sometimes varying to brown; elytron with dense white pubescence interrupted by patches of brown pubescence as follows: a small patch between striae 1-4 near base, a large lateral patch about 0.5 from base between striae 4-10, a small patch between striae 2-3 about 0.6 from base and all apex ....*A. cuernavaca* Johnson
10'. Body usually red orange, sometimes varying to black; elytron with sparse golden pubescence except for patches of dense white pubescence near base between striae 2-5 and a large crescent-shaped patch of dense white pubescence extending from striae 2-9..... .....*A. mazatlan* Johnson
11. Large subapical spine of hind femur about 1.2 times as long as width of tibial base ..... *A. pertinax* (Sharp)
11'.Large subapical spine of hind femur about 2 times as long as width of tibial base ..... *A. puelliopsis* Johnson
12. First abdominal sternum of males with large median patch of pubescence or an elongate sulcus..... 13
12'. First abdominal sternum of males without patch of pubescence or sulcus .....*A. stylifer* (Sharp)
13. Large subapical spine of hind femur about as long as width of tibia base; first abdominal sternum of males with elongate medial sulcus ..... *A. desmoditus* Johnson
13'. Large subapical spine of hind femur about 1.5 times as long as width of tibia base; first abdominal sternum of males with large medial patch of pubescence .... *A. howdenorum* Johnson

Key to *Meibomeus* species of the New World

1. Hind femur with several basal minute spines; pecten without wide gap, a large tooth and with three to four subapical acuminate spines; apical meta-sternal spines..... 2
1'. Hind femur with basal minute spines; pecten with-out gap, a large tooth and with three to five much smaller spines 3
2. Tibial mucro inconspicuous or small, sharp $\pm$ 0.1 mm length of first tarsomere 4
2'. Tibial mucro small approximately 0.1 mm as long as first tarsomere 5
3. Length (pronotum-elytra) $\leq$ 2.08 mm 6
3'. Length (pronotum-elytra) more than 2.80 mm 7
4. First abdominal sternum without polished lateral apical band; stria four expressed far before base and ended by strong tooth .....*M. musculus* (Say)
4'. First abdominal sternum with polished lateral apical band; stria four expressed slightly before base but not ended by tooth ..... *M. campbelli* Kingsolver & Whitehead
5. Eyes shiny black; antennae extending less or up to 0.33 mm the length of elytron; hind femur without basal minute spines; pecten with a wide gap, a large tooth and with three sub-apical acuminate spines; apical meta-sternal spines .....*M. dirli* Romero & Johnson
5'. Eyes dark red to shiny black; antennae extending to close to 1.00 mm the length of elytron; hind femur with several basal minute spines; pecten with a wide gap, a large tooth and with four sub-apical acuminate spines; apical meta-sternal spines ....*M. rodneyi* Romero & Johnson
6. Internal lateral margin often with two or three anterior spines on pectin, without gap, and a large tooth followed by four to five spines 8
6'. Internal lateral margin often with two anterior spines on pecten without gap, a large tooth followed by four to eight spines..... 9

7. Femur with basal minute spines; pecten with moderately or large tooth, without gap and followed by three to four smaller spines 10
7'. Femur with basal minute spines; pecten with large tooth, without gap and followed by three to five smaller spines 11
8. Elytral stria four basally starting at the same height of striae three and five; originating from an inconspicuous tooth .....*M. surrubresus* (Pic)
8'. Elytral stria four basally shorter than three and five striae; originating from a conspicuous tooth ....*M. funebris* (Boheman)
9. Pygidium with basal band of dense, pale vestiture ....*M. serraticulus* (Sharp)
9'. Pygidium with basal band of moderately dense, pale .... *M. panamensis* Kingsolver & Whitehead
10. Elytra striae three and five less pronounced extended basally to approximately 0.5 mm of base, beyond base of stria four; pygidium vestiture with pale dense basal band ..... *M. mitchelli* Kingsolver & Whitehead
10'.Elytral striae three and five extended to close base; pygidium vestiture evenly distributed ....*M. hidalgoi* Kingsolver & Whitehead
11. Elytral interval three with small intense white spot; median lobe of male genitalia fractured, ventral valve semicircular, truncate and lateral lobe superficially divided . .....*M. apicicornis* (Pic)
11'.Elytral interval three without small intense white spot; median lobe of male genitalia not fractured, ventral valve bluntly circular, not truncated and lateral lobe deeply divided.....*M. desmoportheus* Kingsolver & Whitehead

