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New species and phylogenetic analysis of *Cryptodacus*, *Haywardina*, and *Rhagoletotrypeta* (Diptera: Tephritidae)

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Abstract

The genera *Cryptodacus*, *Haywardina*, and *Rhagoletotrypeta* are revised, and the cladistic relationships among their species are analyzed. *Cryptoplagia* Aczél is synonymized with *Haywardina*, and *Lezca* Foote with *Cryptodacus*. Twenty-one species, including ten new species, are recognized. Keys, diagnoses, and illustrations to identify them are presented. *Solanum trichoneuron* is reported as a host plant of *H. cuculi*, and *Celtis iguanaea* as a host of *R. pastranai*.

Resumen

Se hace una revisión de los géneros *Cryptodacus*, *Haywardina*, y *Rhagoletotrypeta*, y se analizan las relaciones filogenéticas entre sus especies. Sinónimos nuevos son *Cryptoplagia* Aczél con *Haywardina*, y *Lezca* Foote con *Cryptodacus*. Se reconocen 21 especies, incluyendo diez nuevas. Se presentan claves y ilustraciones para la identificación de todas las especies. *Solanum trichoneuron* se registra como un huésped de *H. cuculi*, y *Celtis iguanaea* como un huésped de *R. pastranai*.

Introduction

The subtribe Carpomyina (Trypetinae: Trypetini) is a mainly Holarctic and Neotropical group of fruit flies that breed in fruits of a variety of plant families (Norrbom 1989a). It consists of the large genus *Rhagoletis* Loew, with more than 60 species, and ten small genera, none of which currently includes more than seven species. *Rhagoletis* has been the focus of intensive applied, taxonomic, and evolutionary studies (e.g., Bush 1966, Foote 1981, Berlocher and Bush 1982), but relationships among its species groups and the other genera are poorly understood. Most of the genera have not been studied by phylogenetic methods, nor shown to be monophyletic. Character data and cladistic analyses are presented here in an attempt to so define *Cryptodacus* Hendel (= *Lezca* Foote, n. syn.), *Haywardina* Aczél (= *Cryptoplagia* Aczél, n. syn.), and *Rhagoletotrypeta* Aczél. These genera and *Zonosemata* Benjamin differ from other Carpomyina in having a white medial scutal stripe or spot.

Materials and Methods

Most morphological terms used in this paper are explained by McAlpine (1981). Wing band ter-

minology follows Foote (1981, Fig. 71). The discal band is defined as that crossing r-m. The subapical band usually covers dm-cu, but is displaced apically in some *Cryptodacus* and *Haywardina*. The following abbreviations and ratios are used: dc - dorsocentral seta; flgm 1 - first flagellomere; pal - postalar seta; psut spal - postsutural supra-alar seta; Tg - abdominal tergite; facial ratio - medial height/ ventral width of face; flgm 1 ratio - first flagellomere length/ width (lateral view); orb ratio - distance between orbital setae/ distance from anterior seta to eye margin; r-m ratio - distance from bm-cu to r-m/ distance from bm-cu to dm-cu (on vein M). Aculeus tip length was measured ventrally, from the end of the medial membranous area of the aculeus to the end of the aculeus. Scutal microtrichial patterns are most visible on dry specimens at oblique anterior or posterior angles. The characters listed at the beginning of the "Diagnosis" distinguish each species from all its congeners. The "Additional description" includes only characters not listed in the diagnosis or Tables 1 and 2 or those for which further detail is useful. Acronyms for specimen depositories are listed by Griffiths (1980) except: CEEA - Comisión Ecuatoriana de Energía

Atómica, Quito; IEXV - Inst. de Ecología, Xalapa; INBio - Inst. Nacional de Biodiversidad, Costa Rica; INPA - Inst. Nacional de Pesquisas da Amazonia; UFPC - Univ. Federal do Paraná; UFRJ - Univ. Federal Rural do Rio de Janeiro (former Escola Nacional de Agronomia); UVG - Univ. del Valle, Guatemala. Methods of cladistic analysis are discussed in the "Relationships" section.

Key to genera of Carpomyina with a white medial scutal stripe

1. Vein Cu_1 bordered with brown between bm-cu and discal band (Fig. 1), **and/or** antenna elongate, extended beyond ventral facial margin. r-m ratio > 0.60 . Subapical band and posterior orbital seta present. Aculeus tip sagittate and finely serrate (Fig. 5B-I). Known hosts *Loranthus* species *Cryptodacus* Hendel
- Vein Cu_1 without brown border between bm-cu and discal band (rarely with short extension from discal band in *Rhagoletotrypeta*). Antenna not extended beyond ventral facial margin. r-m ratio < 0.60 , or if greater (*Haywardina cuculi*), subapical band and posterior orbital seta absent. Aculeus tip neither sagittate nor serrate. 2
2. Scutum similar to Fig. 2D, without white postsutural lateral stripe or band on transverse suture. Thorax mostly brown. Aculeus tip length $> 1/2$ aculeus length (Fig. 10A-B,D-E). Known hosts *Celtis* species *Rhagoletotrypeta* Aczél (in part)
- Scutum with white postsutural lateral stripe and/or band on transverse suture (Fig. 7, or similar to 2C,E). Thorax mostly yellow or brown. Aculeus tip length $< 1/3$ aculeus length (Fig. 8H, 10C,G) 3
3. dc seta closer to level of pal seta than level of psut spal seta. Usually 4 or more frontal setae. Outer surstylus short, without mesal lobe, and in lateral view, part apical to prensisetae about as long as wide (Bush 1965, Fig. 25, 27). Spermathecae elongate, saclike (Bush 1965, Fig. 22). Known hosts Solanaceae species *Zonosemata* Benjamin
- dc closer to level of psut spal than level of pal seta. Usually 3 frontal setae. Outer surstylus elongate, with mesal lobe, and in lateral view, part apical to prensisetae longer than wide (Fig. 8A-E, 9C-D). Spermathecae spherical, with short neck (Fig. 10K) 4

4. flgm 1 with small dorsoapical point. Thorax brown except yellow propleuron and anepisternum (*H. obscura*) or mostly yellow. Aculeus tip entire or with minute subapical notches (Fig. 8H). 2 spermathecae. Inner surstylus long, extended well beyond epandrium (Fig. 8A-E). Known hosts *Solanum* species *Haywardina* Aczél
- flgm 1 rounded apically. Thorax usually mostly brown. Aculeus tip deeply trilobed (Fig. 10C,G). 3 spermathecae. Inner surstylus short, extended slightly beyond epandrium (Fig. 9C-D). Known hosts *Celtis* species *Rhagoletotrypeta* Aczél (in part)

Genus *Cryptodacus* Hendel

Cryptodacus Hendel 1914a:84 (Type species: *C. obliquus* Hendel, orig. desig.); Aczél 1950:192 (cat.); Foote 1967:21 (cat.); Foote 1980:24 (in part; review).

Cryptodacus Hendel 1914b:12 (Type species: *C. obliquus* Hendel, orig. desig.); Preocc. Hendel 1914a.

Lezca Foote 1978:27 (Type species: *L. tau* Foote, orig. desig.); Foote 1980:34 (review). **N. syn.**

Description. Mostly brown. **Head:** Frons, except in *obliquus*, with brown mark between ocelli extended laterally. 2-3 frontal setae. 2 orbital setae, usually well separated (close together in *obliquus*). Ocellar seta usually small (large in *obliquus*). Face usually with brown spot or spots (entirely yellow in *obliquus*). Antenna relatively long, often extended beyond ventral margin of face; flgm 1 ratio 3.0-7.0; apex rounded, without dorsoapical point, tapered or slightly expanded and flattened in sagittal plane. **Thorax** (Fig. 2C-D): Entirely microtrichose or with bare areas (*lopezi*, *parkeri*, *quirozi*) and mostly brown or dark orange. With at least following white areas: dorsal or posterior margin of anepisternum; medial scutal stripe or spot; and apical 1/2 or more of scutellum. Postpronotal lobe usually with white area (small in *parkeri*, absent in *quirozi*). Often with additional white stripes or bands on scutum laterally, transverse suture, notopleuron, and katepisternum. dc posterior to psut spal, sometimes closer to pal. **Wing** (Fig. 1): r-m ratio > 0.60 . Subbasal band broad, filling most or all of cell bm and all of cell bcu. Discal band broad, anterior end basally curved, filling base of cell r_{2+3} and at least part of cell c, usually with narrow basal and apical borders darker than medial part. Vein Cu_1 bordered with brown between bm-cu and discal band (except in *quirozi* and some *tau*). Subapical band

usually faint or weaker anteriorly. Apical band often faint or absent in cells r_1 and r_{2+3} . Posterior apical band absent. Accessory costal band usually absent (faintly present in *obliquus*). *Male terminalia*: Outer surstylus (Fig. 3) elongate, with small mesal lobe near prensisetæ. Inner surstylus elongate. *Female terminalia*: Aculeus tip (Fig. 5B-I) sagittate and finely serrate. 2 spermathecae (Fig. 5J-K), ovoid or barrelshaped, with long sclerotized base.

Remarks. See Relationships section for justification for the synonymy of *Lezca* with *Cryptodacus*. A host is known for only one of the eight species of *Cryptodacus*. *C. silvai* Lima breeds in fruit of a species of *Loranthus* (Loranthaceae). The specimens "from Colombia" that Foote (1980; including Fig. 52) considered *Cryptodacus* species are actually from Mexico and belong to an undescribed genus near *Pseudophorellia* Lima. *Cryptodacus scutellatus* Hendel belongs in *Zonosemata* (Norrbon 1989b) as Lima (1947) suggested, although his comments were long unnoticed.

Key to the species of *Cryptodacus*

1. Frons brown only between ocelli. Face entirely yellow. Scutum without white band along transverse suture and without lateral white stripe or spot at intra-alar seta (Fig. 2D). Discal band not extended across dm-cu (Fig. 1B). orb ratio < 1. (Bolivia, Peru) *obliquus* Hendel
- Frons with brown mark extended beyond ocelli (Fig. 2A-B). Face with brown spot or spots. Scutum with white band on transverse suture and with lateral white stripe (Fig. 2E) or at least a spot at intra-alar seta (Fig. 2C). Discal band extended across posterior end or more of dm-cu (Fig. 1A,C-G). orb ratio > 1 (Fig. 2A-B) 2
2. Tg5 (and female Tg6) with sublateral white areas bordering medial brown stripe or stripes. dm-cu entirely covered by discal or subapical band (Fig. 1A,F). Postgena entirely yellow. (Mexico, Guatemala) 3
- Tg5 (and female Tg6) without sublateral white areas. dm-cu not bordered by brown medially (Fig. 1C-E), except in *tigreroi* (Fig. 1G). Postgena entirely yellow (*quirozi*) or brown except anterior margin. (Costa Rica, S. America) 4
3. Discal band extended across only posterior end of dm-cu (Fig. 1A). r-m ratio < 0.75. Face with single, medial brown spot. Gena without brown spot. Tg1+2 and Tg3 each brown with narrow white apical band. Female Tg5-6 with undivided medial brown stripe. Syntergosternite 7 brown. (Guatemala) *lopezi* Norrbom, n. sp.
- Discal band extended across all of dm-cu (Fig. 1F). r-m ratio > 0.80. Face with pair of sublateral brown spots. Gena with brown spot. Tg1+2 yellow with white apical band. Tg3 white basally, brown apically. Female Tg5-6 with 2 narrowly separated medial brown stripes. Syntergosternite 7 orange. (Mexico, Guatemala) *tau* (Foote)
4. Cell dm with only apical corner hyaline (Fig. 1C). Tg3-4 each with apical white band. Scutum with white spot at base of intra-alar seta, not extended anteriorly to level of psut spal seta (Fig. 2C). Face with 2 or 4 brown spots, each side with large dorsal and small ventral spot (Fig. 2B) or 1 elongate spot. Frons with distinct brown stripe extended anteriorly from mark on ocelli (Fig. 2B). (Colombia, northern Brazil) *ornatus* Norrbom, n. sp.
- Cell dm with basal and apical hyaline areas (Fig. 1D,E,G). Tg3-4 without apical white bands. Scutum with lateral white stripe extended anteriorly to at least level of psut spal seta, except in *quirozi*. Face with 3-4 brown spots, sometimes fused into 1 U-shaped mark. Frons sometimes with irregular brownish areas (Fig. 2A), but without distinct brown stripe extended anteriorly from mark on ocelli 5
5. Postgena brown except anterior margin. Scutum with lateral white stripe extended anteriorly to at least psut spal seta. Postpronotal lobe with at least small white spot (possibly variable in *parkeri*) 6
- Postgena entirely yellow. Scutum with white spot posterior to intra-alar seta, not extended anteriorly to level of psut spal seta (similar to Fig. 2E). Postpronotal lobe entirely brown *quirozi* Norrbom, n. sp.
6. Subapical band (Fig. 1G) connected to discal band posteriorly, covering all of crossvein dm-cu. flgm 1 ratio > 6. Tg3-4 with uninterrupted medial white stripe. Aculeus tip (Fig. 5C,I) stout, serrate part slightly wider than long but narrower than aculeus width at apices of 8th sternites. (Ecuador) *tigreroi* Norrbom, n. sp.
- Subapical band (Fig. 1D) not connected to discal band, middle part of dm-cu not bordered by brown. flgm 1 ratio < 5.5. Tg3-4 with or without uninterrupted medial white stripe. Aculeus tip (Fig. 5B) slender basally, serrate part as long as wide and broader than aculeus width at apices of 8th sternites (female unknown in *parkeri*) 7

tau in having sublateral white areas on Tg5-6, but they extend only slightly onto Tg4 and the medial brown stripe is solid whereas it is divided by a white stripe in *tau*.

Additional description. *Head*: 3 frontal setae. orb ratio 1.5. Facial ratio 0.59-0.61. flgm 1 ratio 4.6. Gena yellow. *Thorax*: White band on transverse suture connected to anepisternal white area and lateral white stripe. dc slightly closer to pal than to psut spal. *Wing* (Fig. 1A): r-m ratio 0.63-0.69. Cell c brown anteriorly, narrowly orange posteriorly. Subapical band connected to discal band posteriorly, faint and broad anterior to vein R_{4+5} . Apical band faint and narrow or absent in cells r_1 and r_{2+3} ; in cell r_{4+5} dark and broad. *Female terminalia*: Syntergosternite 7 brown. Aculeus 0.70 mm long; tip (Fig. 5D) moderately broad basally, serrate part 0.75 times as long as wide, 0.042 mm long, 0.055 mm wide, broader than aculeus width at apices of 8th sternites.

Etymology. Named for Jorge Lopez.

Holotype. f (at USNM, for eventual deposit in Guatemala), GUATEMALA: Sacatepequez: Finca Capetillo, 26.X.1990, E. Muñiz, McPhail trap.

Paratypes. GUATEMALA: Sacatepequez: Finca Tempixque, 9.X.1990, J. Lopez, McPhail trap, 1f (USNM). Escuintla: Palín, 1992, J. Lopez, 2f (USNM, UVG).

Cryptodacus obliquus Hendel (Fig. 1B, 2D, 3A-B, 4A)

Cryptodacus obliquus Hendel 1914a:84 (Lectotype m (MNM), BOLIVIA: Songo); Lima 1947:153; Aczél 1950:192 (cat.); Foote 1967:21 (cat.); Foote 1980:24.

Cryptodacus obliquus Hendel, 1914b:12 (Holotype m (MNM), BOLIVIA: Songo); Preocc. Hendel 1914a.

Diagnosis. See couplet 1 of key. Also, ocellar seta moderately strong, longer than posterior orbital seta; ventral margin of face slightly concave, facial ratio 0.80; flgm 1 entirely yellow, tapered and not strongly sagittally flattened apically; flgm 1 ratio 3.0; notopleuron and katepisternum without white marks; entire dorsal margin of anepisternum white; and Tg1+2 entirely brown.

