Morphological differences among *Drosophila paraguayensis* **Duda**, 1927 and its close relatives (Diptera, Drosophilidae)

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*Drosophila mediosignata* **Dobzhansky & Pavan**, 1943, a Neotropical species belonging to the *tripunctata* group, has been considered a junior synonym of *D. paraguayensis* **Duda**, 1927 since 1990. However, the detailed morphological analysis of the offspring of two recently established isofemale lines and the reanalysis of the type series of both nominal species in addition to that of another junior synonym, namely *D. medionotata* **Frotta-Pessoa**, 1954, allowed the recognition of three closely related species, two of them identified under the binomial *D. paraguayensis* **sensu Vilela & Bächli**, 1990. Accordingly, *Drosophila mediosignata* is revalidated and redescribed while *D. medionotata* remains a junior synonym of *D. paraguayensis*, which is also redescribed. *Drosophila cuaso* sp. nov. (type locality: Cidade Universitária “Armando de Salles Oliveira”, São Paulo City, state of São Paulo, Brazil), a cryptic species of the two preceding ones, is described. Photomicrographs of wings and tergites as well as of some features of the male and female terminalia useful to the identification of the three closely related species are included. An analysis of the holotype and associated specimens included in the original description of *D. prosimilis*, a species supposed to be closely related to *D. medionotata* and whose identity is as yet unclear, as well as the analysis of some specimens most probably used by **Dobzhansky & Pavan** in the redescription of *D. prosimilis* published in 1943, is also included.

Keywords: abdominal pattern, *Drosophila cuaso* sp. nov., *Drosophila mediosignata*, *Drosophila paraguayensis*, *D. prosimilis*, male terminalia, revalidation, inner spermaticheal capsule.

**INTRODUCTION**

*Drosophila paraguayensis* was described by **Duda** in 1927 from one female specimen collected on 06.X.1907 in Hohenau, Paraguay and one male caught (collection date unknown) in Petrópolis, state of Rio de Janeiro, Brazil. In the last paragraph of the description, **Duda** (1927) mentions that he was not quite sure as to whether the species he had described was new or not, for it could be just a variety of *D. angustibucca* **Duda**, 1925, described by himself from Suiza de Turrialba, Costa Rica.

In his revision of the *tripunctata* species group of *Drosophila*, **Frotta-Pessoa** (1954) redescribed *D. angustibucca* based on specimens collected in three Brazilian states (Rio de Janeiro [then Distrito Federal], São Paulo and Rio Grande do Sul); however, he mentioned that he did not analyze any [type] specimens either of *D. angustibucca* or *D. paraguayensis*; instead, he included a comparative list of the differences he found between *D. angustibucca* and *D. paraguayensis* based on their original descriptions (**Duda**, 1925, 1927, respectively).

In the cited paper, **Frotta-Pessoa** described *D. medionotata* as a probable synonym of *D. prosimilis* **Duda**, 1927 (type locality: Pto. [Puerto] Bermudes, Pichis, Peru) based on its redescriptions by **Dobzhasnky & Pavan** (1943). The redescription

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of *D. prosimilis*, made with much doubt by the latter authors, was not based on the holotype but on specimens collected in 1943 in the Brazilian states of São Paulo (Vila Atlântica [Mongaguá] and Iporanga) and Rio de Janeiro (Rio de Janeiro City: Jacarepaguá). Moreover, a redescription of *D. prosimilis* was made later on by VILELA & BÄCHLI (1990) based on the female holotype.

VILELA & BÄCHLI (1990) also published detailed drawings of the male terminalia of type specimens of *D. medionotata* FROTA-PESSOA, 1954, *D. mediosignata* DOBZHANSKY & PAVAN, 1943, and *D. paraguayensis*, interpreted some subtle differences as due to intraspecific variability and synonymized the first two under the last binomial.