Key to *Bruchidius* species of the Old World

1. Posterior legs entirely black (sometimes a red tinge on mesal side and/or tarsomeres 3-4 more or less reddish).. 2
1'. Posterior legs partly reddish or brown..... 3
2. Pronotum slightly campaniform; with tubercule at base of striae 3 and 4, with minute tooth visible at base of stria 4; antenna more or less darkened centrally, last segment lighter than previous ones; vestiture black and white or with dark brown setae ..... *B. nebulatus* Delobel
2'. Pronotum wide campaniform; two teeth at base of interstriae 3 and 5; antennal segments 5-8 subrectangular; small species (1.2-1.4 mm), with grey and black vestiture ..... *B. vinhanensis* Delobel
3. Vestiture with black, white or pale hairs 4
3'. Vestiture with uniform pale colors 5
4. Antennae almost reaching body length (excluding head); without a large black area surpassing middle of elytron. 6
4'. Antennae short ranging between 0.50-0.75 mm body length; with or without a large black area surpassing middle of elytron..... 7
5. Antennal segments 5-10 longer than wide; elytral base without tooth..... *B. mendosus* (Gyll.)
5'. Antennae long and slightly thick; base of antennae black, four anterior legs testaceous, but with the base of the intermediate dark; elytra moderately short, small pygidium ..... *B. diversimembris* (Pic)
6. Smaller species (1.2-1.3 mm); with posterior legs partly red and tarsi black; elytra length 1.2 times longer than wide together; with a small basal tooth or a blunt tubercle; its apical segments black .....*B. anderssoni* Decelle
6'. Larger species (1.4-1.7 mm); mesal side of posterior legs partly brown or yellow; fore and middle legs yellow; base of mid femora yellow; elytra length1.12 times longer than wide together; at base of stria 4 a small indistinct bulge; 3 basal segment of antennae yellow, antennal segment 4 reddish and the remaining of antenna dark brown .... *B. ivorensis* Delobel
7. Elytral vestiture variegated, whitish with dark markings .....*B. brincki* Decelle
7'. Elytral mainly whitish with square like dots on interstriae 3, 5, 7 and 9; in some specimens, striae 1 and 2 are yellowish..... *B. alacer* Delobel

Discussion

The Old World was noted for its high richness in bruchid genera (5) distributed in 12 species, but with a limited geographic distribution, because *Desmodium* species are present only in Africa and Asia. The most abundant genus in species was *Bruchidius* (8). In the New World there were only 3 genera, but it was the more diverse in species (27), which had a wider geographical distribution. The most numerous genera in species were *Acanthoscelides* (14) and *Meibomeus* (12). In general, the feeding behavior of bruchids on *Desmodium* species was mostly specialist rather than generalist. The four generalist species in the world were *Acanthoscelides biustulus*, *A. desmoditus*, *Meibomeus desmoportheus*, and *M. musculus*.

In this research the genus *Acanthoscelides* was the most diverse species in the bruchid-*Desmodium* relationship of the New World (Table I), this result reflects similar findings of a high number of species reported for the Neotropical region (Johnson, 1981; Borowiec, 1987; Kergoat *et al*., 2005b); the same tendency was also found in the genus *Bruchidius* of the Old World (Borowiec ,1987; Kergoat *et al*., 2005b). It is interesting, that *Acanthoscelides biustulus*, *A. desmodicola* and *A. mazatlan* shared a common host plant (*Desmodium tortuosum*) (Table I); therefore, it is believed that they are similar to some degree in their parental lineages (Alvarez *et al*., 2006).