Additional description. *Head*: Gena yellow. *Thorax* (Fig. 2D): Anapleural suture narrowly, and sometimes parts of meron and metapleuron yellow. dc slightly closer to pal than to psut spal. *Wing* (Fig. 1B): r-m ratio 0.67. Cell c with large posteromedial hyaline area. Subapical band connected to discal band posteriorly. Apical band faint and narrow in cells r_1 , r_{2+3} and r_{4+5} . Accessory costal band sometimes faintly present in cell r_1 . *Abdomen*: Tergites brown, except Tg5 with narrow white medial stripe, broadly expanded on posterior margin; in cleared specimen, Tg3-4 with faint yellow medial stripe.

Remarks. In 1986 at the MNM, I briefly compared the examined specimens with the holotype of *obliquus* Hendel 1914b, which is here designated as lectotype of *obliquus* Hendel 1914a, described from an unstated number of specimens from Bolivia.

Specimens examined. BOLIVIA: Suapi, 1m (USNM). PERU: Vilcanota, 1m (MNM).

Cryptodacus ornatus, n. sp. (Fig. 1C, 2B-C, 5A,E,J,L)

Diagnosis. Cell dm without basal hyaline area; frons with distinct brown stripe extended to anterior orbital seta from ocellar mark (frons of *parkeri* and *silvai* may have irregular pale brown marks); scutal microtrichia even in density; Tg4 with apical white band; and syntergosternite 7, in lateral view (Fig. 5A), with strong dorsal hump. Only *quirosi* also has the lateral scutal white stripe reduced to a small posterior spot.

Additional description. *Head* (Fig. 2B): 2 frontal setae. orb ratio 3. Face on each side with elongate spot (Colombian females) or large dorsal and tiny ventral spot (Brazilian female). Facial ratio 0.50. flgm 1 ratio 5. Gena with brown spot touching eye. *Thorax* (Fig. 2C): White band on transverse suture extended to posterior notopleural seta but separate from anepisternal white area. Lateral white stripe spotlike, extended only slightly anterior to intralar seta. dc closer to psut spal than to pal. *Wing* (Fig. 1C): r-m ratio 0.68-0.70. Cell c entirely brown. Subapical band not connected to discal band, ended at or slightly posterior to vein M on anterior end of dm-cu; faint or absent anterior to vein R_{4+5} . Apical band faint in cell r_1 , narrow and dark in cells r_{2+3} and r_{4+5} . Cell dm brown except anteroapical corner.

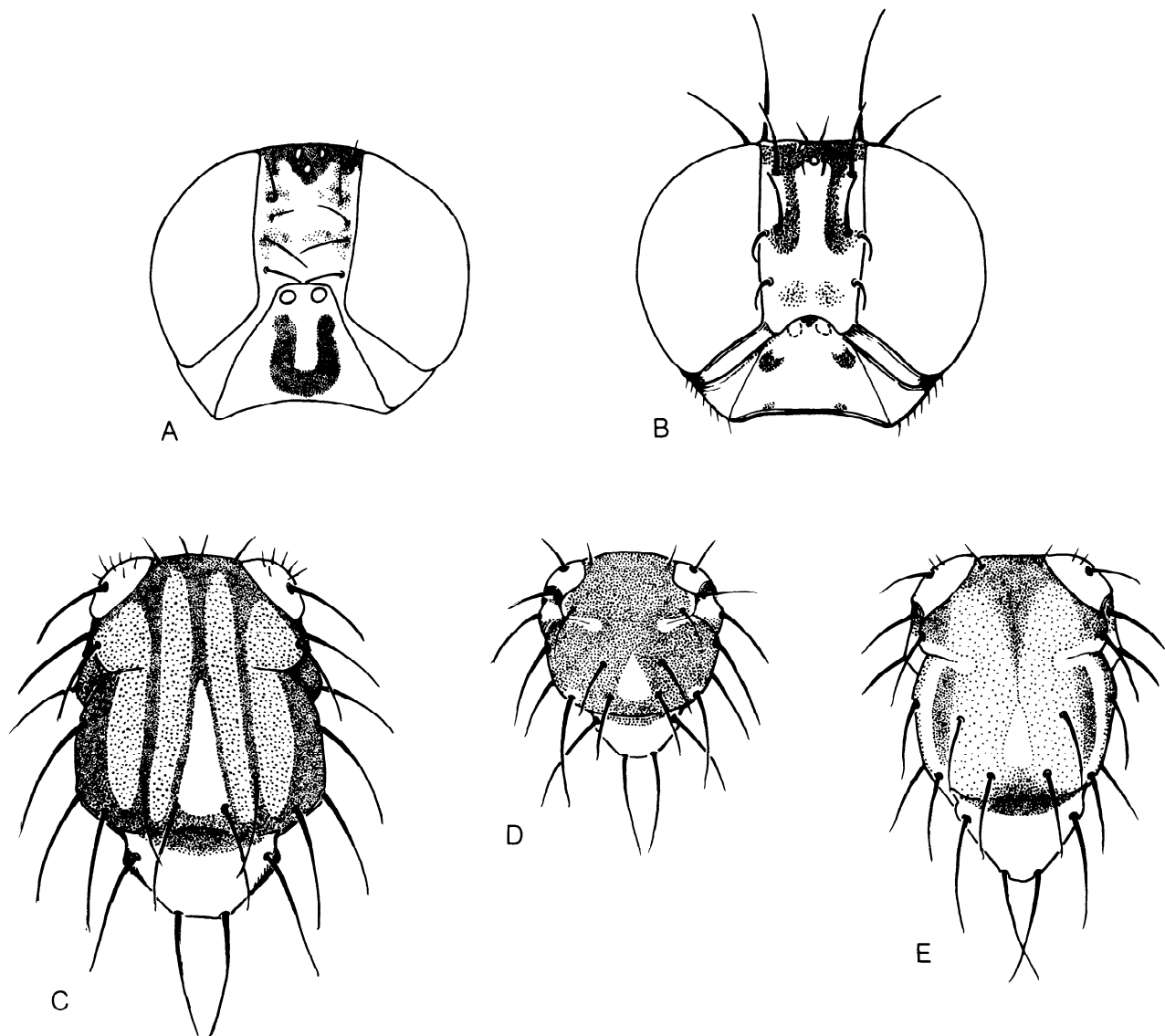


Figure 2. Heads (anterodorsal) and thoraxes (dorsal), *Cryptodacus*: A, *silvai*, paratype male; B-C, *ornatus*, Manaus, Brazil; D, *obliquus*, Vilcanota, Peru; E, *tau*, Cuernavaca, Mexico. Light stipling indicates areas of dense microtrichia in D, dark orange areas in E.

Abdomen: Tg1-5 each with narrow white apical band. Tg6 with white medial stripe, narrowly expanded on posterior margin. **Female terminalia:** Syntergosternite 7 brown. Aculeus 0.57 mm long; tip (Fig. 5E) slender basally, serrate part 1.60 times as long as wide, 0.08 mm long, 0.05 mm wide, broader than aculeus width at apices of 8th sternites. **Egg** (Fig. 5L) - Length 0.53-0.67 mm, widest diameter 0.10-0.14 mm. Micropyle end with short lobe 0.03-0.06 mm long.

Remarks. The aculeus tip is missing on the Brazilian paratype. The measurements are based on the Colombian paratype. Egg measurements are based on 7 eggs dissected from the 2 paratypes.

Etymology. The name refers to the striking coloration of this species.

Holotype. f (ZMHU), COLOMBIA: "Cordill. v. Columbien, terra caliente", Thieme. **Paratypes.** Same data as holotype, 1f (USNM). BRAZIL:

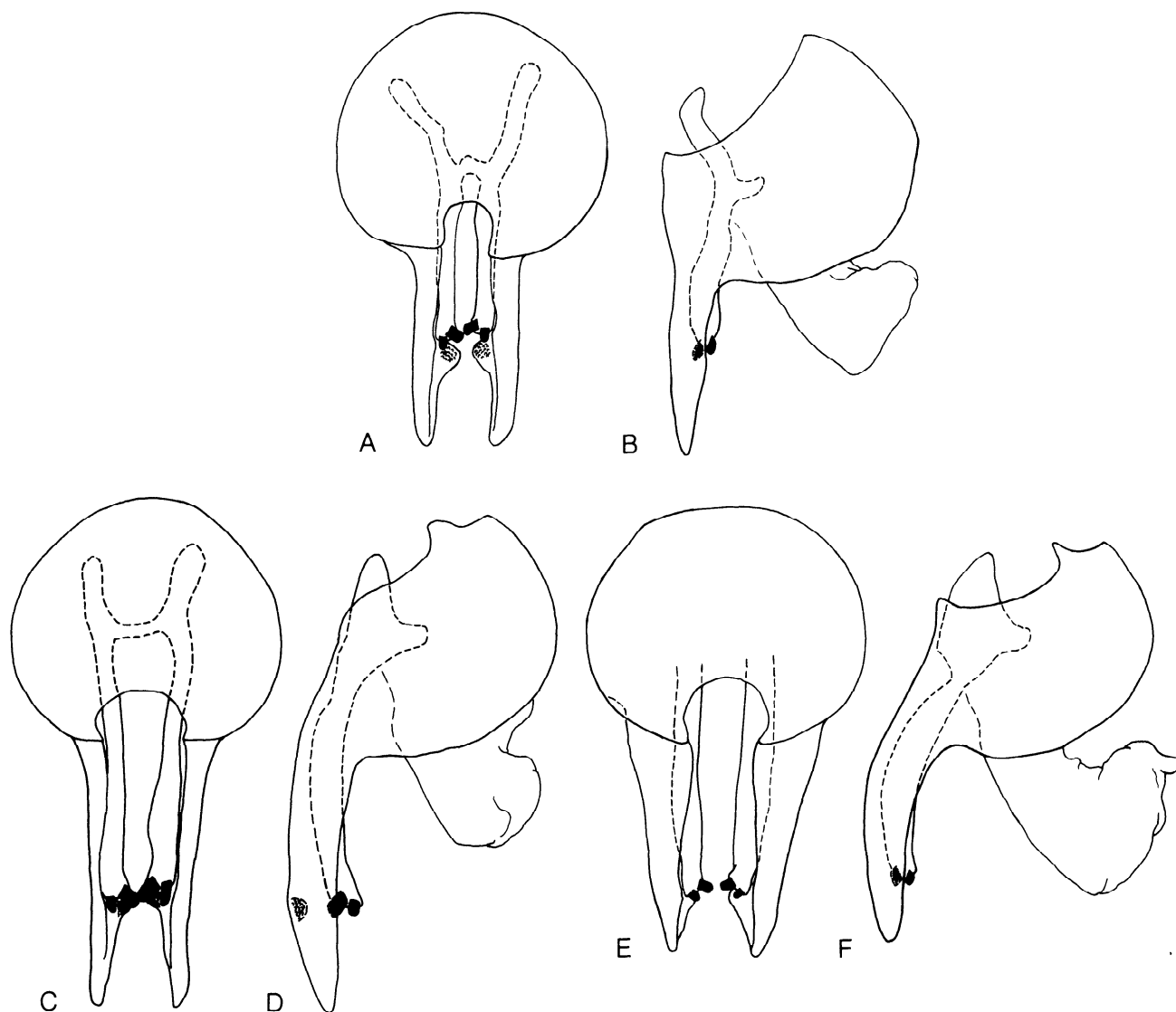


Figure 3. Male terminalia, *Cryptodacus*: A-B, *obliquus*, Suapi, Bolivia; C-D, *parkeri*, holotype; E-F, *tau*, Morelos, Mexico; A,C,E, posterodorsal (proctiger omitted); B,D,F, lateral.

Amazonas: [Manaus], Campus Univ., 20.I.1973, J.A. Raphael, 1f (INPA).

Cryptodacus parkeri, n. sp.
(Fig. 1D, 3C-D, 4B)

Diagnosis. The brown postgena and larger scutal white stripe distinguish *parkeri* from *quirozi*, the only other *Cryptodacus* with 4 large facial spots (1 of 3 types of *ornatus* has 2 large dorsal and 2 small

ventral spots), mostly brown postpronotal lobe (entirely brown in *quirozi*; with small white spot in *parkeri*), large sublateral areas of scutum nonmicrotrichose, or a similar abdominal pattern (brown except apical band on Tg1+2 and medial white stripe interrupted on Tg3).

Additional description. *Head*: Frons with irregular pale brown marks at bases of frontal and anterior orbital setae. 3 frontal setae. orb ratio 1.5. Facial ratio 0.61. flgm 1 ratio 4.7. Gena yellow. *Thorax*: Postpronotal lobe with only posterior 1/4

white. Much of thoracic pleuron nonmicrotrichose. White band on transverse suture connected to anepisternal white area, but narrowly separated from lateral white stripe. dc midway between psut spal and pal. *Wing* (Fig. 1D): r-m ratio 0.67. Cell c entirely brown. Subapical band not connected to discal band, ended posteriorly on vein M at anterior end of dm-cu, pale brown anterior to vein R_{4+5} . Apical band dark in cell r_{4+5} . *Abdomen*: Tg1+2 with apical white band. Tg3-4 with small medial white spot on posterior margin. Tg5 with medial white stripe, not expanded posteriorly. *Male terminalia*: Distiphallus (Fig. 4B) moderately long and slender; in ventral view, apex of sinuous internal tube bilobed, similar to Fig. 4D.

Etymology. Named for Frank Parker.

Holotype. m (USU), COSTA RICA: Guanacaste: 3 km SE R. Naranjo, 15-13.XII.1992, F.D. Parker.

Cryptodacus quirozi, n. sp.
(Fig. 1E, 5E)

Diagnosis. (Also see Diagnosis of *parkeri*). The entirely yellow occiput and postgena distinguish *quirozi* from other *Cryptodacus* except *lopezi* and *tau*, which differ in facial pattern (1-2 spots, vs. 4 in *quirozi*) and abdominal pattern (*quirozi* lacks sublateral yellow areas). The small, spotlike lateral scutal white stripe distinguishes *quirozi* from other *Cryptodacus* except *ornatus*, although the stripe is absent in *obliquus*. In the holotype of *quirozi*, vein Cu_1 lacks the brown border present in most other *Cryptodacus*, but this character may vary as in *tau*.

Additional description. *Head*: 3 frontal setae. orb ratio 2.0. Facial ratio 0.71. flgm 1 ratio 4.6. Gena yellow. *Thorax*: Postpronotal lobe entirely brown. White band on transverse suture connected to anepisternal white area. Lateral stripe reduced to small spot posterior to intra-alar seta. dc slightly closer to psut spal than to pal. *Wing* (Fig. 1E): r-m ratio 0.71. Cell c entirely brown. Subapical band not connected to discal band, ended posteriorly on anterior end of dm-cu, pale brown anterior to vein R_{4+5} . Apical band dark in cell r_{4+5} . *Abdomen*: Tg1+2 with apical white band. Tg3 with medial white spot on posterior margin. Tg4-6 with medial white stripe, very narrow on Tg4. *Female terminalia*: Syntergosternite 7 brown. Aculeus 0.65 mm long; tip (Fig. 5E) slender, serrate part 1.1 times as long

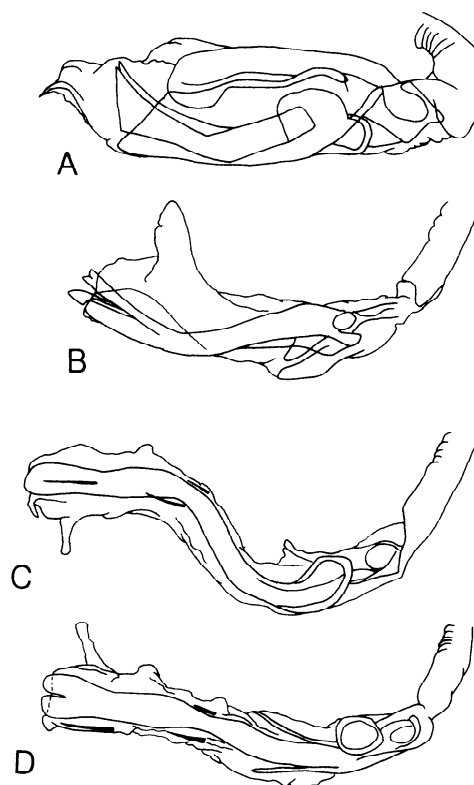


Figure 4. Distiphalli, *Cryptodacus*: A, *obliquus*, Suapi, Bolivia; B, *parkeri*, holotype; C-D, *tau*, Morelos, Mexico; A-C, lateral; D, ventral.

as wide, 0.055 mm long, 0.050 mm wide, slightly narrower than aculeus width at apices of 8th sternites.

