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# A revision of the *striatella* species group of the genus *Rhagoletis* (Diptera: Tephritidae)

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# A revision of the *striatella* species group of the genus *Rhagoletis* (Diptera: Tephritidae)

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Abstract: A taxonomic revision of species of the *striatella* group, including descriptions of three new species from Mexico, Nicaragua and Costa Rica is presented. To date we recognize 6 species in this group: *Rhagoletis striatella*, *R. jamaicensis*, *R. macquartii*, *R. triangularis* n. sp., *R. nicaraguensis* n. sp., and *R. solanophaga* n. sp. Information and records about their distribution, known host plants, and morphological relationships among the species are discussed. A key to the species within the group is presented.

Resumen: Se presenta una revisión taxonómica de las especies del grupo striatella, la cual incluye descripciones de tres nuevas especies provenientes de México, Nicaragua y Costa Rica. A la fecha reconocemos 6 especies en este grupo: Rhagoletis striatella, R. jamaicensis, R. macquartii, R. triangularis n. sp., R. nicaraguensis n. sp., and R. solanophaga n. sp.. Se discute información sobre su distribución, plantas hospederas conocidas, y las relaciones morfológicas entre sus especies. Además se presenta una clave para separar todas las especies del grupo.

#### Introduction

In North America the genus *Rhagoletis* is represented by 24 species widely distributed in temperate regions of Canada and the U.S.A. (Bush, 1966; Berlocher & Bush, 1982; Berlocher, 1984; Foote *et al.*, 1993). Twenty-three species have been recorded from Mexico to South America (in Brazil, Argentina, and Chile) (Foote, 1981; Hernández-Ortiz, 1985 and 1993; Frías, 1992). Of these species only six are shared with North America: *R. striatella* Wulp, *R. cingulata* (Loew), *R. pomonella* (Walsh), *R. completa* Cresson, *R. juglandis* Cresson and *R. boycei* Cresson.

Most of the known species with Central and South American distribution belong to the *nova* group (6 species), the *psalida* group (3 species), the *striatella* group (3 species) and the *ferruginea* group (3 species) (*sensu* Foote, 1981). Our knowledge of their host plants shows that most of them are mainly associated with the Solanaceae (Smyth, 1960;

Bush, 1966; D'Araujo e Silva *et al.*, 1968; Munro, 1968; Foote, 1981; Frías *et al.*, 1984 and 1992).

The *striatella* species group as characterized by Bush (1966) included just one species. But in the later revision of the genus *Rhagoletis* south of the United States by Foote (1981), two other species were recognized from Central and South America.

In this study we make a taxonomic revision of the *striatella* species group (*sensu* Foote, 1981), and describe three new species. We add new locality records and biological data of host plants for one of them. Interspecific relationships within the group are discussed, and a key for segregation of all known species is provided.

### Materials and Methods

Specimens examined are from the following regions: states of Chiapas and Veracruz, Mexico; the province of Guanacaste, Costa Rica, and from the Meseta de los Pueblos, Nicaragua.

The general terminology used in the text is based on McAlpine (1981). For specific nomenclature associated with the wing pattern and the terminalia we followed Foote (1981), and Norrbom and Kim (1988). Identification of botanical samples was made by Gonzalo Castillo from the Department of Sistematica Vegetal (IdeE, Xalapa).

Acronyms used in the text correspond to the following institutions: CNIN= National Collections of Insects, Nicaragua; IBUNAM= Instituto de Biología, Universidad Nacional Autónoma de México, México, DF.; IEXA= Instituto de Ecología A.C., Xalapa, Veracruz; INBIO= Instituto Nacional de Biodiversidad, Costa Rica; USNM= United States National Museum, Washington, DC.

### The striatella species group

Currently the striatella group includes three species (sensu Foote, 1981): R. striatella Wulp, R. macquartii (Loew) and R. jamaicensis Foote, but to date these have not been fully characterized, mainly because the males and host plant relationships of the latter two species remain unknown. Foote (1981) hypothesized the relationships among species, mainly based on the following characters: the absence of the accessory costal band of wing pattern; by the uneven darkening of the hind tibiae and by the presence of spherical spermathecae. To this we must include the presence of the three complete transverse bands; the anterior and posterior apical bands well developed; apical extreme of the posterior apical band ending away from apex of vein M; and prensisetae located a short distance from the apex of outer surstyli.