During a two years survey (IX.1995–VIII.1997) of the *Drosophila* species attracted to banana-baited traps, made once a month, in a remnant of the Atlantic rain forest located in the Cidade Universitária “Armando de Salles Oliveira”, within São Paulo City, state of São Paulo, Brazil, two of us (CRV and VR) have suspected that a pair of sympatric sibling species could probably be involved under the binomial *D. paraguayensis* sensu VILELA & BÄCHLI (1990). The suspicion arose during the processes of identifying the males. It was observed that the variability, attributed to a polymorphism, in the spotting pattern of the tergites V and VI of two groups of specimens at first identified as *D. paraguayensis* never overlapped. Then, looking for additional reliable traits it was realized that in living specimens the most convenient method to tell the two kinds of males apart consisted in inspecting the outline of the aedeagus in ventral instead of lateral view, as generally used for the identification of most species of Neotropical *Drosophila*.

To make a detailed, comparative, morphological analysis of this putative pair of sibling species two isofemale lines were established which are currently kept in the Laboratório de Drosofilídeos, Departamento de Biologia, Instituto de Biociências, Universidade de São Paulo (IBUSP), São Paulo City, Brazil. Samples of different generations of these strains, as well as the two parental wild-caught females, were pinned and used in the comparison with the type specimens of the three nominal species, namely *D. medionotata*, *D. mediosignata* and *D. paraguayensis*, as well as with the type specimens of *D. prosimilis* and five non-type specimens most probably used by DOBZHANSKY & PAVAN (1943) in their redescription of *Drosophila prosimilis*.

The main purposes of the present work are: 1) to revalidate the binomial *Drosophila mediosignata* DOBZHANSKY & PAVAN, 1943, currently considered to be a junior synonym of *D. paraguayensis* DUDA, 1927; 2) to restrict the concept of VILELA & BÄCHLI (1990) for *D. paraguayensis*; 3) to describe a new species closely related to them and 4) to present new morphological data that allow to identify them.

MATERIAL & METHODS

We based our study on the analysis of 20 type specimens in addition to 212 non-type specimens plus 32 removed abdomens. The latter and most of the non-type flies were sampled from two laboratory isofemale lines (coded as I73F170 and I76F16), both from wild-caught females collected at São Paulo City and maintained in the Departamento de Biologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, state of São Paulo, Brazil. The type series of the following species were analyzed: *D. mediosignata* DOBZHANSKY & PAVAN, 1943 (♀ holotype plus 4 paratypes: two ♀♀ and two ♂♂); *D. paraguayensis* DUDA, 1927 (♂ lectotype
Drosophila paraguayensis

Fig. 1. Right wing of *Drosophila paraguayensis*: A, São Paulo City, isofemale line 173F170, generation F₁, ♂; B, idem, ♀ undetermined generation; C, Praia Grande, state of São Paulo, V.1943, ♂; D, idem, ♀.
and ♀ paralectotype; *Drosophila medionotata* FROTA-PESSOA, 1954 (♂ holotype plus 11 paratypes: seven ♂ ♂ and four ♀ ♀) and *D. prosimilis* DUDA, 1927 (♀ holotype). The non-type specimens are listed in the item “Material examined” under each binomial.

Label data attached to each specimen are cited in full with a slash indicating a label change. Our own notes or interpretations are included in brackets (also in other items throughout the text).

The method proposed by SPASSKY (1957) of gently pressing the tip of the abdomen of males was used for the identification of living specimens. However, their aedeagi were analyzed regarding the outline as seen in ventral view instead of the usual analysis of their profiles, as seen in lateral view.

The isofemale lines are kept at 18 ± 1 °C and 13:11 h (L:D) photoperiod in a special culture medium (powdered milk-agar) whose recipe (apparently unpublished) was kindly sent to us, a couple of decades ago, by the retired Professor Dr. Antonio Rodrigues CORDEIRO, then at the Universidade Federal do Rio Grande do Sul. This medium is adequate for keeping some species of *Drosophila* belonging to the *tripunctata* and *cardini* groups that do no breed in the usual banana-agar culture medium and, with small modifications, is prepared as follows:

The agar (10 g) and white sugar (20 g) are dissolved in water (1 liter), slowly brought to the boil, stirred once in a while. Meanwhile, the powdered milk (Nestle®) of Nestle®, 10 g) is first mixed with brewer yeast (10 g) and then the uniform mixture is dissolved in water (90 ml). As soon as the water (plus agar and sugar) starts boiling, the fire is turned off and the liquid mixture (cold water, milk and yeast) is poured into the hot water mixture (water, agar and sugar) which must be stirred until the food is uniform. After ca. 20 min, 8 ml of 10% alcoholic (ethanol) solution of Nipagin® are added to the food which must be uniformly stirred and then poured (about 3 ml food) into the usual cylindric glass tubes (20 x 100 mm), which are stoppered with foam plugs. After cooling at room temperature they must be kept in the refrigerator (ca. 4 °C). When no more water drops are seen on the inner glass wall (usually 1–2 days after the food has been prepared) they are ready to be used.