Etymology. Named for Luis Quiroz.

Holotype. f (IEXV), MEXICO: Veracruz: Apazapan, McPhail trap, 13.XI.1991, G. Quintero & L. Quiroz.

Cryptodacus silvai Lima
(Fig. 2A, 5B)

Cryptodacus silvai Lima 1947:153 (Holotype f (UFRRJ, no. 9836), BRAZIL: Rio Grande do Sul: Rio Grande, 1945, A. D'Araujo e Silva); Aczél 1951b:133 (cat.); Foote 1967:21 (cat.).

Diagnosis. Differs from other *Cryptodacus* except *tigreroi* by the facial pattern (2 dorsal and 1 ventral brown spots, sometimes fused into large U-shaped mark) and abdominal pattern (brown except for complete white T-shaped mark). Differs from *tigreroi*

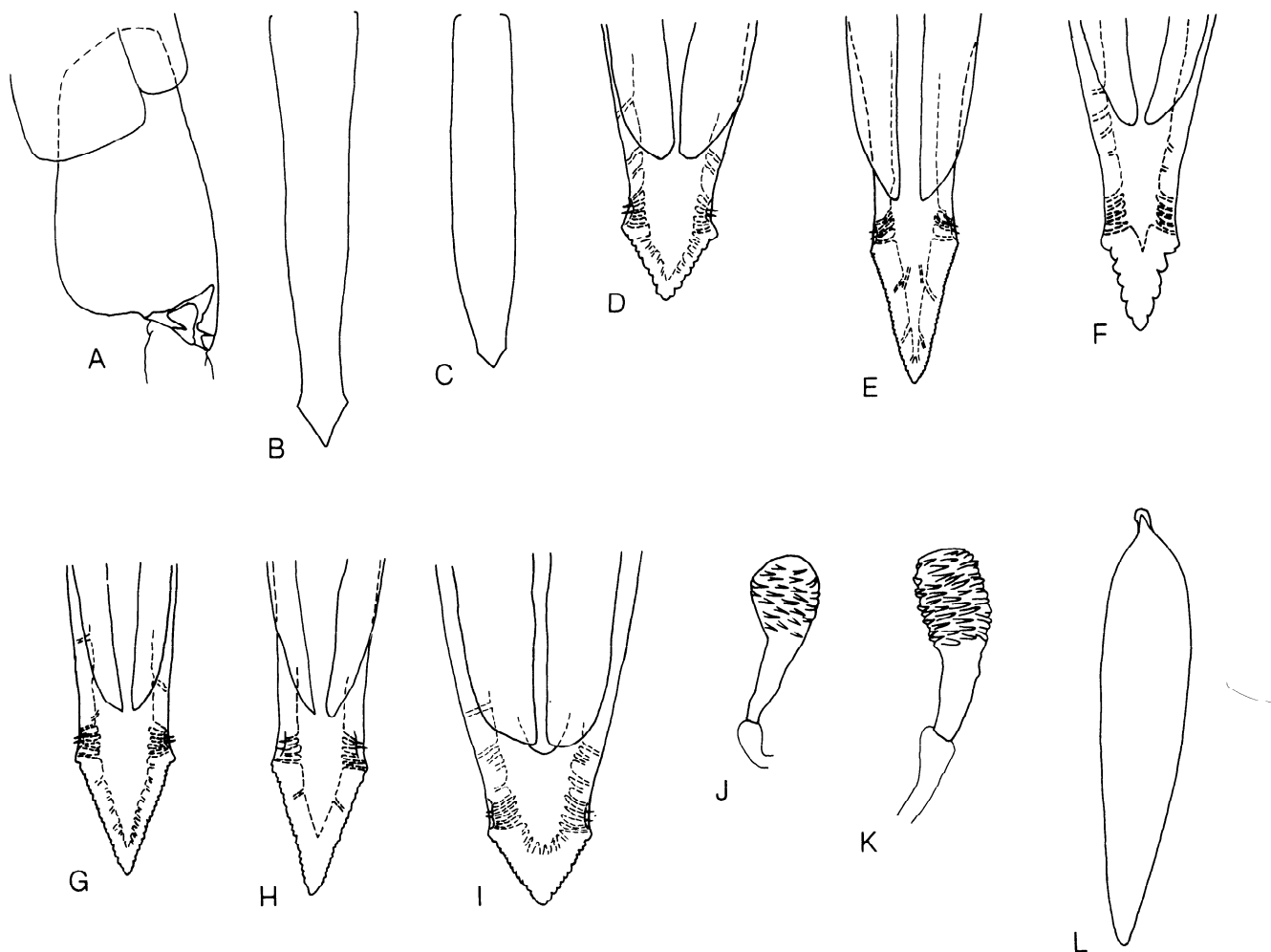


Figure 5. Female terminalia, *Cryptodacus*: A,E,J,L, *ornatus*, paratype, Colombia; B, *silvai* (copied from Lima 1947, Figure 4); C,I, *tigreroi*, holotype; D, *lopezi*, paratype; F, *quirozi*, holotype; G, *tau*, Palín, Guatemala; H,K, *tau*, Morelos, Mexico; A, syntergosternite 7, right lateral view; B-C, aculeus (ventral); D-I, aculeus tip (ventral); J,K, spermatheca; L, egg.

as follows: subapical band not connected posteriorly to discal band; flgm 1 ratio 5.0; and aculeus tip narrower basally.

Additional description. *Head* (Fig. 2A): Frons with irregular pale brown marks sometimes forming bands or irregular stripes between frontal and/or orbital setae. 2-3 frontal setae, posterior seta small if present. orb ratio 2.0. Facial ratio 0.67. Gena yellow. *Thorax*: White band on transverse suture connected to anepisternal white area, connected to or narrowly separated from lateral white stripe. dc slightly closer to pal than to psut spal. *Wing* (Lima 1947, Fig. 3): r-m ratio 0.67. Cell c entirely brown. Subapical band not connected to discal band, ended just posterior to vein M on dm-

cu, sometimes pale brown anterior to vein R_{2+3} or R_{4+5} . Apical band faint and narrow in cells r_1 and r_{2+3} ; dark in cell r_{4+5} . *Abdomen* (Lima 1947, Fig. 1-2): with broad white apical band on Tg1+2 and medial stripe on Tg3-5 (3-6 in f) forming large T-shaped mark. *Male terminalia* not examined. *Female terminalia* (data from Lima 1947): Syntergosternite 7 brown. Aculeus tip (Fig. 5B) slender basally, serrate part approximately as long as wide, broader than aculeus width at apices of 8th sternites.

Host. The type series was reared from fruits of "herva de passarinho (*Loranthus* sp.)" (Lima 1947).

Specimens examined. 3m paratypes (UFRRJ) [with only following labels: "Paratipo", "Cryptodacus

silvai n. sp. 1947 Costa Lima det., "Def. San. Veg. 7642", and "Larvas en frutos de herva de passarinho"] [examined at laboratory of R.A. Zucchi (USP, Piracicaba)].

***Cryptodacus tau* (Foote), n. comb.**
(Fig. 1F, 2E, 3E-F, 4C-D, 5G-H,K)

Lezca tau Foote 1978:27 (Holotype f (USNM), MEXICO: Morelos: Cuernavaca, 3.III.57, O. Hernandez); Foote 1980:34.

Diagnosis. Discal band extended across most or all of dm-cu; r-m ratio > 0.80 ; subapical band ended apical to dm-cu; and abdomen (Foote 1978, Fig. 2) with Tg1+2 yellow (except apical white band), Tg3 mostly brown but white basally, and sublateral white areas extended across Tg4 (present only on Tg5-6 and apex of Tg4 in *lopezi*, absent in other species), leaving 2 narrowly separated medial brown stripes on Tg4-5 (4-6 in female).

Additional description. *Head*: 3 frontal setae. orb ratio 2.0. Gena with brown spot touching eye. Face with 1 medial brown spot on each side, medial height 0.67 ventral width. flgm 1 often yellow basally; flgm 1 ratio 4.5-5.0. *Thorax* (Fig. 2E): Mostly dark orange or brown. White band on transverse suture connected to anepisternal white area and lateral white stripe. dc slightly posterior to psut spal to almost midway between it and pal. *Wing* (Fig. 1F): r-m ratio 0.86-0.90. Cell c brown basally, pale brown or hyaline apically. Subapical band not connected to discal band, ended posteriorly apical to dm-cu at vein M or usually in middle of cell r_{4+5} ; faint anterior to vein R_{4+5} or entirely pale brown. Apical band faint and narrow or absent in cells r_1 and r_{2+3} ; dark and broad in cell r_{4+5} . *Male terminalia*: Distiphallus (Fig. 4C-D) elongate and slender; in ventral view, apex of internal tube bilobed. *Female terminalia*: Syntergosternite 7 orange. Aculeus 0.71-0.79 mm long; tip (Fig. 5G-H) slender basally, serrate part 1.14-1.33 times as long as wide, 0.075-0.080 mm long, 0.060-0.065 mm wide, broader than aculeus width at apices of 8th sternites.

Remarks. In most Guatemalan specimens, the dark scutal areas are entirely brown rather than largely dark orange as in the Mexican specimens (Fig. 2E), but I found no consistent differences in the white part of the pattern nor any other characters.

Specimens examined. Holotype (see synonymy) and 1m1? (USNM) with same data. GUATEMALA: Escuintla: Palín, Granja El Coronel, 1992, J. Lopez, 2f (USNM); Palín area, 1992, J. Lopez, 2m2f (USNM, UVG). Sacatepequez: Jocotenango, Finca Portal, 1989, J. Lopez, 1f (USNM). MEXICO: MORELOS: Cuernavaca, VI-VIII. 1942, D. Starr, 1m1f (USNM); "probably Morelos", 1957, 1m1f (USNM). SINALOA: Escuinapa, Tinajitos, 14.III.1988, C. Campos, 2m2f (IEXV). SONORA: Huatabampo, La Sabila, 7.III.1989, R. Hernandez P., 1f (USNM).

***Cryptodacus tigreroi*, n. sp.**
(Fig. 1G, 5C,I)

Diagnosis. flgm 1 ratio 6.8 (< 5.5 in other species). Differs from all *Cryptodacus* except *lopezi* by the stout aculeus tip (Fig. 5C,I), from all species except *obliquus* and *lopezi* in having a complete subapical band that covers all of dm-cu, and from all species except *silvai* in facial pattern (1 broad ventral and 2 dorsal brown spots) and abdominal pattern (brown except for white T-shaped mark formed by apical band on Tg1+2 and complete medial stripe on Tg3-6).

Additional description. *Head*: 2 frontal setae. orb ratio 2.5. Face with lateral margin narrowly brown. Facial ratio 0.54. Gena with ventral brown spot not extended to eye. *Thorax*: Mostly brown except posterior margin of scutum orange (extent of orange and brown areas probably variable as in *tau*). Postpronotal lobe with only posterior 2/3 white. White band on transverse suture connected to anepisternal white area, narrowly separated from lateral white stripe. dc slightly closer to pal than to psut spal. *Wing* (Fig. 1G): r-m ratio 0.74. Veins R_{2+3} , R_{4+5} and M with spur veins in subapical band, R_{4+5} also with one in discal band. Cell c entirely brown. Subapical band connected to discal band, pale brown anterior to vein R_{2+3} . Apical band narrow in cells r_1 and r_{2+3} ; in cell r_{4+5} slightly broader and darker. *Female terminalia*: Syntergosternite 7 brown. Aculeus 0.70 mm long; tip (Fig. 5C,I) relatively stout, especially basally, serrate part 0.83 times as long as wide, 0.05 mm long, 0.06 mm wide, narrower than aculeus width at apices of 8th sternites.

Etymology. Named for Juan Oswaldo Tigrero (CEEA).

Holotype. f (at USNM, for eventual deposit in Ecuador), ECUADOR: Pichincha: Valle de Tumbaco, 2348 m, 11.I.1992, "No. TH-02".

Genus *Haywardina* Aczél

Haywardina Aczél 1951c:258 (Type species: *Tomoplagia cuculi* Hendel, orig. desig.); Foote 1967:25 (cat.), 1980:31 (review).

Cryptoplagia Aczél 1951c:265 (Type species: *C. cuculiformis* Aczél, orig. desig.); Foote 1967:21 (cat.), 1980:24 (review). **n. syn.**

Description. *Head:* Yellow except brown between ocelli. 3 frontal setae. 1-2 reclinate orbital setae, orb ratio < 1. Ocellar seta strong. Face with distinct carina. Antenna short to medium length, never extended to ventral margin of face; flgm 1 tapered, with small dorsoapical point; flgm 1 ratio 1.7-3.2. *Thorax* (Fig. 7): Usually mostly yellow with brown marks on scutum and often on scutellum, anepisternum, katapisternum, katatergite, or mediotergite, or mostly brown with orange anepisternum (*obscura*). Scutal brown spots on mesal side of lateral white stripe not connected posteriorly (not forming U-shaped mark). Also with following white areas: medial scutal stripe or spot; narrow lateral postsutural scutal stripe, usually not extended along transverse suture (except in *cuculiformis*); postpronotal lobe (except in *obscura*); apex of scutellum; and dorsal anepisternal stripe. Notopleuron and katapisternum without white markings. Thorax usually entirely microtrichose (bare in *cuculiformis*). dc slightly to distinctly posterior to psut spal but closer to it than to pal. *Wing* (Fig. 6A-B): r-m near middle of cell dm, ratio < 0.60, except in *cuculi*. Subbasal, discal, and apical crossbands present. Discal band with anterior end basally curved, usually connected to subbasal band in cells c, r₁, and/or r₂₊₃; not extended over dm-cu, except in *cuculi*. Subapical band present (except in *cuculi*), connected to or separate from discal band at posterior wing margin. Apical band connected to subapical band at anterior wing margin or isolated. Posterior apical band absent. Accessory costal band present or absent. *Abdomen:* Tergites mostly yellow with brown spots, usually at least Tg5 with basal submedial pair. *Male terminalia:* Outer surstylus (Fig. 8A-E) elongate, with distinct mesal lobe near prenisetae. Inner surstylus elongate. *Female terminalia:* Aculeus tip slender, acute, en-

tire or with small subapical notches (Fig. 8H). 2 spermathecae, small, ovoid or spherical, with short base (Fig. 8I).

Remarks. See Relationships section for justification for the synonymy of *Cryptoplagia* with *Haywardina*.

Key to the species of *Haywardina*

1. Postpronotal lobe and scutum, except for white postsutural stripes, brown (Fig. 7B). Pleuron brown except for yellow anepisternum. Scutellum brown except apical 2/5 white. (Argentina) *obscura* Norrbom, n. sp.
- Postpronotal lobe white. Scutum, except for postsutural brown spots and white stripes, yellow. Pleuron mostly yellow, at most with brown spots on anepisternum, katapisternum and katatergite. Scutellum yellow at least basomedially 2
2. Scutellum entirely yellow. Discal band extended across r-m and dm-cu. Subapical band absent. Posterior orbital seta absent. (Argentina) *cuculi* (Hendel)
- Scutellum with large basal brown spots on sides (Fig. 7A). Discal band extended only across r-m (Fig. 6A-B). Subapical band present, extended over dm-cu. Posterior orbital seta present 3
3. Anepisternum, katapisternum, katatergite and mediotergite each with large brown spot. Accessory costal band absent. Subapical band with anterior end strongly basally curved and separate from apical band. Aculeus tip without subapical notches. (Peru) *cuculiformis* (Aczél)
- Anepisternum, katapisternum, and katatergite yellow except for white areas. Accessory costal band present (Fig. 6A). Subapical band straight anteriorly and narrowly connected to apical band. Aculeus tip with small subapical notches (Fig. 8H). (Peru, Ecuador) *bimaculata* Norrbom, n. sp.

Haywardina bimaculata, n. sp.
(Fig. 6A, 7A, 8A-B, F, H-I)

Cryptoplagia sp. Foote 1980:24.