This group has a certain resemblance in the wing pattern with species of the *cingulata* group, which differs in several characters such as spermathecae elongated; prensisetae located at middle of length of outer surstyli; a different shape of apical appendage of distiphallus; and the apical extreme of the posterior apical band touching the apex of vein M.

Meanwhile, the species of Central and South American distribution within the *nova*, *psalida* and *ferruginea* groups differ by the presence of the accessory costal band developed, and the anterior and posterior apical bands, or both usually are incomplete or absent.

# Key to the *Rhagoletis* species of the *striatella* group

- 2(1). Mesonotum black with a whitish pollinosity pattern forming two well-defined, conspicuous broad bands (Fig. 2A); discal band usually very narrow at posterior extreme (in cell CuA<sub>1</sub>); discal and subapical bands separated along vein CuA<sub>1</sub>, but sometimes weakly joined at posterior extreme of both bands ......... R. striatella Wulp
- 3(1'). Mesonotum distintively red-yellowish and with a weak pollinosity pattern of four longitudinal stripes (Fig. 2C); second costal cell hyaline on apical third near pterostigma (only with a small spot at proximal base); sub-basal and discal bands completely separated along entire length; discal and subapical bands broadly joined along most of width of cell CuA, ......
- 4(3'). Pollinosity pattern of mesonotum with all stripes completely separated; sub-basal and discal bands broadly connected along entire length forming a big compact spot; second costal cell mostly blackish; anterior apical band with a slender hyaline fascia along costal margin of cell  $\mathbf{r}_3$  (Fig. 1A) R. macquartii (Loew)
- 4'. Pollinosity pattern of mesonotum with stripes connected anteriorly in pairs but separated in

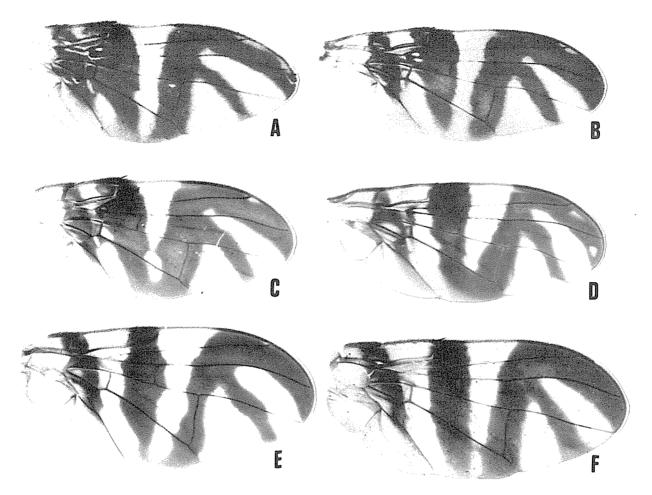


Figure 1. Wing pattern of Rhagoletis species of the striatella group: A) R. macquartii; B) R. jamaicensis; C) R. nicaraguensis n. sp.; D) R. solanophaga n. sp.; E) R. striatella; F) R. triangularis n. sp. (Figures A-B after Foote, 1981).

- 5(4'). Discal and subapical bands broadly connected at posterior margin of wing in most of cell  $\mathrm{CuA}_1$ ; subapical and posterior apical bands broadly connected throughout width of cell  $\mathrm{r}_5$  (Fig. 1C); scutellum mostly whitish with only very narrow black fascia along scuto-scutellar suture (Fig. 2D).....

# Rhagoletis striatella Wulp Fig. 1E, 2A

Rhagoletis striatella Wulp, 1899: 408. Biologia Centrali Americana Zool. Insecta, Diptera Vol 2.