Five bruchid genera (*Acanthoscelides*, *Bruchidius*, *Bruchus*, *Callosobruchus*, and *Meibomeus*) found in this study resulted to be host specific on *Desmodium* species (Table I); our results seem to coincide with the discovery of Kergoat *et al*. (2005b) who reported that the genera *Acanthoscelides* and *Bruchidius* are host specific with strong taxonomic conservatism in host plant use and that during their evolutionary process they have experienced various host shifts, which induced them to believe that both genera have undergone parallel evolution, based on the fact, that they colonized similar host plants in their geographical areas. The diversification time-frame was consistent with the hypothesis of contemporary radiation with respect to the diversification of their legume hosts. However, *Amblycerus perfectus* displayed a marginal feeding habit on *Desmodium* plants (Table I); they showed feeding preferences on members of Myrtaceae (1 sp.); but, these species mostly feeds on family members of Combretaceae (2) (Table III).

Acanthoscelides desmoditus, *A. mazatlan* and *A. musculus* demonstrated to be strong feeders on *Desmodium,* these

findings were consistent with the results obtained by Kergoat *et al*. (2005b); the latter bruchids also had *Desmodium tortuosum* and the genus *Aeschynomene* (*A. americana*) (Tables I and III) as their common host plants. Nevertheless, those three *Acanthoscelides* species were marginal feeders on genera *Aeschynomene* (1sp.), *Ornithopus* (1 sp.) and *Lespedeza* (1 sp.), respectively. On the other hand, *Desmodium* species served as marginal host plants of *Acanthoscelides longistilus* and *A. modestus* (Table I), but separately, each species presented a strong feeding preference towards de genera *Lespedeza* (5 sp.) and on genus *Aeschynomene* (7 sp.), respectively (Table III). Also, *Acanthoscelides pertinax* prefers *Dalea* species rather than *Desmodium* species; *Meibomeus hidalgoi* feeds indiscriminately on *Desmodium* species and on genus *Aeschynomene* (Table III). The species in the genus *Meibomeus* seem to follow the same trend on host plants specificity, as reported in other phylogenetic studies of the genera *Acanthoscelides*, *Bruchidius* and *Bruchus* (Kergoat *et al*., 2004, 2005a, 2005b).

Delobel (2010a) reported 14 *Bruchidius* species reared from pod samples of several Desmodieae collected in the southern part of Vietnam. However, in our study, we found eight species related to the genus *Desmodium* in the Old World. *Bruchidius alacer*, *B. ivorensis* and *B. nebulatus* have other alternative host plants (Table III) (Delobel, 2007, 2010a, 2010b); however, *Bruchidius alacer* has an alternative host plant (*Desmodium triflorum*) (Delobel, 2010b), as well as *B. nebulatus* (*Pycnospora lutescens*), and *Conicobruchus caeruleus* (*Campylotropis stenocarpa*) (Delobel, 2010a).

It is important to comment that, according to Ohashi (2005), the two major centers of diversity of the genus *Desmodium* are Southeastern Asia and Mexico; nonetheless, no bruchids were detected in Southeastern Asia (H. Ohashi, Biological Institute, Tohoku University, Sendai, Japan, personal communication 2010). The bruchids registered for the Old World are reported fundamentally from Africa (Table II); however, recently three new bruchid species (*Bruchidius nebulatus*, *B. vinhanensis*, and *B. alacer*) were reported feeding on new host record *Desmodium* species (*Desmodium heterocarpon*, *D. styracifolium* and *D. triflorum*) in Vietnam (Delobel, 2010a). In Mexico, 31 *Desmodium* species are present, from the 47 totally registered in the world, that are well known food resources for bruchids (Romero & Johnson, 2004), this confirms a strong bruchid-*Desmodium* association, which makes it a very interesting subject for future studies.

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Table I. Species of Bruchidae found feeding on *Desmodium* seeds.

Table I. (cont.)