Diagnosis. Differs from *obscura* by the mostly yellow thorax, and from *cuculi* by the large brown

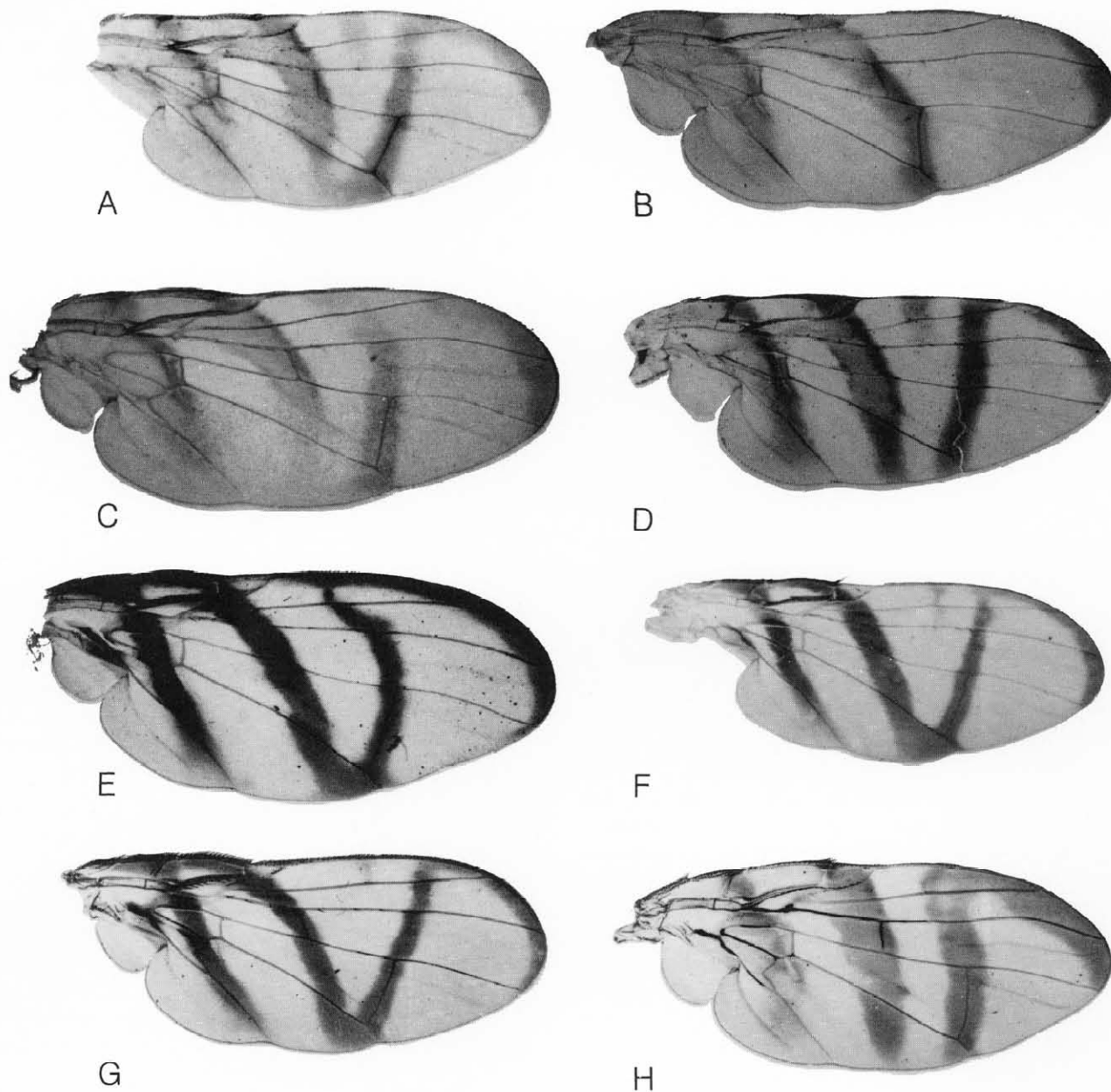


Figure 6. Wings, *Haywardina* and *Rhagoletotrypeta*: A, *H. bimaculata*, paratype, Cochabamba, Peru; B, *H. obscura*, holotype; C, *R. argentinensis*, Argentina; D, *R. intermedia*, holotype; E, *R. morgantei*, holotype; F, *R. parallela*, holotype.

spots on the scutellum, and by r-m and the discal band not apically displaced (see diagnosis of *cuculi*). Differs from both *cuculi* and *cuculiformis* in lacking brown spots on the anepisternum, katapisternum, katatergite and mediotergite, having an accessory costal band, and by the small subapical notches on the aculeus tip.

Additional description. *Head*: 2 orbital setae. flgm 1 ratio 2.3-2.4. *Thorax* (Fig. 7A): Scutal white stripes narrow; lateral stripe complete but not extended mesally along transverse suture. Scutum with broad brown spot on mesal side of lateral white stripe. Scutellum with large brown spot covering basal 3/4 of side and extended onto disc; yellow basomedially, gradually becoming white on apical 1/4-1/3. *Wing* (Fig. 6A): r-m ratio 0.54-0.56. Discal

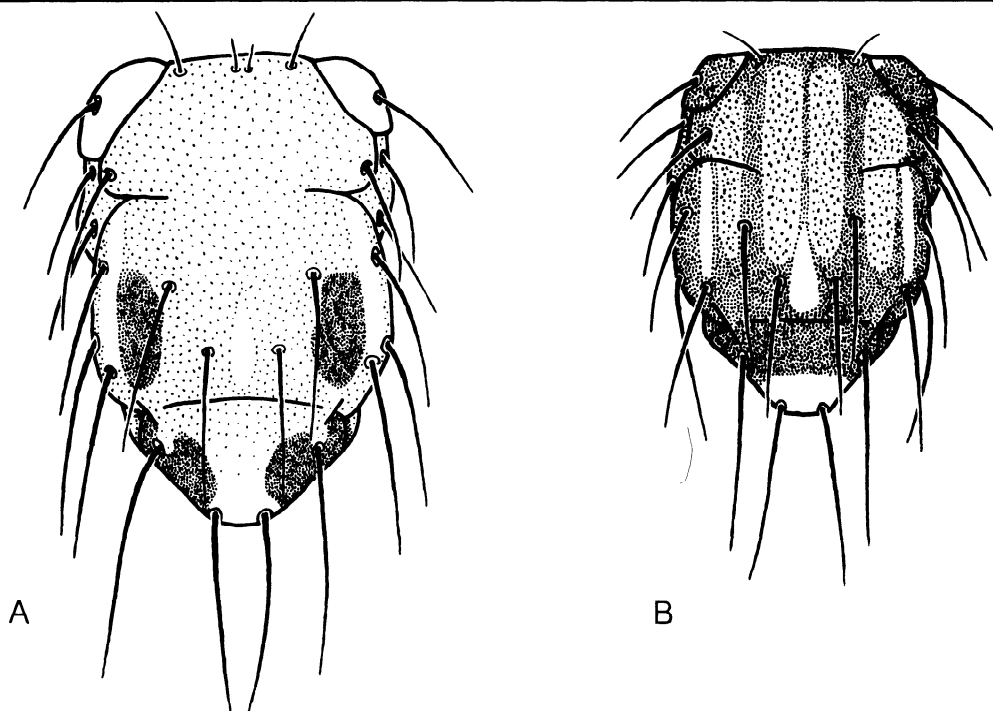


Figure 7. Thoraxes (dorsal), *Haywardina*: A, *bimaculata*, paratype, Cochabamba, Peru; B, *obscura*, holotype. Light stippling indicates yellow areas in A, areas of dense microtrichia in B.

and subapical bands connected in cell cu_1 . Apical band narrowly connected to subapical band in cell r_1 . *Abdomen*: Tg4-5 and sometimes Tg3 with pair of submedial brown spots; Tg4-5 (and Tg6 in female) also with lateral brown spot. *Male terminalia*: Distiphallus (Fig. 8F) relatively slender; apical membranous part broad in ventral view. *Female terminalia*: Syntergosternite 7 orange. Aculeus 1.01-1.10 mm long; tip (Fig. 8H) 0.19-0.21 mm long, with small subapical notches.

Etymology. The name refers to the two large spots on the scutellum.

Holotype. m (USNM), PERU: Cajamarca: Cochabamba, 1650 m, 18.II.1968, P.G. Casanova. **Paratypes.** Same data as holotype, 2f (USNM). ECUADOR: Loja: Parroquia Nambacola, 1238 m, II-VII.1991, "No. TH-01", 2f (CEEA, USNM).

Haywardina cuculi (Hendel) (Fig. 8C,G)

Tomoplagia cuculi Hendel 1914b:35 (Syntypes 1m1f (MNM, NMW), ARGENTINA: Tucumán, XI; Aczél 1950:242 (cat.).

Haywardina cuculi: Aczél 1951c:259 (redescr.); Foote 1967:25 (cat.); Hardy 1968:118 (types); Foote 1980:31.

Diagnosis. Posterior orbital seta and subapical band absent; r-m ratio > 0.80 ; and both r-m and dm-cu covered by discal band. Species of *Cryptodacus*, especially *tau*, resemble *cuculi* in the apical displacement of r-m and the discal band, but have a posterior orbital seta, at least a small subapical band, a brown border along vein Cu_1 (sometimes absent in *tau*), a serrate aculeus tip, and no dorsoapical point on flgm 1.

In thoracic markings, *cuculi* resembles *cuculiformis* in having a brown spot on the anepisternum, katepisternum, and katatergite, but it has no brown marks on the scutellum and only one pair on the scutum (mesal to the lateral white stripe). The medial brown spot on the mediotergite is sometimes absent. The distiphallus (Fig. 8G) is relatively stout, with a stout internal tube with a sharp 90° bend. The membranous apical part tapers to a slender lobe in both ventral and lateral views.

The third instar larva possesses small, sclerotized, preoral teeth near the stomal organ as do other species of *Carpomyia*.

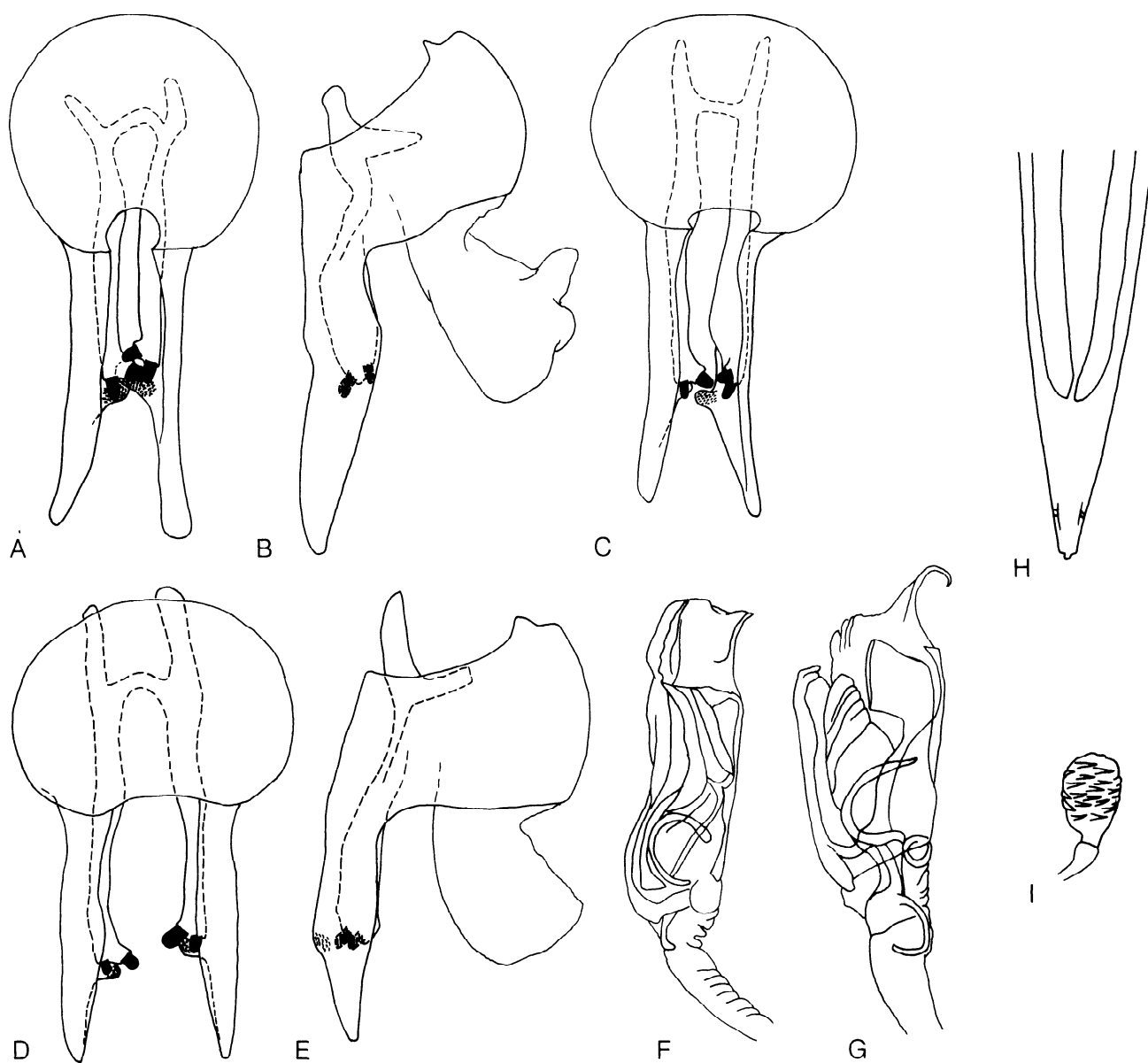


Figure 8. Male and female terminalia, *Haywardina*: A-B,F, *bimaculata*, holotype; C,G *cuculi*, Cafayate, Argentina; D-E, *obscura*, holotype; H,I, *bimaculata*, paratype, Cochabamba, Peru; A,C-D, male genitalia (posterodorsal, proctiger omitted); B,E, same (lateral); F-G, distiphallus (ventral); H, aculeus tip, (ventral); I, spermatheca.

Host. *Solanum trichoneuron* Lillo is the only confirmed host. Numerous adults, some in copulation, were collected on *S. argentinum* Bitter & Lillo, which also may be a host (Aczél 1951c). The rearing records from orange and guava (Hayward 1942) seem doubtful. "Piquillin", on the labels of several examined specimens, is a name in Argentina for species of *Condalia* (Rhamnaceae) (Bodenbender 1940), which I doubt are hosts.

Specimens examined. ARGENTINA: Las Heras, "s/ fruto piquillin", 12.XI.1942, 3m2f (MACN, USNM). Salta: 1200 m, II.1905, J. Steinbach, 1m (ZMHU); Cafayate, 1165 m, II.1951, K. Haywood, 1m1f (USNM) 1f (DEI); Cafayate, 4.II.1960, Ajmat-Bennasar, 1m1f (IML); Yacochuya (Cafayate), 1950 m, 1-15.II.1969, Willink, Terán & Stange, 1m (IML). Tucumán: Burruyacu, V. Padre Monti, 17.I-7.II.1948, R. Golbach, 1m (DEI); Burruyacu, Taruca

Pampa, Finca San Augustine, reared ex. fruit of *Solanum trichoneuron* Lillo (voucher in USNM herbarium) collected 18.V.1991, A.L. Norrbom, 10m9f 4 larvae (USNM, IML); Tafi del Valle, 12.XII.1947, R. Golbach, 1f (USNM); Tucumán, 21.I.1928, H.E. Box, 1f (MACN).

Haywardina cuculiformis (Aczél), n. comb.

Cryptoplagia cuculiformis Aczél 1951c:265 (Holotype m (USNM), PERU: Piura, 5.V.1937, J.E. Wille); Foote 1967:21 (cat.), 1980:24.