Known distribution. CANADA: Ontario. U.S.A.: Michigan, Wisconsin, Illinois, Iowa, New Mexico and Texas (Bush 1966: 518). MEXICO: Guerrero, Amula (Wulp 1899: 408); México, El Yukón, 8800 ft, 4-VIII-1962 ex. *Physalis* sp.; Agua Bendita, Tenango del Valle; Tlaxcala, Huamantla (Bush 1966: 516,518). Jalisco, Guadalajara, 15 mi NE, 17-IX-1970, G.E., R.M. Bohart; Durango, Navíos, 26 mi E El Salto, 2-VIII-1964, 8000 ft, J. F. McAlpine (Foote (1981: 37).

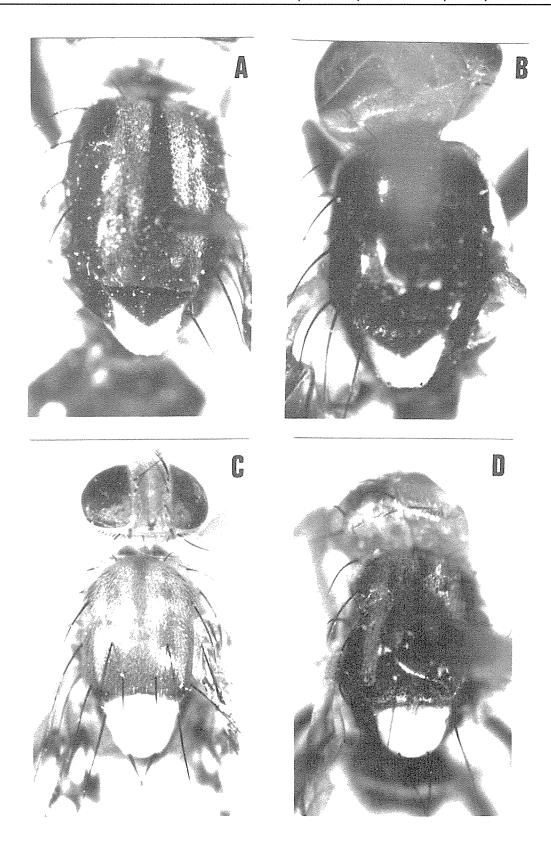


Figure 2. Mesonotum showing general coloration and polinosity pattern: A) R. striatella; B) R. triangularis n. sp.; C) R. solanophaga n. sp.; D) R. nicaraguensis n. sp.

New records. MEXICO. México, Tequesquinahuac, C. Tlaloc 2600 m, 21-VIII-1984, A. Ibarra y J. Butze cols. (1 female IEXA); Morelos, Km 49 Carr. Xochimil-co-Oaxtepec, 6-X-1984, A. Ibarra col. (1 female IEXA); Michoacán, Gabriel Zamora, CESV (1 female IEXA).

Diagnosis. Head yellow with frons reddish; facial carina well developed; third antennal segment dorsoapically pointed; arista covered with short hairs; postocellars yellow or black. Mesonotum black covered by whitish pollinosity forming a pattern of two separated broad longitudinal stripes; scutellum whitish with a triangular black spot on base of disc, and basal sides of same color; all femora mostly black, tibiae yellowish but slightly darkened gradually to hind tibia; all tarsi yellow.

Wing pattern with three transverse, completely separated bands; hyaline fascia between anterior and posterior apical bands reaching vein  $R_{4+5}$ . Abdomen mostly black; tergites 2-4 in males and 2-5 in females with a slender white stripe along posterior margin of each; females with tergite 6 and syntergosternite 7 wholly black; aculeus very long (2.5 - 2.8 mm) and spermathecae spherical. Male with outer surstyli robust and broad from its base and rounded in apex in lateral view; prensisetae very close to apex; distiphallus elongated and broad, with a long, bare apical appendage.

Host plants. Physalis spp. (Bush 1966; Foote 1981).

Remarks. This species has the most northern distribution for the *striatella* group in continental America, mainly associated with temperate regions. *Rhagoletis striatella* has an unusually long aculeus, longer than in any other species, and it can be separated using the key.

# Rhagoletis triangularis Hernández & Frías, new species

Figs. 1F, 2B, 3E-G

Type material. HOLOTYPE male (IEXA). MEXICO: Chiapas, Unión Juárez, 10-III-1985, F. Arias col.