Bruchidae specie ● Host plants
Acanthoscelides bisignatus (Horn)
● *Desmodium lindheimeri* Vail
Acanthoscelides biustulus (Fall)
● *Desmodium angustifolium* (Kunth) DC.
● *Desmodium batocaulon* A. Gray
● *Desmodium cinerascens* A. Gray
● *Desmodium densiflorum* Hemsl.
● *Desmodium grahamii* A. Gray
● *Desmodium hartwegianum* Hemsl.
● *Desmodium hartwegianum* Hemsl. var. *hartwegianum*
● *Desmodium leptoclados* Hemsl.
● *Desmodium lindheimeri* Vail
● *Desmodium molliculum* (Kunth) DC.
● *Desmodium neomexicanum* A. Gray
● *Desmodium nitidum* M. Martens & Galeotti
● *Desmodium psilophyllum* Schltdl.
● *Desmodium sericophyllum* Schltdl.
● *Desmodium tortuosum* (Sw.) DC.
Acanthoscelides cuernavaca Johnson
● *Desmodium distortum* (Aubl.) J.F. Macbr.
● *Desmodium orbiculare* Schltdl.
● *Desmodium tortuosum* (Sw.) DC.
Acanthoscelides desmodicola Johnson
● *Desmodium tortuosum* (Sw.) DC.
Acanthoscelides desmoditus Johnson
● *Desmodium amplifolium* Hemsl.
● *Desmodium angustifolium* (Kunth) DC.
● *Desmodium cajanifolium* (Kunth) DC.
● *Desmodium cinereum* (Kunth) DC.
● *Desmodium conzattii* Greenm.
● *Desmodium densiflorum* Hemsl.
● *Desmodium distortum* (Aubl.) J.F. Macbr.
● *Desmodium grahamii* A. Gray
● *Desmodium lindheimeri* Vail
● *Desmodium neomexicanum* A. Gray
● *Desmodium nicaraguense* Oerst.
● *Desmodium orbiculare* Schltdl.
● *Desmodium orbiculare* Schltdl. var. *rubricaule* (Rose & Painter) B.G. Schub & McVaugh
● *Desmodium orbiculare* Schltdl. var. *salvinii* (Hemsl.) B.G. Schub. ex Standl. & Steyerm.
● *Desmodium plicatum* Schltdl. & Cham.
● *Desmodium saxatile* (Morton) B.G. Schub. & McVaugh
● *Desmodium skinneri* Benth. ex Hemsl.
● *Desmodium skinneri* Benth. ex Hemsl. var. *flavovirens* B.G. Schub. & McVaugh
● *Desmodium sumichrastii* (Schindl.) Standl.
● *Desmodium tortuosum* (Sw.) DC.
Acanthoscelides howdenorum Johnson
● *Desmodium cinereum* (Kunth) DC.
● *Desmodium conzattii* Greenm.
● *Desmodium densiflorum* Hemsl.
● *Desmodium sericophyllum* Schltdl.
Acanthoscelides longistilus (Horn)
● *Desmodium illinoense* A. Gray
● *Desmodium caum* DC.
Acanthoscelides mazatlan Johnson
● *Desmodium cinereum* (Kunth) DC.
● *Desmodium distortum* (Aubl.) J.F. Macbr.
● *Desmodium glabrum* (Mill.) DC.
● *Desmodium scorpiurus* (Sw.) Desv.
● *Desmodium tortuosum* (Sw.) DC.
Acanthoscelides megacornis Kingsolver
● *Desmodium cinereum* (Kunth) DC.
● *Desmodium tortuosum* (Sw.) DC.
Acanthoscelides modestus (Sharp)
● *Desmodium caum* DC.
Acanthoscelides pertinax (Sharp)
● *Desmodium tortuosum* (Sw.) DC.
Acanthoscelides puelliopsis Johnson
● *Desmodium adscendens* (Sw.) DC.
● *Desmodium barbatum* (L.) Benth.
● *Desmodium caum* DC.
● *Desmodium intortum* (Mill.) Urb. var. *apiculatum* B.G. Schub.
Acanthoscelides schubertae Johnson
● *Desmodium caum* DC.
Acanthoscelides sp.
● *Desmodium arizonicum* S. Watson
Acanthoscelides stylifer (Sharp)
● *Desmodium grahamii* A. Gray
Amblycerus perfectus (Sharp)
● *Desmodium cinereum* (Kunth) DC.
Bruchidius alacer Delobel
● *Desmodium triflorum* (L.) DC.
Bruchidius anderssoni Decelle
● *Desmodium gangeticum* (L.) DC.
Bruchidius brincki Decelle
● *Desmodium heterocarpon* (L.) DC.
Bruchidius diversimembris (Pic)
● *Desmodium ramosissimum* G. Don
Bruchidius ivorensis Delobel
● *Desmodium velutinum* (Willd.) DC.
Bruchidius mendosus (Gyllenhal)
● *Desmodium triflorum* (L.) DC.
Bruchidius nebulatus Delobel
● *Desmodium heterocarpon* (L.) DC.
Bruchidius vinhanensis Delobel
● *Desmodium styracifolium* (Osbeck) Merr.
Bruchus multivariegatus Pic
● *Desmodium salicifolium* (Poir.) DC.
Callosobruchus anjaliae Singal & Pajni
● *Desmodium* sp.
Conicobruchus caeruleus (Champion)
● *Desmodium elegans* DC.
Meibomeus apicicornis (Pic)
● *Desmodium caum* DC.
Meibomeus campbelli Kingsolver & Whitehead
● *Desmodium glabrum* (Mill.) DC.
● *Desmodium tortuosum* (Sw.) DC.
Meibomeus desmoportheus Kingsolver & Whitehead
● *Desmodium campyloclados* Hemsl.
● *Desmodium caripense* (Kunth) G. Don
● *Desmodium grahamii* A. Gray
● *Desmodium mollicullum* (Kunth) DC.
● *Desmodium retinens* Schltdl.
● *Desmodium sumichrastii* (Schindl.) Standl.
Meibomeus dirli Romero & Johnson
● *Desmodium cajanifolium* (Kunth) DC.
Meibomeus funebris (Boheman)
● *Desmodium caum* DC.
Meibomeus hidalgoi Kingsolver & Whitehead
● *Desmodium* sp.
Meibomeus mitchelli Kingsolver & Whitehead
● *Desmodium* sp.
Meibomeus musculus (Say)
● *Desmodium canescens* (L.) DC.
● *Desmodium caum* DC.
● *Desmodium tenuifolium* Torr. & A. Gray
● *Desmodium tortuosum* (Sw.) DC.
● *Desmodium triflorum* (L.) DC.
Meibomeus panamensis Kingsolver & Whitehead
● *Desmodium caum* DC.
Meibomeus rodneyi Romero & Johnson
● *Desmodium glabrum* (Mill.) DC.
Meibomeus serraticulus (Sharp)
● *Desmodium bellum* (S.F. Blake) B.G. Schub.
Meibomeus surrubresus (Pic)
● *Desmodium caum* DC.
● *Desmodium tortuosum* (Sw.) DC.