Diagnosis. Subapical band anterobasally curved; scutum without microtrichia; scutal lateral white stripe moderately broad and extended along transverse suture; and apical part of outer surstylus relatively short. In thoracic markings resembles *bimaculata* and *cuculi*, but differs from the former as indicated in the key and the diagnosis of *bimaculata*, from the latter in having a pair of large brown spots on the scutellum, and from both in having 3 pairs of brown spots or stripes on the scutum bordering the medial and lateral white stripes. The distiphallus is more slender than in *cuculi*, but has a similar slender, membranous, apical lobe.

Host. The types were reared from fruits of an undetermined plant, which Aczél (1951c) suggested was a *Solanum*.

Specimens examined. Holotype (see synonymy). PERU: Piura, 30.III.1937, J.E. Wille, 1f paratype (USNM).

Haywardina obscura, n. sp.
(Fig. 6B, 7B, 8D-E)

Diagnosis. Thorax brown except white areas and most of propleuron and anepisternum yellow; postpronotal lobe brown except extreme mesal and lateral corners. *Rhagoletotrypeta pastranai* and *R. xanthogastra* resemble *obscura* in wing pattern and body color, but differ as follows: most of anepisternum brown; lateral scutal stripe extended mesally along transverse suture; inner surstylus short; and flgm 1 rounded apically.

Additional description. *Head:* 2 orbital setae. flgm 1 ratio 1.7. *Thorax* (Fig. 7B): Scutal white

stripes narrow; lateral stripe complete but not extended mesally along transverse suture. Scutellum with apical 2/5 white. dc slightly posterior to psut spal. *Wing* (Fig. 6B): r-m ratio 0.52. Discal and subapical bands not connected in cell cu₁. Apical band very narrowly connected to subapical band in cell r₁. *Abdomen:* Tg1+2 with transverse sublateral brown spot. Tg3 with small submedial, Tg4 with small lateral, Tg5 with small submedial and large lateral brown spots. *Male terminalia:* Distiphallus relatively slender; apical membranous part broad in ventral view.

Etymology. The name refers to the mostly dark thorax.

Holotype. m (MCZ), ARGENTINA: Cordoba, W.M. Davis.

Genus *Rhagoletotrypeta* Aczél

Rhagoletotrypeta Aczél 1951a:313 (Type species *R. xanthogastra* Aczél, orig. desig.); Aczél 1954:138 (key, n. spp.); Foote 1966:803 (revision); Foote 1967:41 (cat.); Foote 1980:46 (review); Steyskal 1981: 707 (key); Foote et al. 1993:365 (U.S.A. spp.).

Serpentinographa Aczél 1951a:308 (Type species *S. argentinensis* Aczél, orig. desig.); Foote 1966:803 (syn.); Foote 1967:41 (cat.).

Chaetorhagoletis Blanchard: Aczél 1954:138 (*nomen nudum*); Foote 1967:41 (cat.).

Description. *Head:* Yellow except brown between ocelli, and often large posterior areas of occiput and postgena brown. 3 (very rarely 2 or 4) frontal setae. 2 reclinate orbital setae, orb ratio < 1. Ocellar seta strong. Face with distinct carina. Antenna short to medium length, never extended to ventral margin of face; flgm 1 tapered, rounded apically or rarely with weak dorsoapical point; flgm 1 ratio 1.7-3.5. *Thorax:* Mostly brown (sometimes partly dark orange), with following white areas: medial scutal stripe or spot; postpronotal lobe (except sometimes in *xanthogastra*); apex of scutellum; and dorsal anepisternal stripe, sometimes extended along posterior margin. Scutum sometimes (*xanthogastra* group) with white spot on transverse suture or postsutural lateral stripe or spot. Notopleuron and katapisternum without white markings (except in *parallela*). dc usually even with or slightly anterior or posterior to psut spal (more posterior in some

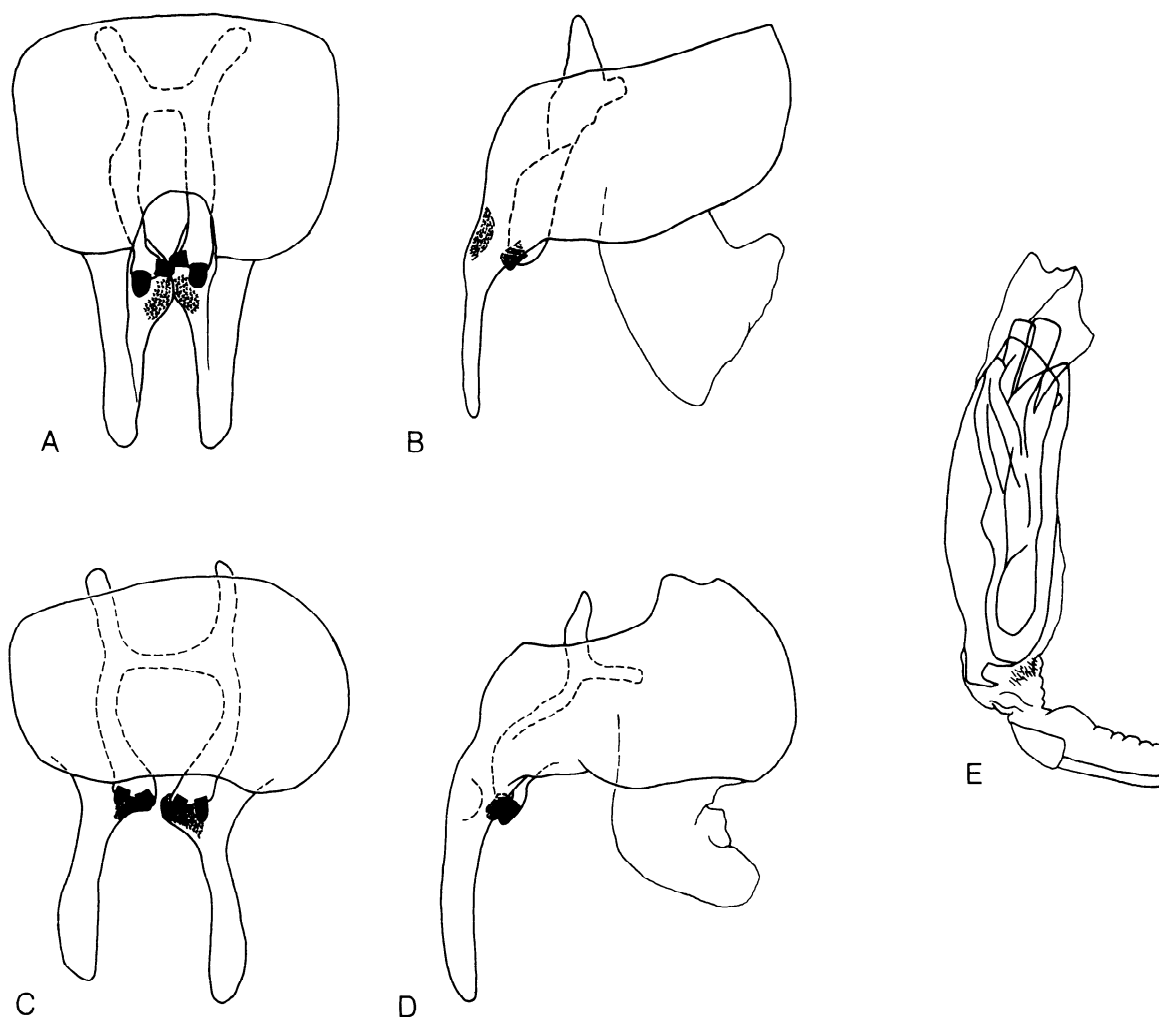


Figure 9. Male terminalia, *Rhagoletotrypeta*: A-B,E, *morgantei*, holotype; C-D, *pastranai*, Coçador, Brazil; A,C, posterodorsal (proctiger omitted); B,D, lateral; E, distiphallus.

annulata, but closer to *psut* *spal* than to *pa*). **Wing** (Fig. 6C-F): *r-m* near middle of cell *dm*, ratio < 0.60. Subbasal, discal, subapical, and anterior apical crossbands present. Discal band with anterior end basally curved, usually connected to subbasal band in cells *c*, *r*₁, and/or *r*₂₊₃. Subapical band usually connected to discal band at posterior wing margin, and connected to apical band at anterior margin. Apical band complete. Posterior apical band absent. Accessory costal band usually present (except in *argentinensis* and *parallela*). **Abdomen**: Tergites mostly brown or mostly yellow with brown spots, usually with apical white bands. **Male terminalia**: Outer surstylus (Fig. 9A-B,C-D) elongate, with mesal lobe near prensisetæ; mesal lobe short and sharply delimited (*xanthogastra* group; Fig. 9C) or

broad and gradually arising from apical part of surstylus (*annulata* group; Fig. 9A). Inner surstylus short, in lateral view (Fig. 9B,D), distance from margin of epandrium to apex of inner surstylus < or = width of outer surstylus. Distiphallus (Fig. 9E) slender, cylindrical. **Female terminalia**: Aculeus tip often (*annulata* group; Fig. 10A-B,D-E) > 0.40 times aculeus length, deeply trilobed (Fig. 10G), flattened in sagittal plane (Fig. 10A,F), or simple (Fig. 10B,D-E,H-I). 2 (*annulata* group) or 3 (*xanthogastra* group) spermathecae (Fig. 10J-K), spherical with short base.

Remarks. *Rhagoletotrypeta* includes nine species, three of which are described here. The six species for which hosts are known breed in fruit of *Celtis*

species (Ulmaceae). The relationship of the *xanthogastra* group with the *annulata* group needs further corroboration (see Relationships section), but seems likely considering their hosts. The name *Serpentinographa* is available for the *annulata* group if these taxa are recognized as separate genera.

Key to the species of *Rhagoletotrypeta*

1. Scutum with white mark on transverse suture, usually extended to intra-alar seta as postsutural lateral stripe (similar to Fig. 2C,E). Aculeus tip length $< 0.4 \times$ aculeus length (Fig. 10C), in ventral view, apex deeply trilobed (Fig. 10G). 3 spermathecae. (Argentina, southern Brazil, Paraguay, Uruguay) 2
- Scutum entirely brown along transverse suture and without lateral postsutural white stripe (similar to Fig. 2D). Aculeus tip length $> 0.4 \times$ aculeus length (Fig. 10A-B,D-E), in ventral view, apex not trilobed. 2 spermathecae 4
2. Accessory costal band absent (Fig. 6F). Discal and subapical bands parallel. White area on transverse suture extended across notopleuron. Scutellar basal seta within white area *parallela* Norrbom, n. sp.
- Accessory costal band at least faintly present. Discal and subapical bands divergent anteriorly. Notopleuron entirely brown. Scutellar basal seta within brown area 3
3. Scutum with complete lateral white stripe from transverse suture to intra-alar seta (similar to Fig. 2E), and anteriorly with pair of submedial stripes of dense microtrichia. Postpronotal lobe entirely white *pastranai* Aczél
- Scutal lateral white mark comma-shaped, not extended posteriorly beyond level of psut. spal seta (see Aczél 1951a, Fig. 2B). Scutum without microtrichia. Postpronotal lobe entirely brown or at least with brown margins *xanthogastra* Aczél
4. Wing bands narrow (Fig. 6D-E); width of discal band at r-m $< 1.2 \times$ length of r-m; width of apical band in cell r_{4+5} usually $< 0.7 \times$ length of r-m. Hyaline area between subapical and apical bands often extended slightly into cell r_1 . Subbasal band usually extended to apex of vein Cu_2+A_1 . Postgena usually brown posteriorly. Aculeus tip simple or flattened in sagittal plane and trilobed in lateral view 5
- Wing bands broad; width of discal band at r-m $> 1.5 \times$ length of r-m; width of apical band in cell

r_{4+5} usually $>$ length of r-m. Hyaline area between subapical and apical bands not extended into cell r_1 . Subbasal band not extended to apex of vein Cu_2+A_1 . Postgena entirely yellow. Aculeus tip not flattened in sagittal plane, simple in lateral view (Fig. 10H,I) 8

5. Only Tg1+2 and Tg5 with apical white band, Tg3-4 entirely brown. (southern Brazil) *morgantei* Norrbom, n. sp.
- All tergites with apical white bands 6
6. Subapical band with anterior end strongly basally curved, reaching costa basal to level of posterior end of dm-cu (Fig. 6C). Accessory costal band absent. Aculeus tip flattened in sagittal plane, trilobed in lateral view (similar to Fig. 10F). (Argentina) *argentinensis* (Aczél)
- Subapical band with anterior end at most slightly basally curved, reaching costa apical to level of posterior end of dm-cu. Accessory costal band at least faintly present. Aculeus tip variable. (Mexico to Costa Rica) 7
7. Aculeus tip flattened in sagittal plane, trilobed in lateral view (Fig. 10F). (Mexico, Costa Rica) .. *annulata* Aczél
- Aculeus tip slender but not flattened in sagittal plane (Fig. 10B), simple in lateral view (similar to Fig. 10I). (Mexico) *intermedia* Norrbom, n. sp.
8. Apical band moderately broad at base, hyaline area between it and subapical band extended at least halfway across cell r_{2+3} . Scutum with submedial stripes of dense microtrichia absent or small and widely separated from lateral microtrichial stripe. Aculeus tip straight in lateral view (Fig. 10I). (New Mexico, Texas) ... *uniformis* Steyskal
- Apical band very broad at base, hyaline area between it and subapical band not extended more than halfway across cell r_{2+3} . Scutum with submedial stripes of dense microtrichia broad and narrowly separated from lateral microtrichial stripe. Aculeus tip with sharp subapical dorsal bend in lateral view (Fig. 10H). (northeastern and midwestern U.S.A.) *rohweri* Foote

Rhagoletotrypeta annulata Aczél (Fig. 10A,F,J)

Rhagoletotrypeta annulata Aczél 1954:142 (Holotype m (USNM), MEXICO: San Luis Potosí: Tamazunchale,

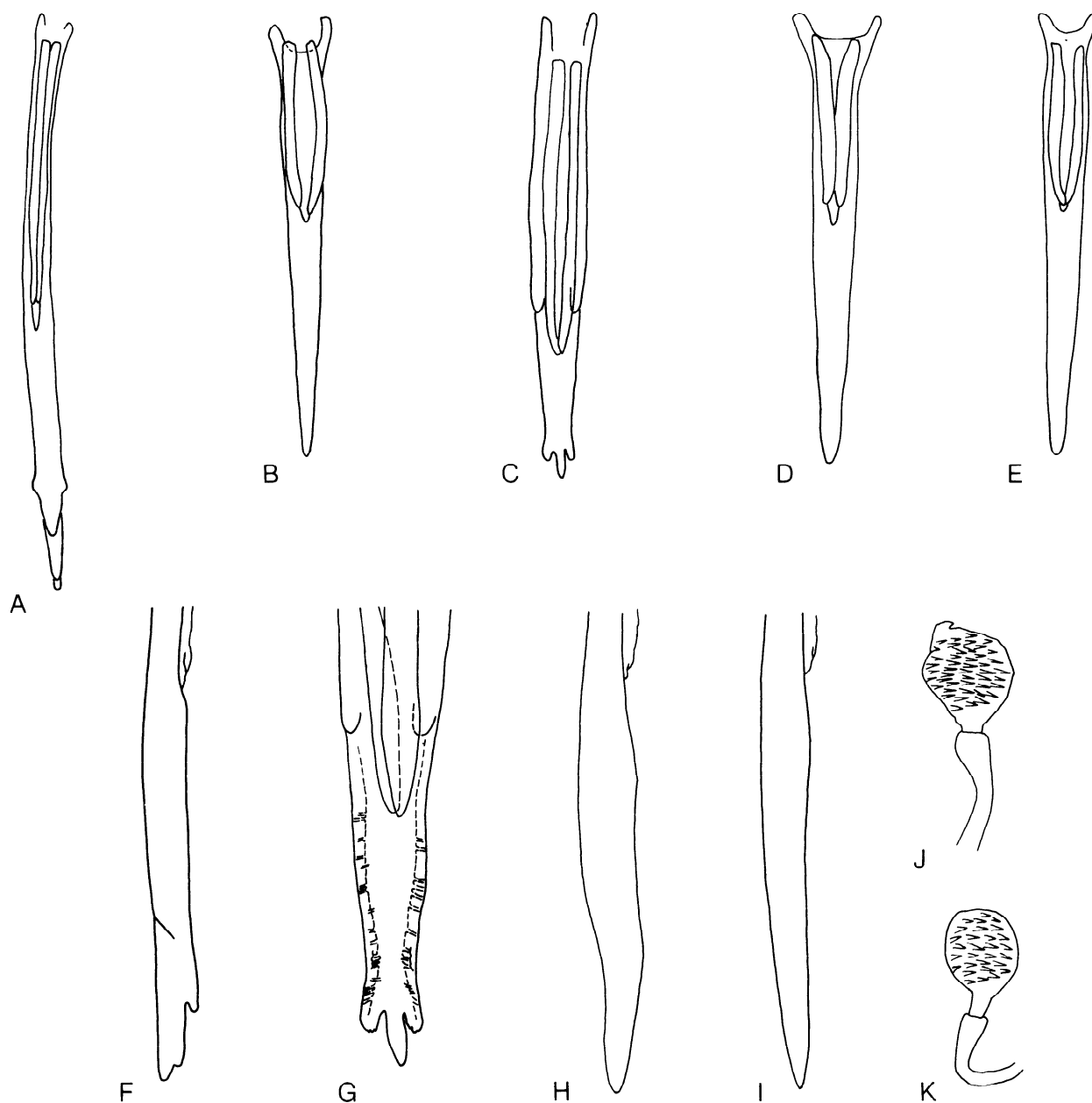


Figure 10. Female terminalia, *Rhagoletotrypeta*: A,F,J, *annulata*, Tamazunchale, Mexico; B, *intermedia*, holotype; C,G,K, *parallela*, paratype; D,H, *rohweri*, Trenton, New Jersey, U.S.A.; E,I, *uniformis*, San Antonio, Texas, U.S.A.; A-E, aculeus (ventral); F,H-I, aculeus tip (lateral); G, aculeus tip (ventral); J-K, spermatheca.

reared ex. fruit *Celtis* sp., 31.X.-19.XI.1939, J.G. Shaw); Foote 1966:804 (in key), 806 (in part, misid. of *uniformis*); Foote 1967:41 (cat.); Steyskal 1981:709 (in key, diag.).