Description. Holotype male: Head yellow; facial carina well developed; inferior half of frons reddish with few short blackish hairs; three pairs of frontal bristles and two pairs of orbitals; third antennal segment dorsoapically pointed; arista yellow with

short hairs along all length; postocellar and genal bristles yellow (Fig. 3G).

Thorax. Mesonotum 2.26 mm long, completely black with scarce polinosity on surface, but without any defined pattern of stripes; scutellum whitish and subquadrate at the apical margin, with a basal triangular shaped spot on disc, and sides of base with black spots including the basal scutellar bristles; subscutellum and mediotergite wholly black. In lateral view pleuron brownish black with a typical whitish stripe just below the notopleuron arising from the postpronotal lobe to base of wing.

All femora mainly black, except for a small apical portion of the fore femur dark yellow; anterior, mid tibiae, and all tarsi yellow, hind tibia blackish

Wing 4.50 mm long; wing pattern with discal and subapical bands very close in cell  $\text{CuA}_1$ , weakly connected at some points; discal band parallel sided from pterostigma to posterior margin of wing; accesory costal band absent; hyaline fascia between anterior and posterior apical bands just reaching the vein  $R_{4+5}$  (Fig. 3F).

**Abdomen.** Mostly black with only fine stripes on posterior margins of tergites 2 and 4.

Male terminalia. Epandrium brownish; in lateral view outer surstyli are strong and wide at base; apical end broad and rounded; in posterior view outer surstyli broad at base and straight; inner surstyli long with prensisetae located very close to apex of outer surstyli; proctiger long but slender at base; distiphallus relatively small provided with an apical slender membranous appendage bare on surface.

Female. Unknown.

Host plants. Unknown.

Etymology. Specific name derived from the Latin *triangulatum* in reference to shape of black spot on basal disc of scutellum.

Remarks. This species is closely related to *R. striatella* Wulp, by the similar morphology of outer surstyli broad at base in both species and the inner surstyli nearly as long as the former; by the presence of a triangular black spot on base of disc of scutellum, and by the distiphallus bare. Differences between the two species are given in the key.

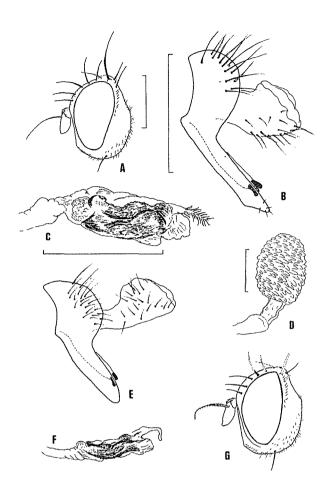


Figure 3. A, G) Head in lateral view (line=1 mm); B, E) Male terminalia showing epandrium, proctiger and surstyli in lateral view (line=0.5 mm); C, F) Distiphallus (line=0.5 mm); D) Spermatheca (line=0.1 mm). Figs. A, B, C, D R. solanophaga n. sp.; Figs. E, F, G R. triangularis n. sp.

# Rhagoletis solanophaga Hernández & Frías, new species

Figs. 1D, 2C, 3A-D

Type material. Holotype male (IEXA): MEXICO, Veracruz, Xalapa, Jardín Botánico 1280 m, 17-X-1990, R. Pérez col. "Ex-larva en frutos de Solanum appendiculatum". Paratypes: Same data as holotype (2 males, 1 female IEXA); Idem, 3-III-1997, V. Hernández col. "Ex: larvas en frutos de Solanum appendiculatum" emerg. 9-IV-1997 (1 male, 3 females IEXA, 1 male, 1 female IBUNAM); Idem, 22-II-1998, V. Hernández col. "Ex: larvas en frutos de Solanum appendiculatum" emerg. 5-III-1998 (2 males, 1 female IEXA); Idem, 31-VIII-1991, L. Delgado y F. Capistrán cols., trampa luz (1 female IEXA). COSTA RICA, Est. Cacao 1000-1400 m SW

side Volcán Cacao, Guan. Pr., Mar. 1988, GNP Blod. Sur. 323300, 375700 (2 males, 4 females INBIO); 2 females USNM, one male and female on same pin).