Preparations of microscope slides were made following WHEELER & KAMBSSELLIS (1966) and KANESHIRO (1969). The abdominal structures, including the disarticulated terminalia, are preserved in microvials filled with glycerin and attached by the stopper to the pin of the respective specimen.

Illustrations of the ventral lobe of epandrium were drawn using an objective 20x and a camera lucida (1.8x). Whenever possible, photomicrographs were taken of the following structures: abdomens (objectives 1.8x and 4x) of newly killed males and females from isofemale lines, right wing (objective 2.5x), aedeagus in ventral and left lateral views, hypandrium in posterior view, oviscap valves, and inner spermathecal capsules in lateral view (objective 6.3x; details of the latter at 20x). Whenever in the same plate (except for Fig. 14), all figures were drawn to the same scale and all photomicrographs were taken and enlarged to the same magnification. The photomicrographs were taken using a black & white film APX25 AgfaPan, except for the abdomens, for which we used Fujichrome 64T.

For measurements and indices see VILELA & BÄCHLI (1990), for morphological terminology see VILELA & BÄCHLI (2000). Averages are followed by ranges (in parentheses). The list of references under each binomial is intended to be exhaustive; however, some papers were intentionally omitted whenever they just repeat data from others already cited.
**Drosophila cuaso**

Fig. 2. Right wing of *Drosophila cuaso* sp. nov.: A, holotype, ♂; B, allotype, ♀; C, Bucaramanga, ♂.

The acronyms of the specimens depository and of the strain keepers are in parentheses and defined as follows: American Museum of Natural History, New York City (AMNH); Departamento de Biologia, Instituto de Biociências, Universidade de São Paulo, São Paulo City (IBUSP); Museu de Zoologia, Universidade de São Paulo, São Paulo City (MZSP); Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro City (MNRJ); Staatliches Museum für Tierkunde, Dresden (SMTD); Zoologisches Museum, Humboldt-Universität, Berlin (ZMHB).

RESULTS

**Drosophila mediosignata** Dobzhansky & Pavan, 1943, sp. revalid.

(Figs 3A; 4A; 5A; 6A, B; 7A, B; 9A; 10A)

*Drosophila (Drosophilata) mediosignata* Dobzhansky & Pavan, 1943: 24, plate 2, figs 27, 29, 30 (metaphase chromosomes), plate 5, fig. 105 (spermathecal capsule), plate 6, fig. 131 (egg); Pavan & Cunha, 1947: 60 (key); Dobzhansky & Pavan, 1950: 2 (collection; under the name medio-group[sic]); Freire-Maia & Pavan, 1950: 22 (included in the *tripunctata* group; updated di-
Drosophila mediosignata  Drosophila paraguayensis

Drosophila paraguayensis  Drosophila cuaso

Drosophila cuaso

![Fig. 3. Epandrium, cerci and decasternum, posterior view: A, Drosophila mediosignata, paratype; B, D. paraguayensis, São Paulo, 173F170, generation F1; C, idem, Praia Grande, V.1943; D, D. cuaso sp. nov., holotype; E, idem, Bucaramanga.](image)