Diagnosis. Except for *argentinensis*, which differs by its very strongly curved subapical band, *annulata* differs from all other *Rhagoletotrypeta* for which

the female is known by the shape of its aculeus tip, which is flattened in the sagittal plane and trilobed in lateral view (Fig. 10A,F). *R. morgantei*, which is known only from the male and also could have this type of aculeus, differs from *annulata* in lacking apical white bands on Tg3-4.

Remarks. The male from Costa Rica has a shorter medial scutal stripe and more extensive brown markings on the back of the head, but is tentatively considered conspecific with the Mexican specimens. Its wing pattern differs from the holotype's in having the subapical band straight anteriorly rather than basally curved, and the hyaline area between the discal and apical bands is extended to vein Cu_1 , but both of these characters vary within the large Tamazunchale series as does the location of the dorsocentral seta (slightly posterior to psut spal to almost midway between it and pal).

Host. *Celtis pallida* Torr., in northern Mexico called granjeno huasteco.

Specimens examined. Holotype (see synonymy) and 1m paratype (USNM) with same data. COSTA RICA: Puntarenas: Res. Biol. Carara, Estac. Quebrada Bonita, 50 m, X.1989, R. Zuniga, 1m (INBio). MEXICO: San Luis Potosí: Tamazunchale, Campo El Sol, reared ex. fruit of granjeno huasteco, emerged X-XI.1939, 5m20f (USNM, IEXV). Tamaulipas: La Libertad, 25.IX.1987, J. Leyva, 1f (USNM); Cañon de Rosario, Santa Engracia, reared from fruit of granjeno huasteco, emerged 26.IX.1939, 1f (USNM).

Rhagoletotrypeta argentinensis (Aczél)
(Fig. 6C)

Serpentinographa argentinensis Aczél 1951a:308 (Holotype f (IML), ARGENTINA).

Rhagoletotrypeta argentinensis: Foote 1966:803 (in key); Foote 1967:41 (cat.); Steyskal 1981:708 (in key).

Diagnosis. Anterior part of subapical band strongly basally curved (Fig. 6C). The aculeus tip (Aczél 1951a, Fig. 1E-G) resembles *annulata* (Fig. 10A,F).

Specimens examined. ARGENTINA: without other data, 1m (IML).

Rhagoletotrypeta intermedia, n. sp.
(Fig. 6D, 10B)

Diagnosis. In wing pattern, closely resembles *annulata*, but differs in aculeus tip shape (not lobed nor flattened in sagittal plane). In aculeus tip shape

resembles *uniformis*, but differs in wing band width (see couplet 4 of key).

Additional description. *Head*: flgm 1 ratio 3.4-3.7. *Thorax*: Entirely microtrichose. Scutal submedial and lateral stripes of denser microtrichia separated by about width of submedial stripe. dc slightly posterior to psut spal. *Wing* (Fig. 6D): r-m ratio 0.47. Discal band about as broad as length of r-m. Apical band in cell r_{4+5} 1/2-2/3 as broad as length of r-m. Subbasal band extended almost to apex of vein A_1+Cu_2 . Accessory costal band faint. *Female terminalia*: Aculeus (Fig. 10B) 1.04 mm long; tip 0.54 mm long, acute and slender but not flattened in sagittal plane, without lobes; in lateral view almost straight (similar to Fig. 10I). *Male terminalia*: Similar to *morgantei*.

Etymology. The name refers to this species' resemblance to both *annulata* and *uniformis*.

Holotype. f (USNM), MEXICO: Morelos: Cañon de lobos, 16.XI.1960, C. Benschoter. **Paratype.** Same locality, 28.VII.1978, J. Butze, m (IEXV).

Rhagoletotrypeta morgantei, n. sp.
(Fig. 6E, 9A-B,E)

Diagnosis. Very similar to *annulata* and *intermedia*, but differs in having Tg3-4 entirely brown.

Additional description. *Head*: flgm 1 moderate brown (perhaps discolored), with minute dorsoapical point; flgm 1 ratio 3.30. *Thorax*: Entirely microtrichose. Scutal submedial and lateral stripes of denser microtrichia separated by > width of submedial stripe. dc aligned with psut spal. *Wing* (Fig. 6E): r-m ratio 0.50. Bands narrower than length of r-m. Subbasal band extended to apex of vein A_1+Cu_2 . Accessory costal band faint. *Abdomen*: Tergites brown except posterior margins of Tg1+2 and Tg5. *Male terminalia*: Distiphallus (Fig. 9E) in lateral view relatively slender, cylindrical.

Etymology. Named for Joao Morgante, whose research and training of students has greatly advanced the study of Neotropical fruit flies.

Holotype. m (USP), BRAZIL: Sao Paulo: Rib. Preto, Guatapar, I.1945, Barretto.

Rhagoletotrypeta parallela, n. sp.
(Fig. 6F, 10C,G,K)

Diagnosis. Posterior 1/3 of notopleuron white, and katepisternum with dorsal white spot; discal and subapical bands parallel. These two wing bands are almost parallel in *argentinensis*, but both are slender (width no greater than length of r-m) and strongly curved or oblique (Fig. 6C), whereas they are broader than the length of r-m and almost perpendicular to the anterior wing margin in *parallela* (Fig. 6F).

Additional description. *Head*: flgm 1 ratio 1.75-2.00. *Thorax*: White band on transverse suture extended across notopleuron to anepisternal white area and connected to postpronotal white area along margin of scutum. dc aligned with psut spal. *Wing* (Fig. 6F): r-m ratio 0.50-0.53. Bands yellow brown. Subbasal band extended to basal 1/3 of vein A_1+Cu_2 . Discal and subapical bands separate or narrowly fused at posterior margin. *Abdomen*: Tergites yellow or orange with 1-2 pairs of brown spots on Tg4-6. *Female terminalia*: Aculeus (Fig. 10C) 1.02 mm long; tip (Fig. 10G) 0.28 mm long.

Host. The types were reared from fruit of "tala", a common name in Argentina for several species of *Celtis*.

Etymology. The name refers to the parallel discal and subapical bands.

Holotype. f (MACN), ARGENTINA: Salta: Cuel. Moldes, de frutos de tala (*Celtis* sp.), 1.1953, M.A. Rosillo. **Paratypes.** Same data as holotype, 2f (MACN, USNM).

Rhagoletotrypeta pastranai Aczél
(Fig. 9C-D)

Rhagoletotrypeta pastranai Aczél 1954:146 (Holotype m (MACN), ARGENTINA: Córdoba: Sierra Zala, San Javier, J.A. Pastrana); Foote 1966:803 (in key); Foote 1967:41 (cat.); Steyskal 1981:708 (in key).

Diagnosis. Differs from all *Rhagoletotrypeta* except *parallela* by the complete lateral scutal white stripe (extended from transverse suture to intralar seta). Differs from all *Rhagoletotrypeta* except *xanthogastra* by the small size of the apical scutellar

lar white area. The basal seta is within the brown area.

Remarks. The thoracic and abdominal color patterns vary considerably in the series from Coçador, Brazil. Specimens on which the dark areas are mostly orange are teneral or are paler colored and probably immature, so this appears to be an age related character. The abdomens of the type series are mostly orange, but these specimens also seem immature (their eyes are wrinkled). The abdomen is mostly brown in the Cuel. Moldes, Argentina female, so this is not geographic variation. The specimens of *xanthogastra* and *parallela* I examined also may be immature, and abdominal color also may vary in those species.

Hosts. The types were reared from fruit of *Celtis tala* Gill. collected Apr., 1938, emerged Nov., 1938 (Aczél 1954). Specimens were reared from fruit of *C. iguanaea* (Jacq.) Sarg. in Brazil by I. Nora (pers. comm.).

Specimens examined. Holotype (see synonymy) and 1m1f paratypes (MACN) 1f paratype (IML) with same data. ARGENTINA: Buenos Aires: La Plata, 1.V.1935, R. Costa, 1m (MACN). Salta: Cuel. Moldes, ex. fruto tala, 1.1953, M.A. Rosillo, 1f (MACN). BRAZIL: Santa Catarina: Coçador, 17.I.1990, I. Nora, 1m (UFPC); Coçador, reared ex. esporão de galo (*Celtis iguanaea*), 16.III.1987, I. Nora, 12m13f (USNM, USP, UFPC); Nova Teutonia, 22.II.1960, F. Plaumann, 1m (CNC). PARAGUAY: Paraguari: Cerro Acahay, 25°53'S 57°08'W, 13-14.III.1986, M. Pogue & M. Solis, 1f (USNM). URUGUAY: Cerro Largo: Sierra de Vaz, Rio Tacuari, 20 km SE Melo, 23-26.III.1963, J.K. Bouseman, 1f (AMNH).

Rhagoletotrypeta rohweri Foote
(Fig. 10D,H)

Rhagoletotrypeta rohweri Foote 1966:804 (Holotype f (USNM), USA: New Jersey: Camden, 2.VIII.1962, S.A. Rohwer); Steyskal 1981:708 (in key); Foote et al. 1993:366 (review).

Diagnosis. Wing bands very broad; aculeus tip with dorsal bend (Fig. 10H).

Host. Many paratypes were trapped on "hackberry" trees on which fruits were infested by

tephritid larvae. This *Celtis* sp., which must be *occidentalis* L., *tenuifolia* Nutt., or *laevigata* Willd., the only *Celtis* that occur in New Jersey, is almost certainly the host plant of *rohweri*, although as noted by Foote et al. (1993), no adults were reared to prove this association.

Rhagoletotrypeta uniformis Steyskal (Fig. 10E,I)

(part) *Rhagoletotrypeta annulata*: Foote 1966:806.

Rhagoletotrypeta uniformis Steyskal 1981:709 (Holotype m (USNM), USA: Texas: San Antonio, emerged V.1973 ex. fruit of *Celtis laevigata* Willd. collected autumn.1972, D.R. Johnston); Foote et al. 1993:367 (review).

Diagnosis. The shape of the aculeus, which is relatively simple, without lobes, unflattened in the sagittal plane, and without a dorsal bend (Fig. 10E,I), distinguishes this species from all *Rhagoletotrypeta* except *intermedia*, which differs from *uniformis* in having much narrower wing bands. Although often difficult to observe, the pattern of dense scutal microtrichia is useful to recognize *uniformis*. The lateral stripes are broad, but the submedial stripes are reduced or absent, whereas in other *Rhagoletotrypeta*, the submedial stripes are broad or microtrichia are entirely lacking.

Host. *Celtis laevigata* Willd.

Specimens examined. Holotype (see synonymy) and 2m11f paratypes (USNM) with same data. USA: New Mexico: Carlsbad, 14.VIII.1989, M.R. Perry, 1f (USNM). Texas: San Antonio, airport, 13.VI.1970, D. Johnston, 1f paratype (USNM); San Antonio, 1.VIII.1956, D.R. Johnston, 1m (USNM).

Rhagoletotrypeta xanthogastra Aczél

Rhagoletotrypeta xanthogastra Aczél 1951a:315 (Holotype f (IML), ARGENTINA: Tucumán: Villa Padre Monti, 17.I-7.II.1948, R. Golbach); Aczél 1954:150 (male; in key); Foote 1966:803 (in key); Foote 1967:42 (cat.); Steyskal 1981:708 (in key).

Chaetorhagoletis bahamondesi Blanchard; Aczél 1954:150 (*nomen nudum*).

Diagnosis. Scutum without microtrichia; lateral scutal white mark comma-shaped, not extended posteriorly beyond psutal seta.

Remarks. The postpronotal lobe is entirely brown in the IML male from San Javier, but is white medially in the other two specimens examined.

Host. *Celtis tala* Gill. (*tala*), was reported by Aczél (1954). The record he reported from "ciruelo" (probably a *Spondias* sp.) seems doubtful.

Specimens examined. ARGENTINA: Córdoba: Sierra Zala, San Javier, reared ex. fruit *Celtis tala* Gill., emerged XI.1938, J.A. Pastrana, 2m "allotype" and "paratype" (IML, MACN). Tucumán: Finca Horco Mde., 11.I.1953, 1f (IML).

Relationships

Phylogenetic analyses were conducted to test if *Cryptodacus*, *Haywardina*, *Rhagoletotrypeta*, *Lezca* and *Cryptoplagia* are monophyletic groups. The latter two names are no longer considered valid, based on the results of the analyses (see below).

The analyses were hindered by the fact that relationships among the genera of Carpomyina are poorly resolved. Because analysis of all carpomyine genera was not within the scope of this study, a working hypothesis was used, that the species with a white medial scutal stripe (i.e. *Cryptodacus*, *Haywardina*, *Rhagoletotrypeta* and *Zonosemata*) are a monophyletic group.

Relationships were analyzed using the mhennig* and bb* options of Hennig86 (Farris 1988). Table 1 lists the 50 characters used, and Table 2 shows the distributions of their states. Intraspecific variation is shown in Table 2, but only one state at a time was assigned in matrices used in Hennig86. Coding for the variable species is discussed in Table 1. Relationships within *Zonosemata* were not analyzed, but for the characters analyzed, the full range of states occurring within *Zonosemata* is represented by the three species included in the matrix. As a convention, in the text and trees, a character number (indicated by "#") refers to state 1 unless followed by a decimal point and an alternative state.

Because relationships among carpomyine genera are uncertain, several different taxa were used as the outgroup in separate analyses. These included: the genus *Paraterellia*, which is possibly

Table 1. Characters studied in cladistic analysis. Unless otherwise indicated, state 0 is plesiomorphic and multistate characters are linear transformation series.