Description. Head yellow with frons reddish; facial carina developed and broadened from mid part to inferior margin; third antennal segment rounded apically; gena with some dark brownish hairs; genal and postocellar bristles yellow; arista bare, only with few short hairs near base (Fig. 3A).

Thorax. Mesonotum 2.90-3.01 mm long, mainly yellow reddish on surface, with small black spots near the scuto-scutellar suture and in the upper portion of wing base; whitish pollinosity pattern weakly differentiated, formed by four longitudinal stripes connected anteriorly in pairs but separated along mid part (Fig. 2C); postpronotal lobes whitish in the anterior half, forming a stripe from wing base to just below notopleuron; scutellum whitish without any dark spot on disc, but with black spots on sides of base not including the scutellar basal bristles; subscutellum and mediotergite black. Pleuron mostly yellow reddish with small brownish dark spots occupying the anterior region of anepisternum, anepimeron and anatergite, and some specimens with a small black spot on the upper portion of katepisternum; anterior and mid legs completely yellow, hind femora blackish with some yellow areas in basal third and apex; hind tibiae darkened.

Length of wing 5.71-6.50 mm; wing pattern with dark brown bands with some paler portions in some of them; sub-basal, discal, subapical, and apical bands present; accessory costal band absent; discal and subapical bands broadly connected in cell CuA<sub>1</sub>; hyaline fascia between anterior and posterior apical bands originates in cell  $\mathbf{r}_3$  very close to vein  $\mathbf{R}_{2+3}$ ; hyaline fascia between subapical and posterior apical band originates in middle of cell  $\mathbf{r}_5$ .

Abdomen. Tergites 1+2 yellow; tergite 2 with a blackish stripe in anterior half; tergites 3 and 4 usually black with a slender whitish line at posterior margin; tergite 5 wholly brownish black.

Male terminalia. Epandrium brownish yellow; outer surstyli in lateral view long and slender, curved posteriorly with an inferior preapical protuberance, apical end acute; inner surstyli with prensisetae very close to apical portion of former; distiphallus moderately broad with an apical membranous appendage covered with numerous spines on surface.

Female. Differing in the following characters: mid femora of some specimens with a medial dorsal

black spot; sclerites of pleuron usually with dark brown coloration in the upper middle of katepisternum; black spots contiguous to scuto-scutellar suture more conspicuous than in males; abdominal tergites blackish with a slender white stripe along posterior margin; syntergosternite 7 1.04-1.14 mm long and usually black; aculeus length of 1.34-1.40 mm some longer than the length of syntergosternite 7; two spermathecae rather larger and spherical with many scale-like papillae on surface.

Host plants. Solanum appendiculatum H.B. & ex Dunal.

**Etymology**. Specific name from the Latin *solanum* + *phagus* meaning that this species breeds in fruits of solanaceous plants.

Remarks. Intraspecific variation is common in this species, mainly in tergite coloration in both sexes, which ranges from yellow reddish with black or mostly blackish. This species can be separated from other species by the broad connection of the discal and subapical bands at the posterior margin of wing, and by the yellow reddish coloration of the mesonotum unique among species of the *striatella* group.

Some relevant information about the life cycle of this species is that all specimens collected from their host plants in Mexico, emerged from the pupae after approximately 30-35 days, without a diapause as in other species of the genus.

# Rhagoletis nicaraguensis Hernández & Frías, new species Figs. 1C, 2D

Type material: Holotype female (IEXA): NICARA-GUA, Meseta de los Pueblos, Carazo, San Marcos, 1-X-1994, M. Niklaus-Ruíz.

Description. Holotype female. Small specimen with most of head yellow; frons brown reddish; genal and postocellar bristles yellow; third antennal segment dorsoapically rounded; arista bare for entire length; three pairs of frontals and two pairs of orbital bristles present.

Thorax. Mesonotum 1.72 mm long; scutum mostly black with a whitish pollinosity on surface forming a well defined pattern of four longitudinal stripes, all of them connected on presutural region; postpronotal lobes and scutellum broadly whitish,

but latter with basal black spot on disc very slender along scuto-scutellar suture and sides of base weakly including the basal scutellar bristles.