Table II. Bruchidae species related to *Desmodium* seeds and its distribution.

Bruchidae species Distribution
Acanthoscelides bisignatus (Horn) Mexico, U.S.A.
Acanthoscelides biustulus (Fall) Mexico, U.S.A.
Acanthoscelides cuernavaca Johnson Mexico.
Acanthoscelides desmodicola Johnson Mexico, U.S.A.
Acanthoscelides desmoditus Johnson Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Mexico, Panama, Venezuela.
Acanthoscelides howdenorum Johnson Mexico.
Acanthoscelides longistilus (Horn) U.S.A.
Acanthoscelides mazatlan Johnson Mexico, Nicaragua.
Acanthoscelides megacornis Kingsolver Costa Rica, Dominica, Dominican Republic, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Peru, Saint. Vincent, U.S.A., Venezuela.
Acanthoscelides modestus (Sharp) Argentina, Brazil, Colombia, Guatemala, Honduras, Mexico, Panama, Puerto Rico, U.S.A.
Acanthoscelides pertinax (Sharp) Antilles, Belize, Colombia, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Venezuela.
Acanthoscelides puelliopsis Johnson Belize, Brazil, Colombia, El Salvador, Panama, Venezuela.
Acanthoscelides schubertae Johnson Belize, Guatemala, Honduras, Mexico.
Acanthoscelides stylifer (Sharp) Mexico, Nicaragua, U.S.A.
Amblycerus perfectus (Sharp) Brazil, Costa Rica, Honduras, Mexico, Venezuela.
Bruchidius alacer Delobel Vietnam.
Bruchidius anderssoni Decelle Sri Lanka, Vietnam.
Bruchidius brincki Decelle Sri Lanka, Vietnam.
Bruchidius diversimembris (Pic) Burundi, Ethiopia, Ivory Coast, DR Congo, Rwanda, South Africa, Tanzania.
Bruchidius ivorensis Delobel Guinea, Ivory Coast, Kenya.
Bruchidius mendosus (Gyllenhal) Vietnam.
Bruchidius nebulatus Delobel Vietnam.
Bruchidius vinhanensis Delobel Vietnam.
Bruchus multivariegatus Pic Ivory Coast, DR Congo, Rwanda.
Callosobruchus anjaliae Singal & Pajni India.
Conicobruchus caeruleus (Champion) India.
Meibomeus apicicornis (Pic) Belize, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, U.S.A.
Meibomeus campbelli Kingsolver & Whitehead Costa Rica, El Salvador, Mexico, Nicaragua, Panama.
Meibomeus desmoportheus Kingsolver & Whitehead Costa Rica, Mexico, U.S.A.
Meibomeus dirli Romero & Johnson Panama.
Meibomeus funebris (Boheman) Argentina, Bolivia, Brazil, Paraguay.
Meibomeus hidalgoi Kingsolver & Whitehead Colombia, Honduras, Mexico.
Meibomeus mitchelli Kingsolver & Whitehead Guatemala, Honduras, Mexico.