agnosis of the group), 60 (key); Pavan, 1950: 33 (key); de Castro, 1953: 368 (tarsal setae); Frota-Pessoa, 1954: plate XV, fig. 12 (♂ terminalia), plate XVII, fig. 32 (oviscept valve) plate XVIII, fig. 61 (spermathecal capsule), plate XX, figs 73–76 (male abdomen), plate XXIII, fig. 99 (wing); da Cunha et al., 1957 [under the name "medio" group (sic)]: 101, 104 (crop yeasts), 103, 104 (yeast attraction); Pavan, 1959: 29 (breeding site); Petersen, 1960: 13 (collection); Mourão et al., 1965: 160 (distribution); Pilares et al., 1981: 162 (distribution [under cardini group]); Wheeler, 1981: 44 (catalogue); Val., 1982: 337 (type series, ♂ terminalia of holotype); Franck & Valente, 1985: 134, 135 (collection); Vilela & Bächli, 1990: 256 (♂ ter-
minalia, paratype; as a junior synonym of *D. paraguayensis* DUDA, 1927); FRANCK & NAPP, 1992: 125, 126 (electrokinetic pattern), 128 (genetic similarity), 129 (dendrogram); LORETO et al. 1998: 155 (collection, transposable elements).

Type locality: Iporanga, São Paulo, Brazil (correction: the citation Apiá, São Paulo, Brazil, in the original description is clearly a mistake; hence, the type locality is hereby considered to be Iporanga, São Paulo, Brazil, for the following reasons: there is no specimen labelled Apiá in the type series and the holotype bears a label which reads Iporanga).

**Material examined.** Type specimens (MZSP). Holotype δ (previously dissected): “δ / Iporanga S. Paulo VII-943 / Drosophila medioignata Type / HOLOTIPO [red label] / D. medioignata holotipo”.

Paratypes (2 δ δ [dissected, one previously], 2 ? ? [one dissected]), same data as holotype.


**Diagnosis.** Aedeagus bearing a pair of subapical, serrate, lateral, ear-shaped expansions which, in ventral view, are noticeably narrower than those present in *D. cuaso* sp. nov. and slightly shorter than those present in *D. paraguayensis* as in Fig. 6. The aedeagus in profile is wider than that of *D. cuaso* sp. nov. It can be distinguished from *D. paraguayensis* by the following features: its aedeagus (in profile) is clearly ellipse-shaped (somewhat triangle-shaped in *D. paraguayensis*), its inner spermathecal capsules (Fig. 9) are pear-shaped (somewhat spherical in *D. paraguayensis*) and the ventral lobe of epandrium is somewhat angular both dorsally and ventrally (finger-shaped in *D. paraguayensis*) (see also VILELA & BÄCHLI, 1990: 255–257, figs 98–100).

**Redescription** (*n*<sub>max</sub> = 3). Characters as in *D. paraguayensis* except: Frontal length 0.29 mm, frontal index 0.74 (0.74–0.75), top to bottom width ratio 1.21 (1.20–1.21). Length ratio of anterior to posterior orbital seta 0.67, of mid to anterior orbital seta 0.37 (0.30–0.40); poc 0.67x (0.61–0.71), oc 0.81x (0.67–0.88) frontal length; vt index 1.29 (1.12–1.40); vibrissal index 0.46. Cheek index about 11. Eye index 1.18 (1.18–1.19). Arista with 7 upper and 3 lower branches, plus terminal fork, inner branches short. Proboscis and palpi yellow.

Thorax length 1.16 (1.15–1.19) mm; h index 0.87; dc index 0.64; scut index 1.07 (0.92–1.17); sterno index 0.52 (0.46–0.61), mid katepisternal seta 0.91x (0.75–1.18) length of the anterior one. Halteres and legs yellow.

Wing length 2.38 (2.28–2.47) mm; length to width ratio 2.29 (2.27–2.30). Indices: C, 4.63 (4.25–5.00); ac, 1.55 (1.50–1.57); hb, 0.35 (0.33–0.36); 4c, 0.52 (0.50–0.54); 4v, 1.48 (1.45–1.50); 5x, 1.23 (1.12–1.43); M, 0.41 (0.38–0.45); prox. X, 0.48 (0.45–0.52).

Abdomen: in many specimens the inner border of the marginal bands is broader on tergite III (t III) and t IV, sometimes forming a median stripe. On t VI there is a large median spot which is much darker than the other abdominal markings.