Notopleuron and most pleural sclerites black, except for a white yellowish stripe from below notopleura to base of wing; fore legs completely yellow including the coxa; mid and hind femora blackish; midtibia yellow and hindtibia darkened; all tarsi yellow.

Wing length 3.76 mm; pattern with three broad transverse bands, with sub-basal and discal bands connected at level of radial section; second costal cell with a black spot on proximal and distal thirds; discal and subapical bands very broad and closer in medial portion of discal cell, but in cell CuA<sub>1</sub> strongly connected; accessory costal band absent; anterior apical band broad with a small hyaline spot at end of vein  $R_{2+3}$ , posterior apical band broadly connected to subapical band occupying entire width of cell  $r_5$ ; hyaline fascia between both apical bands narrow to level of vein  $R_{4+5}$  and extending into cell  $r_5$ .

Abdomen. Tergites mainly blackish with whitish posterior marginal stripes on tergites 2-5; tergite 6 and syntergosternite 7 completely black and the latter 0.44 mm long; aculeus 0.65 mm long; aculeus tip tapering gradually to apex.

Male. Unknown.

Host plants. Unknown.

**Etymology**. This species is named in reference to the country where it was collected the first time.

**Remarks.** This species is closely related to R. jamaicensis by the following combination of characters: pollinosity pattern of scutum with stripes connected on presutural region; sub-basal and discal bands partially connected between  $B_m$  and costal cells; presence of small hyaline spot at end of vein  $R_{2+3}$ ; and by darkened coloration of basal and distal portion of costal cell.

R. nicaraguensis is proposed as a new species by the following combination of characters differing from other species: a broad connection in the discal and subapical bands at their posterior extremes (most of cell CuA<sub>1</sub>); posterior apical band and subapical band broadly connected in cell r<sub>5</sub>; and by the extremely slender discal spot on the base of scutellum.

## Rhagoletis jamaicensis Foote Fig. 1B

Rhagoletis jamaicensis Foote, 1981: 39. U.S. Dept. Agric. Tech. Bull. 1607.

Known distribution. JAMAICA: Hardwar Gap, 4000 ft, 25-VII-1966, Howden & Becker (type locality); COSTA RICA: Prov. San José, 7-VII-1978, L.F. Girón (Foote 1981: 40).

Diagnosis. Third antennal segment rounded apically but with a slight suggestion of point dorsoapically; arista bare; postocellar bristles yellow; mesonotum black and with a pattern of whitish pollinosity forming four longitudinal stripes which are joined on each side in the presutural region, but separated in the middle; scutellum whitish with a black spot on basal disc straight occupying a half of base, sides of base black; anterior scutellar bristles inserted well within black area. Females with anterior legs completely yellow, mid and hind femora mostly blackish except extreme apices of both yellow; midtibia yellow; hindtibia darkened basally and apically.

Wings with three transverse bands present; sub-basal and discal bands partially connected; hyaline fascia between anterior and posterior apical bands extended beyond vein  $\mathbf{R}_{4+5}$ ; base of posterior apical band connected to subapical band shorter than width of cell  $\mathbf{r}_5$ ; accessory costal band absent.

Abdominal tergites black in most part with slender whitish stripes along posterior margins of tergites 2-5; tergite 6 blackish; syntergosternite 7 black on basal two thirds becoming dark brown apically; aculeus about 1.0 mm long, apex rather bluntly rounded; spermathecae spherical with prominent papillae clustered at base.

Male. Unknown.

Host plants. Unknown.

**Remarks.** This species is very similar to *R. nicara-guensis* n. sp., as previously discussed. They can be separated using the key.

### Rhagoletis macquartii (Loew) Fig. 1A

Trypeta macquartii Loew, 1873: 267. Smith. Inst. Misc. Coll. 11(3) (publ. 256).

Urophora scutellaris Macquart, 1851:261 (p. 288). Suppl. Mem. Soc. Royal Sci., Agr. Arts Lille (supl. IV). (Preoccuped Wiedemann 1830).

Known distribution. BRASIL: Goiás (Macquart 1851: 267). Ouro Prêto, Minas Gerais, IV-1954, N.L.H. Krauss (Foote 1981: 38).