1. Frons color - 0) yellow except ocellar tubercle; 1) with brown mark extended laterally from ocellar tubercle.	24. r-m ratio - 0) < 0.60; 1) > 0.63.
2. Number of frontal setae - 0) 2-3; 1) 4 or more. <i>R. striatella</i> was coded 0 in the Hennig86 matrix because there are only 3 frontal setae in other species of the <i>striatella</i> group, so the occasional occurrence of 4 in <i>striatella</i> is probably homoplasy.	25. Vein Cu ₁ with brown border between bm-cu and discal band - 0) no; 1) yes. If <i>C. tau</i> is coded 0 vs. 1 in the Hennig86 matrix, the trees have same topology but are 1 step longer. <i>P. immaculata</i> sometimes has a band along Cu ₁ that is doubtfully homologous with state 1.
3. orb ratio - 0) < or = 1; 1) > 1.	26. Wing band width - 0) at least subbasal band and usually others moderately to very broad; 1) all bands narrow, including subbasal band in cells bm and bcu. <i>P. superba</i> Foote has narrow bands, but this is probably homoplasy.
4. Ocellar seta - 0) at least as large as posterior orbital seta; 1) smaller than posterior orbital seta.	27. Discal band - 0) not crossing dm-cu; 1) crossing at least posterior end of dm-cu.
5. Face color - 0) entirely yellow; 1) with 1-2 brown spots; 2) with 4 spots or 2 elongate spots; 3) with 3 spots arranged in inverted triangle or fused into U-shaped mark.	28. Subapical band - 0) covering all of dm-cu; 1) ending at anterior end of dm-cu or in cell r ₄₊₅ .
6. Facial ratio - 0) at least 0.80; 1) less than 0.70.	29. Subapical band - 0) as strong anteriorly as posteriorly; 1) faint or absent anterior to vein R ₄₊₅ . <i>Paraterellia</i> was coded 0 in the Hennig86 matrix because this state is found in most <i>Carpomyia</i> .
7. flgm 1 ratio - 0) < 3.5; 1) > 4.0.	30. Accessory costal band - 0) present; 1) absent. Coded state 0 in <i>C. obliquus</i> . State 1 is plesiomorphic with <i>R. striatella</i> as outgroup. <i>Paraterellia</i> was coded 0 because the anterior end of the discal band (the apical fork in <i>P. ypsilon</i> Foote) may be homologous with the accessory band. If it is coded state 1 (or the polarity is reversed), tree topology is not effected.
8. flgm 1 shape - 0) tapered, tip with distinct dorsoapical pointed lobe; 1) tapered, tip at most slightly flattened, rounded or with weak dorsoapical point; 2) not tapered, tip strongly flattened, rounded or slightly expanded, without dorsoapical point. With <i>Paraterellia</i> as outgroup, state 1 is plesiomorphic, with states 0 and 2 independently derived. With either <i>Rhagoletis</i> species as outgroup, state 0 is plesiomorphic.	31. Abdomen color - 0) mostly orange, at least Tg5 usually with paired basal submedial brown spots; 1) mostly orange, often with lateral brown spots; 2) mostly brown. Coded nonadditive. State 1 is plesiomorphic with <i>R. ferruginea</i> as outgroup; state 2 with <i>R. striatella</i> . The coding for <i>R. pastranai</i> slightly effects tree topology (see discussion of <i>xanthogastra</i> group).
9. flgm 1 color - 0) yellow; 1) at least tip brown.	32. Apical white bands on tergites - 0) present except sometimes on apical tergite; 1) present on Tg1+2 and Tg3; 2) only Tg1+2 with apical white band; 3) absent. Species with orange abdomens were coded state 0, because the bands are difficult to see. They are faint or possibly absent in <i>Paraterellia</i> , <i>Haywardina</i> and <i>Zonosemata</i> .
10. Occiput and postgena color - 0) without brown areas; 1) with large brown area(s). The coding for <i>R. annulata</i> slightly effects tree topology (see discussion of <i>annulata</i> group).	33. Abdominal medial white stripe - 0) present only on apical tergite or absent; 1) present on Tg3-5 (male) or Tg3-6 (female); 2) faint or reduced to posterior spot on Tg3-4.
11. dc location - 0) closer to level of pal than to level of psut spal; 1) closer to level of psut spal than level of pal. With either <i>Rhagoletis</i> species as outgroup, state 1 is plesiomorphic.	34. Sublateral white areas on tergites - 0) absent; 1) present on at least Tg5-6.
12. Scutal microtrichia - 0) entirely bare; 1) evenly microtrichose; 2) with 4 stripes of more dense microtrichia; 3) with only 2 submedial denser stripes; 4) with submedial stripes and with sublateral bare areas. With <i>Paraterellia</i> as outgroup, state 1 is plesiomorphic; with either <i>Rhagoletis</i> species, state 2 is plesiomorphic.	35. Male sternite 6 with medial, usually mostly membranous lobe - 0) no; 1) yes.
13. Postpronotal lobe - 0) mostly or entirely white; 1) mostly or entirely brown. If <i>R. xanthogastra</i> is coded 0 vs. 1 in the Hennig86 matrix, the trees have the same topology but are 1 step shorter.	36. Outer surstylus, shape apical to inner surstylus (posterior view) - 0) tapered or truncate; 1) slightly expanded apically.
14. Notopleuron - 0) entirely brown or yellow; 1) with white posterior area.	37. Outer surstylus, mesal lobe - 0) short and sharply delimited; 1) broad and gradually arising from apical part of surstylus. The lobe is absent in <i>Zonosemata</i> , which was coded state 0.
15. Thorax color (excluding white markings) - 0) mostly yellow or orange; 1) mostly brown. With <i>R. striatella</i> as outgroup, state 1 is plesiomorphic.	38. Outer surstylus, length apical to mesal lobe - 0) at least 2x width of outer surstylus; 1) < 2x width of outer surstylus; 2) absent. State 1 is plesiomorphic with <i>R. striatella</i> as outgroup.
16. Medial scutal white stripe or spot - 0) absent; 1) present. <i>P. immaculata</i> Blanc and <i>varipennis</i> (Coquillett) have a broad, faint, posterior white mark that probably is not homologous with state 1.	39. Inner surstylus - 0) relatively long (in lateral view, distance from margin of epandrium to apex of inner surstylus at least 2x width of outer surstylus); 1) relatively short (above ratio < or = 1).
17. Lateral scutal white stripe - 0) absent; 1) present, at least as anterior or posterior spot; 2) slender, not extended along transverse suture. If <i>Paraterellia</i> is coded 0 vs. 1 in the Hennig86 matrix, the same trees result except they are 1 step longer, with 17.1 a basal synapomorphy.	40. Distiphallus - 0) with distinct, complex internal sclerotization; 1) relatively simple, with little distinct internal sclerotization.
18. Lateral scutal white stripe - 0) extended to transverse suture (or absent); 1) extended to psut spal, but not to transverse suture; 2) reduced to white spot at or posterior to intra-alar seta. <i>C. silvai</i> was coded 1 in the Hennig86 matrix.	41. Distiphallus - 0) short to moderately long, without sinuous internal tube; 1) elongate, with sinuous internal tube.
19. Postsutural scutal brown spots - 0) scutum brown or orange except for white areas, or with U-shaped brown spot extended from posterior margin; 1) scutum with isolated brown spot bordering lateral white stripe.	42. Apical membranous part of distiphallus - 0) broad in ventral and/or lateral views; 1) tapered to single lobe slender in both views.
20. Anepisternum color (excluding white area) - 0) mostly brown or yellow (if yellow with brown spot, spot located medially or ventrally); 1) yellow with brown dorsal spot.	43. Aculeus tip length/ aculeus length - 0) < 0.4; 1) > 0.4.
21. Anepisternum dorsal white area - 0) linear or narrowly triangular, entire dorsal margin, but no more than 1/2 of posterior margin white; 1) broadly triangular, entire dorsal margin and > 1/2 of posterior margin white; 2) anterior part of dorsal margin dark, most or all of posterior margin white. <i>H. cuculi</i> , which has brown spot extended to dorsal margin anteriorly, but white area narrow posteriorly, was coded 0.	44. Aculeus with lateral barb basal to tip - 0) no; 1) yes.
22. Katepisternum dorsal margin - 0) brown or yellow; 1) with broad white spot or stripe.	45. Aculeus tip sagittate and finely serrate - 0) no; 1) yes.
23. Scutellum color - 0) white area small, basal seta in brown area on sides and disc; 1) white area large, basal seta not in brown areas on sides and disc; 2) sides with large brown basal area, but disc yellow basally and medially. State 1 is plesiomorphic, with states 0 and 2 derived independently.	46. Aculeus tip with small subapical notches - 0) yes; 1) no. State 1 is plesiomorphic with either <i>Rhagoletis</i> species as outgroup.
	47. Aculeus tip deeply trilobed in ventral view - 0) no; 1) yes.
	48. Aculeus tip flattened in sagittal plane and trilobed in lateral view - 0) no; 1) yes.
	49. Number of spermathecae - 0) 3; 1) 2. State 1 is plesiomorphic with either <i>Rhagoletis</i> species as outgroup.
	50. Spermathecal shape - 0) small, spherical, usually with short neck, normally sclerotized; 1) large, elongate, and weakly sclerotized.

Table 2. Character states in species of *Cryptodacus*, *Haywardina*, *Rhagoletotrypeta*, and *Zonosemata*.

	Character number																																													
Taxa	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0						
Outgroup																																														
<i>Paraterellia</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
<i>R. ferruginea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
<i>R. striatella</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Z. minuta</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Z. scutellata</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Z. vidrapennis</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>H. cuculi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>H. cuculiformis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>H. bimaculata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>H. obscura</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>R. parallela</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>R. xanthogastra</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>R. pastranai</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>R. annulata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>R. argentiniensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>R. morgantei</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>R. intermedia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>R. rohweri</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>R. uniformis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>C. obliquus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>C. lopezi</i>	1	0	1	1	1	1	2	1	0	0	3	0	1	1	1	0	0	0	0	2	1	1	0	1	0	1	1	2	1	0	1	1	2	1	0	1	1	2	1	0	1	1	2	1	0	1
<i>C. tau</i>	1	0	1	1	1	1	2	1	0	0	3	0	1	1	1	0	0	0	0	2	1	1	0	1	0	1	1	2	1	0	1	1	2	1	0	1	1	2	1	0	1	1	2	1	0	1
<i>C. ornatus</i>	1	0	1	1	1	1	2	1	0	0	3	0	1	1	1	0	0	0	0	2	1	1	0	1	0	1	1	2	1	0	1	1	2	1	0	1	1	2	1	0	1	1	2	1	0	1
<i>C. parkeri</i>	1	0	1	1	1	1	2	1	0	0	3	0	1	1	1	0	0	0	0	2	1	1	0	1	0	1	1	2	1	0	1	1	2	1	0	1	1	2	1	0	1	1	2	1	0	1
<i>C. quirozi</i>	1	0	1	1	1	1	2	1	0	0	3	0	1	1	1	0	0	0	0	2	1	1	0	1	0	1	1	2	1	0	1	1	2	1	0	1	1	2	1	0	1	1	2	1	0	1
<i>C. silvai</i>	1	0	1	1	1	1	2	1	0	0	3	0	1	1	1	0	0	0	0	2	1	1	0	1	0	1	1	2	1	0	1	1	2	1	0	1	1	2	1	0	1	1	2	1	0	1
<i>C. tigreroi</i>	1	0	1	1	1	1	2	1	0	0	3	0	1	1	1	0	0	0	0	2	1	1	0	1	0	1	1	2	1	0	1	1	2	1	0	1	1	2	1	0	1	1	2	1	0	1

related to the Carpomyina and may indicate the carpomyine groundplan for the characters analyzed; and two Solanaceae-breeding species of *Rhagoletis*, *ferruginea* Hendel and *striatella* Wulp, whose hosts might suggest that they are closely related to *Haywardina* and *Zonosemata*.

Depending upon the outgroup used, the resulting cladograms vary greatly in how the genera are grouped. The two trees shown (Fig. 11-12) are included mainly to indicate relationships within each genus, rather than among them. With *Paraterellia* as outgroup, *Cryptodacus* is hypothesized as the sister group of *Haywardina* + *Rhagoletotrypeta*, with *Zonosemata* as the sister group of these three genera (Fig. 11). With the species of *Rhagoletis* as outgroup, almost all possible sister group relationships among the four genera are equally parsimonious. In some trees the *xanthogastra* and *annulata* groups of *Rhagoletotrypeta* are not sister taxa (i.e. *Rhagoletotrypeta* not monophyletic), and/or *Haywardina* is not hypothesized as monophyletic. Furthermore, when either or both of species of *Rhagoletis* is included in the matrix with *Paraterellia* as outgroup, they are grouped with

only some taxa (*striatella* with *Cryptodacus* and the *annulata* group; *ferruginea* variously), thus the four genera with the medial white scutal stripe might not be a monophyletic group. Considering that the basal nodes of all the trees are defined by only a few characters, and that those characters are highly variable in the Tephritidae (e.g., thorax and abdomen color (#15, #31), dc seta location (#11), and antennal flagellomere shape (#8)), I have little confidence in any of the trees below the genus level.

Although the relationships among *Cryptodacus*, *Haywardina*, *Rhagoletotrypeta*, and *Zonosemata* are not resolved by this analysis, *Cryptodacus*, the *R. xanthogastra* group, the *R. annulata* group, and *Zonosemata* are hypothesized as monophyletic groups in all resulting trees. Each of these groups is based on apomorphies that are unique or nearly unique to it, so no matter what outgroup is used they probably are monophyletic.

Synapomorphies of *Cryptodacus* include: wing vein Cu₁ bordered by brown band between bm-cu and the discal band (#25), although it is lost in *quirozi* and variable in *tau*; and r-m displaced apically (#24), which occurs as homoplasy in *H. cuculi*. The subapical band faint anteriorly (#29),

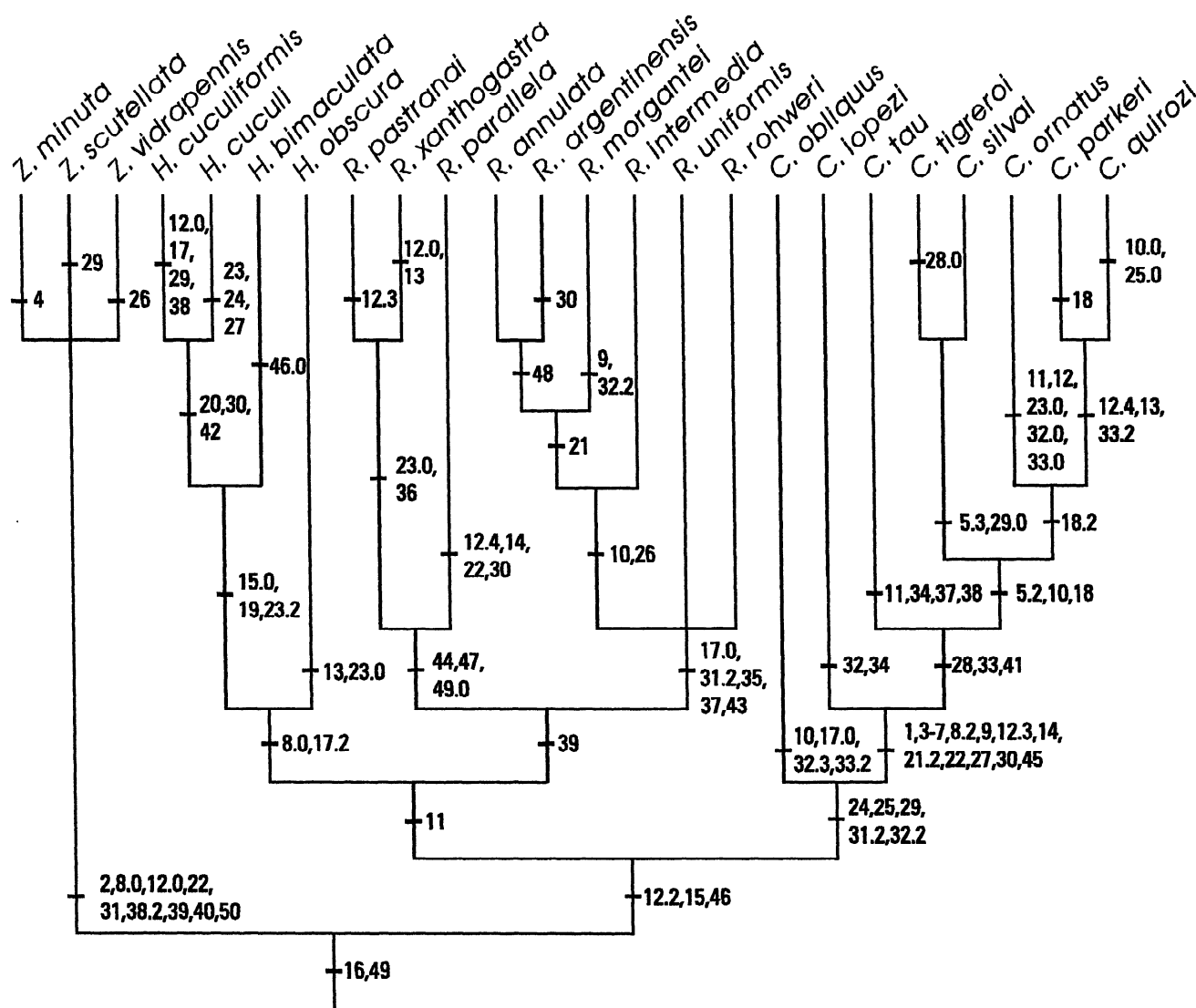


Figure 11. Possible relationships among species of *Cryptodacus*, *Rhagoletotrypeta*, *Haywardina*, and *Zonosemata*. One of 24 trees (length 122 steps, ci 53, ri 80) with *Paraterellia* as outgroup; other trees differ only within *R. annulata* group, within *R. xanthogastra* group, and/or within *Cryptodacus*. Numbers separated by commas refer to characters listed in Table 1. State 1 is assumed unless character number is followed by a decimal point and an alternative state number.

which occurs as homoplasy in *Z. scutellata* and *H. cuculiformis*, and loss of the white apical band on at least tergite 4 (#32), which occurs as homoplasy in *R. morgantei* and is difficult to code in the species with yellow abdomens, are also interpreted as synapomorphies on all trees, with reversal in #29 in *silvai* + *tigreroi*, and in #32 in *ornatus*. Another possible synapomorphy of all *Cryptodacus* species is the slightly sagittate and finely serrate aculeus tip (#45), but unfortunately, no females of *obliquus*

are known, so whether this is a synapomorphy for the entire genus or only the seven other species is uncertain. A similar but convergent shape occurs in four species of the *Rhagoletis nova* group (Foote 1981), in which the tip is sagittate, but with much larger serrations (Frias 1986).