Table II. (cont.)

Bruchidae species Distribution
Meibomeus musculus (Say) U.S.A., Canada.
Meibomeus panamensis Kingsolver & Whitehead Bolivia, Colombia, Honduras, Mexico, Panama, Trinidad & Tobago, Venezuela.
Meibomeus rodneyi Romero & Johnson Mexico.
Meibomeus serraticulus (Sharp) Mexico.
Meibomeus surrubresus (Pic) Argentina, Belize, Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Paraguay, Trinidad & Tobago, U.S.A., Venezuela.

Table III. Alternative bruchid host plants.

Bruchids ● Host plants (Family)
Acanthoscelides desmoditus
● *Aeschynomene americana* L. (Leguminosae)
Acanthoscelides longistilus
● *Lespedeza capitata* Michx. (Leguminosae)
● *Lespedeza hirta* (L.) Hornem. (Leguminosae)
● *Lespedeza intermedia* (S. Watson ex A. Gray) Britton (Leguminosae)
● *Lespedeza texana* Britton (Leguminosae)
● *Lespedeza virginica* (L.) Britton (Leguminosae)
Acanthoscelides mazatlan
● *Ornithopus* sp. (Leguminosae)
Acanthoscelides megacornis
● *Aeschynomene americana* L. (Leguminosae)
● *Aeschynomene sensitiva* Sw. (Leguminosae)
Acanthoscelides modestus
● *Aeschynomene ciliata* Vogel (Leguminosae)
● *Aeschynomene incana* G. Mey. (Leguminosae)
● *Aeschynomene indica* L. (Leguminosae)
● *Aeschynomene montevidensis* Vogel (Leguminosae)
● *Aeschynomene rudis* Benth. (Leguminosae)
● *Aeschynomene scabra* G. Don (Leguminosae)
● *Aeschynomene sensitiva* Sw. (Leguminosae)
Acanthoscelides pertinax
● *Aeschynomene americana* L. (Leguminosae)
Dalea aff. *submontana* (Rose) Bullock
● *Dalea leporina* (Aiton) Bullock (Leguminosae)
● *Galactia striata* (Jacq.) Urb. (Leguminosae)
● *Marina scopa* Barneby (Leguminosae)
Amblycerus perfectus
● *Callistemon citrinus* (Curtis) Skeels (Myrtaceae)
● *Combretum farinosum* Kunth (Combretaceae)
● *Combretum fruticosum* (Loefl.) Stuntz (Combretaceae)
Bruchidius alacer
● *Alysicarpus vaginalis*(L.) DC. (Leguminosae)
Bruchidius ivorensis
● *Pseudarthria hookeri* Wight & Arn. (Leguminosae)
Bruchidius nebulatus
● *Pycnospora lutescens* (Poir.) Schindl. (Leguminosae)
Conicobruchus caeruleus
● *Campylotropis stenocarpa* (Klotzsch) Schindl. (Leguminosae)
Meibomeus hidalgoi
● *Aeschynomene brasiliana* (Poiret) DC. (Leguminosae)
Meibomeus musculus
● *Lespedeza hirta* (L.) Hornem. (Leguminosae)
Meibomeus surrubresus
● *Aeschynomene americana* L. (Leguminosae)
● *Peltaea* sp. (Malvaceae)
● *Rhynchosia calycosa* Hemsl. (Leguminosae)