Diagnosis. Third antennal segment gently dorsoapically pointed; postocellar and genal bristles yellow. Mesonotum mostly black with white pollinosity pattern forming four longitudinal stripes all of them completely separated anteriorly; scutellum whitish with a black discal spot covering the basal third, and margin straight; basal sides of scutellum black including the basal bristles; medial half of postpronotal lobes yellowish brown.

Females with forelegs and midtibia yellow; mid and hindfemur mostly blackish except their extreme apices; hindtibia darkened in their proximal and apical thirds.

Wings with three transverse bands present; sub-basal and discal bands broadly connected along most of their lengths; second costal cell mostly blackish with only a small hyaline spot on the middle; anterior and posterior apical bands complete, the first with a narrow hyaline fascia along distal margin of cell  $\mathbf{r}_3$ ; discal and subapical bands completely separated; hyaline fascia between anterior and posterior apical bands extending beyond vein  $\mathbf{R}_{\text{dag}}$ .

Abdominal tergites mostly blackish with whitish slender stripes on posterior margins of tergites 2-5; tergite 6 black with a central yellow spot on posterior margin; aculeus 0.9 mm long, apex rather bluntly rounded; spermathecae spherical with some scale-like papillae clustered at base.

Male. Unknown.

Host plants. Unknown.

Remarks. This species appears to be closely related to R. jamaicensis and R. nicaraguensis, but can be differentiated by the solid connection of the subbasal and discal bands darkening completely the bm, cup, and most of the second costal cells; and by the hyaline fascia along distal margin of cell  $r_a$ .

#### Discussion

The *striatella* species group is more widely distributed in Continental America than any other

group of Rhagoletis as a whole. It has representatives from southern Canada to Brazil and the Antilles.

Rhagoletis striatella has been recorded from temperate regions of Canada, in the USA, and Mexico in the "Mexican High Plateau", having as its southern limit the mountain ranges of the "Eje Volcánico Transversal" in Central Mexico; R. macquartii is the only known species of the group occurring in South America, where it has been recorded from the central region of Brazil.

The remaining species of the group could have a Mesoamerican origin: *R. triangularis* only known by the holotype from southern Mexico near the border with Guatemala; *R. solanophaga* is described from material collected in a locality of the coastal slope of the Gulf of Mexico, and in Guanacaste Province in Costa Rica.

Rhagoletis jamaicensis is the only species of the genus known from the Antilles, and currently is recorded from Jamaica and Costa Rica. Rhagoletis nicaraguensis is known only from Nicaragua.

Knowledge of host plants of species of the *striatella* group is certainly poor. Larvae of *R. striatella* have been found developing in fruits of *Physalis* species (Solanaceae) (Bush, 1966; Foote, 1981), and all specimens of *R. solanophaga* collected in Mexico were found as larvae breeding in fruits of *Solanum appendiculatum* (Solanaceae). This confirms that species with Central and South American distribution are strongly related with this plant family.

The discovery of the three new species, suggests that the striatella species group can be separated at least into two subgroups; first comprising  $R.\ striatella$  and  $R.\ triangularis$  related by the following combination of characters: arista covered by short pilosity along entire length; third antennal segment sharply dorsoapically pointed; the hyaline fascia between anterior and posterior apical bands reaching just to vein  $R_{4+5}$ ; the presence of a triangular shaped black spot on the discal base of scutellum; by the shape of outer surstyli which are broad from its base and rounded in the apex (in lateral view); and by the apical membranous appendage of distiphallus bare.

The second subgroup includes the species R. macquartii, R. jamaicensis, and R. nicaraguensis, which can be distinguished by the following characters: third antennal segment rounded dorsoapically or sometimes gently pointed; the hyaline fascia between anterior and posterior apical bands extending anterior to vein  $R_{4+5}$  (inside cell  $r_3$ ); discal

basal spot of scutellum straight; and by the partial or complete fusion of the sub-basal and discal bands.

Finally, *R. solanophaga* appears most different from the others, based on the coloration of the mesonotum and by the spines on the membranous appendage of the distiphallus. It would be necessary to obtain the currently unknown males in order to define complete relationships within the group.

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