Within *Cryptodacus*, the hypothesis that *obliquus* is the sister taxon of the other species is well supported. The positions of the other species are consistent in all trees, except for *ornatus* and

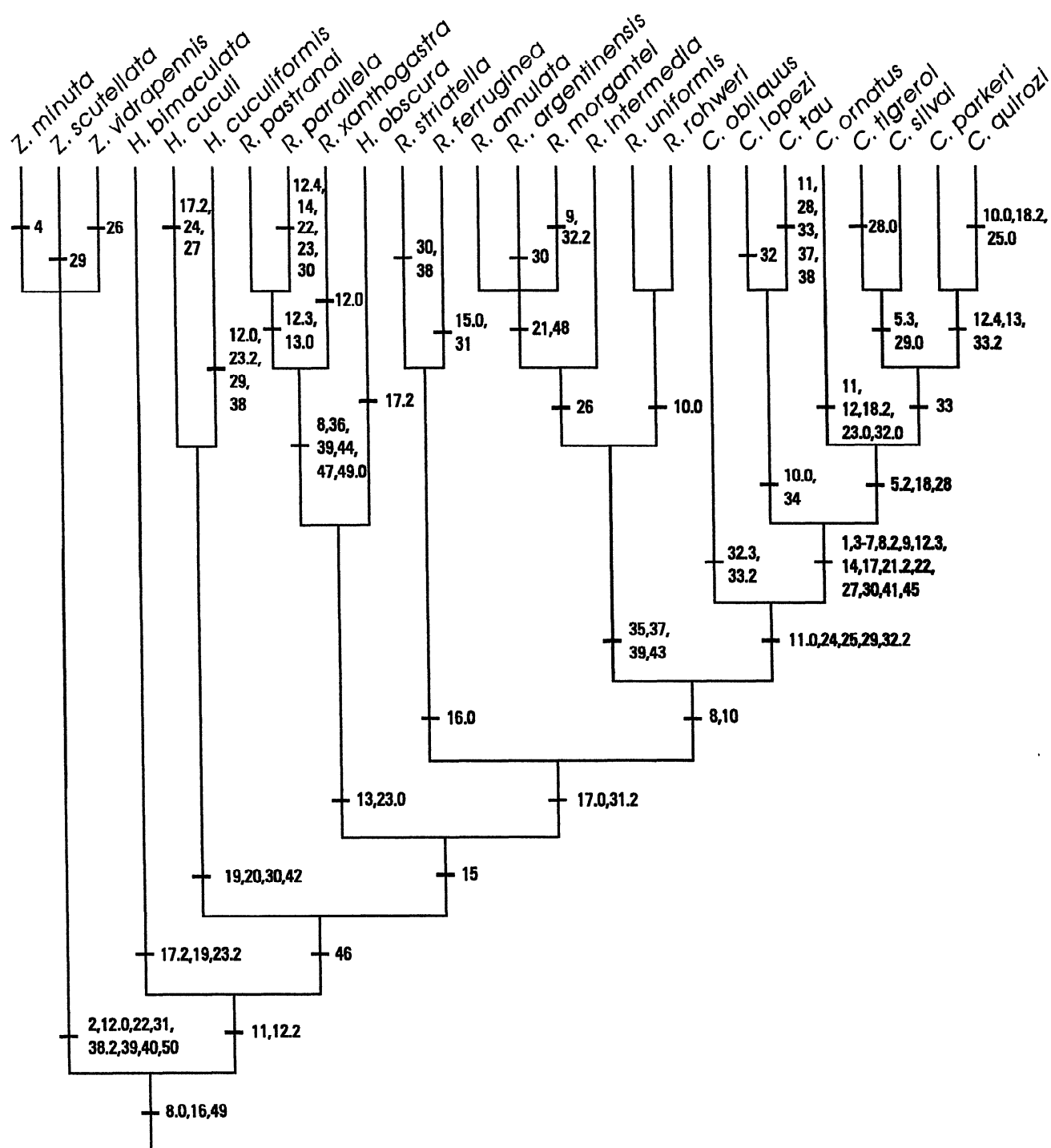


Figure 12. Possible relationships among species of *Cryptodacus*, *Rhagoletotrypeta*, *Haywardina*, and *Zonosemata*. One of 36 trees (length 128 steps, ci 50, ri 79) with *Paraterellia* as outgroup and two *Rhagoletis* species included in matrix; other trees differ only in position of *H. bimaculata* (alternately as sister group of *H. cuculi* + *H. cuculiformis*), within *R. xanthogastra* group, and/or within *Cryptodacus*.

tau. *C. ornatus* is variously hypothesized as the sister group of *silvai* + *tigreroi*, of *parkeri* + *quirozi*, or of all four species. *C. tau* is either the sister group of those five species (Fig. 11), which are always grouped together, or the sister group of *lopezi* (Fig. 12).

I consider *Lezca* a subjective synonym of *Cryptodacus*. Continued recognition of *Lezca* as a monotypic taxon for *tau*, would make *Cryptodacus* paraphyletic. *C. silvai* and the five new species instead could be placed in *Lezca*, leaving only *obliquus* in *Cryptodacus*, but since the close relationship of all of these species is well supported, I see no reason to divide them into separate genera.

Haywardina is not well defined by synapomorphies as are the other three genera. Support is weak for the inclusion of *obscura* (Fig. 11), but the female of this species is unknown and it otherwise has mostly plesiomorphic character states, so there are few apomorphies grouping it with any other taxon. Discovery of the female and host plant may clarify its relationships. The shape of the lateral scutal white stripe (#17.2) suggests that *obscura* is related to *bimaculata* and *cuculi*, but if so, there is reversal in this character because the stripe is broader and more extensive anteriorly in *cuculiformis*. All four species have a similar abdominal color pattern (#31.0), but this is plesiomorphic with *Paraterellia* as outgroup. It is apomorphic with either *Rhagoletis* species as outgroup, but occurs as homoplasy in the *R. xanthogastra* group. With *Paraterellia* as outgroup, the shape of the antennal flagellomere (#8.0) appears to be a synapomorphy for *Haywardina*, but given that this state is present in other carpomyine genera except *Cryptodacus*, *Rhagoletotrypeta*, and *Goniglossum*, it probably is not a true synapomorphy at this level. With *Rhagoletis ferruginea* as outgroup, in some trees *obscura* is hypothesized as the sister taxon of a clade including *Cryptodacus* and the *xanthogastra* and *annulata* groups, supported by the mostly brown thorax (#15); in other trees it is placed as the sister group of the *xanthogastra* group, based on #15, #31 and #23.0 (scutellum white area small), or within the *xanthogastra* group (but this assumes states 44.1, 47.1, and 49.0 for *obscura*). With all three outgroup taxa included in the matrix, *obscura* is placed as the sister taxon of the *xanthogastra* group (Fig. 12), but this is supported only by #13 and #23.0, in which there is reversal within the clade.

The close relationship of *bimaculata*, *cuculiformis*, and *cuculi* (Fig. 11) is suggested by

their scutal markings. These species have isolated brown marks bordering the lateral white stripe (#19). Some species of *Zonosemata* may have brown markings in this area, but if so they are usually connected posteriorly to form a broad U. The brown lateral marks on the scutellum (#23.2) may be interpreted as a synapomorphy for *bimaculata* + *cuculiformis* + *cuculi*, with reversal to state 1 in *cuculi* (Fig. 11), or as homoplasy in *bimaculata* and *cuculiformis*. The unique pattern of brown spots on the thoracic pleuron (#20), the loss of the accessory costal band (#30), which occurs as homoplasy in some species of *Cryptodacus* and *Rhagoletotrypeta*, and the slender apical lobe on the distiphallus (#42) are synapomorphies indicating the close relationship of *cuculi* and *cuculiformis*.

The aculeus tip is notched in *Paraterellia*, *Zonosemata*, and *H. bimaculata* (#46.0), although the different shapes of the tip in these taxa may indicate that this is convergence. With all three outgroup taxa included in the matrix, in some trees (Fig. 12) *H. bimaculata* is hypothesized as the sister group of all the other taxa except *Paraterellia* and *Zonosemata*, for which #46 is the only synapomorphy. Trees with *bimaculata* as the sister group of *cuculi* + *cuculiformis* are equally parsimonious, however, and the former hypothesis of relationship is not supported with any of the other taxa as outgroup. With either species of *Rhagoletis* as outgroup, #46.0 could be interpreted as a synapomorphy for *bimaculata* and *Zonosemata*, but other character distributions do not support that hypothesis. If *obscura* has the same type of aculeus tip, this state could be the groundplan condition for a clade including *Haywardina* and *Zonosemata* (with reversal in *cuculi* + *cuculiformis*). *H. cuculiformis* also shares an apomorphic state with *Zonosemata*, the absence of scutal microtrichia (#12.0), which is also interpreted here as homoplasy because of other character state distributions. Either species possibly could be a plesiomorphic member of *Zonosemata*, but, based on the characters analyzed, no trees result with either of them grouped with *Zonosemata*.

I consider *Cryptoplagia* a subjective synonym of *Haywardina*. By the generic limits proposed by Aczél, *bimaculata* (and perhaps *obscura*) would be included in *Cryptoplagia*, but the latter would be paraphyletic, because *cuculiformis*, the type species of *Cryptoplagia*, is more closely related to *cuculi*, the type species of *Haywardina*, despite the distinctive autapomorphies of the latter species.

Rhagoletotrypeta includes two well defined monophyletic species groups, whose relationship to

each other (Fig. 11) is suggested mainly by the short inner surstylus (#39), a character that also occurs in *Zonosemata*. The fact that species of both species groups breed in *Celtis* species, a host taxon not known to be attacked by any other Carpomyina, also suggests their relationship. With either *Rhagoletis* species as outgroup, in some trees the *xanthogastra* group forms a clade with *Zonosemata* and *Haywardina*, or it is hypothesized as the sister group of the *annulata* group + *Cryptodacus*. Also, with all three outgroup taxa included in the matrix, the *xanthogastra* and *annulata* groups are not hypothesized as sister taxa (Fig. 12).

The *xanthogastra* group includes *parallela*, *pastranai*, and *xanthogastra*. Its monophyly is indicated by at least three synapomorphies: aculeus with lateral barbs (#44); aculeus tip deeply trilobed (#47); and 3 spermathecae present (reversal to #49.0). The shape of the apex of the outer surstylus (#36), which is unknown in *parallela*, and the abdominal color pattern (#31), which varies in *pastranai*, may be additional ones. The relationships among these three species are not well resolved. In most trees, either *parallela* is the sister taxon of *pastranai* + *xanthogastra* (Fig. 11), for which #23.0 and perhaps #36 are synapomorphies, or *xanthogastra* is the sister group of *parallela* + *pastranai* (Fig. 12), if *parallela* is assumed to have state #36.1. With either *Rhagoletis* species as outgroup, if *pastranai* is coded state 2 for #31, the same trees result as when it is coded state 0, but there are additional trees in which *pastranai* is the sister taxon of the other two species.

The *annulata* group of *Rhagoletotrypeta* includes *annulata*, *argentinensis*, *intermedia*, *morgantei*, *rohweri*, and *uniformis*. Synapomorphies for this group include: male sternite 6 with a medial lobe (#35); outer surstylus with mesal lobe not sharply differentiated (#37); and aculeus tip length more than half the length of the aculeus (#43). There is homoplasy in #37 in *C. tau*. The absence of the lateral scutal stripe (#17.0), also absent in *C. obliquus* and *Rhagoletis*, may be another synapomorphy. Within the *annulata* group, *intermedia* is the sister group of *morgantei* + *annulata* + *argentinensis*. The shape of the aculeus tip, flattened in the sagittal plane and trilobed in lateral view (#48), may be a synapomorphy of *annulata* and *argentinensis* (Fig. 11), but this character is unknown in *morgantei*, so it could be a synapomorphy of all three species (Fig. 12). If *annulata* is coded state 0 for #10, the shortest trees are one step longer, and additional trees result with

annulata and *morgantei* reversed in their positions in Fig. 11. In the latter trees, state 1 is assumed for #48 in *morgantei*, and #10 is a synapomorphy for it and *argentinensis*. The relationships of *uniformis* and *rohweri* are not well resolved. Only in trees in which *Cryptodacus* and the *annulata* group are hypothesized as sister taxa (Fig. 12), state #10.0 can be interpreted as a synapomorphy for these two species.

Zonosemata is a well defined monophyletic taxon of seven species that breed in Solanaceae (Bush 1965, Norrbom 1989b, Hernández 1989). Autapomorphies for it include: 4 or more frontal setae (#2), which occurs as homoplasy in some specimens of *Rhagoletis striatella*; scutum without microtrichia (#12.0), which occurs as homoplasy in *H. cuculiformis* and *R. xanthogastra*; outer surstylus short and without medial mesal lobe (#38.2) (its apex is rugose and may be homologous with the mesal lobe); distiphallus relatively simple, evenly sclerotized, with little distinct internal sclerotization (#40); and spermathecae large, elongate, and weakly sclerotized (#50). Other possible synapomorphies (i.e. states of characters whose polarity depends upon the outgroup) are the posterior location of the dc seta (#11) and the notched aculeus tip (#46.0). There is homoplasy in some *Cryptodacus* and some *Rhagoletis* species in the former character, and because the aculei of *Paraterellia* and *H. bimaculata* have similar notches, the latter character state could have evolved at a lower level (see discussion of *Haywardina*). Bush (1966) also suggested that there are apomorphic traits in chromosome shape for *Zonosemata*, but karyotypes have not been studied in other carpomyine genera except *Rhagoletis*.

Berlocher and Bush (1982) indicated that *R. striatella* and perhaps other solanaceous breeding species of *Rhagoletis* may be more closely related to *Zonosemata* than to their congeners. Their hypothesis does not necessarily conflict with hypotheses of *Zonosemata*'s relationships discussed here, because Berlocher and Bush were unable to include species of *Cryptodacus*, *Rhagoletotrypeta*, or *Haywardina* in their electrophoretic study.

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