δ Terminalia (Figs 3A; 4A; 5A; 6A, B). Ventral lobe of epandrium apically slightly concave, dorsally obtuse-angled and ventrally roundish (Fig. 4A) bearing about six setae; distoventral membranous area of aedeagus somewhat U-shaped, as seen with the method by SPASSKY (1957) in anesthetized living specimens under stereomicroscope. According to VILELA (1984: 247) there are some similarities between the male terminalia of *D. medioignata* (subgroup II of FROTA-PESSOA, 1954) and those of *D. albirostris* (subgroup III), although they are currently included in different subgroups.

♀ Terminalia (Figs 7A, B; 9A; 10A). Valves of oviscapt (Figs 7A, B) with about 14 marginal and 6 discal peg-like ovisensilla. Spermathecal capsule pear-shaped (Figs 9A; 10A), sclerotized.


Notes. Dobzhansky & Pavan (1950) refer collectively to the following three species: *D. mediostriata, D. mediopunctata* and *D. mediosignata* as medio-group, so the distribution records for *D. mediosignata* in several Brazilian states, especially those located in the Amazonian region, could not be enumerated.

**D. paraguayensis** **Duda, 1927**

(Figs 1: 3B, C; 4B, C; 5B, C; 6C–F; 7C–F; 9B, C; 10B; 11A, B; 12A–H; 13A–H; 14A–D)

*Drassophila paraguayensis* **Duda, 1927**: 185; Bächli, 1984: 250 (syntypes depository).
Fig. 5. Hypandrium, gonopods and paraphyses, posterior view: A, Drosophila mediosignata, paratype; B, D. paraguayensis, São Paulo, 173F170, generation F1; C, idem, Praia Grande, V.1943; D, D. cuaso sp. nov., holotype; E, idem, Bucaramanga.


*Drosophila prosimilis* (sensu DOBZHANSKY & PAVAN, 1943, misidentification, not *Drosophila prosimilis* DUDA, 1927; see material examined).

*Drosophila (Drosophila) medionotata* FROTA-PESSOA, 1954: 288, plate XV, fig. 13 (♂ terminalia), plate XVII, fig. 32 (left oviscap valve, dotted line), plate XVIII, fig. 65 (misspelled as *medionotata*), spermathecal capsule, plate XXIII, fig. 100 (wing); DE CASTRO, 1955: 366 (manuscript name, tarsal setae,); CLAYTON & WASSERMAN, 1957: 126 (as *D. medionotata* ?) strains, metaphase and polytene chromosome numbers); PATTERSON, 1957: 8, 9 (table 2, interspecific
hybridization tests); Pipkin, 1965: 5 (collection); Pipkin et al. 1966: (breeding sites); Wheeler, 1981: 44 (catalogue); Val, 1982: 336 (type series, δ terminalia of holotype and paratype); Val & Kaneshiro, 1988: 193, 194 (collection); Vilela & Bächli, 1990: 257 (δ terminalia, paratype [as a junior synonym of D. paraguayensis Duda, 1927]) (synonymized by Vilela & Bächli, 1990: 102); Sevenster & van Alphen, 1993: 723, 724 (survival time, developmental period); Hoennisberg, 1995: 87 (collection [misspelled as D. medionotata]).

Type locality: Vila Atlântica [located in Mongaguá], state of São Paulo, Brazil.


Additional specimens. MZSP = 4 δ, 1 ♀: "Praia Grande S. Paulo V–943": although not individually labelled as to species these 5 specimens are kept together in the MZSP in the same small box which is collectively labelled prosimilis, and there is strong evidence [collection date, handwritten, and method of double mounting] that the specimens were among those used by Dobzhansky & Pavan (1943) to redescribe D. prosimilis (misidentification, non D. prosimilis Duda, 1927). MZSP = 36 δ, 35 ♀ offspring from first and second generations (including some of undetermined generation) of one isofemale line [date of collection of the wild-caught female]: "BRASIL SP São Paulo Cid. Universitária / Isofemale line IBUSP 173F170 / RATCOV & VILELA leg. 26–28.VII.1997 / [date of emergence and death (variable)] / Drosophila paraguayensis [♀ / ♂] BACCHI, VILELA & RATCOV det. 1999": 1 ♀: idem but mother of isofemale line IBUSP 173F170; (abdomens of 8 δ, ♀ and 8 ♀ taken randomly from the isofemale line 173F170 were photographed on 29.IX.1999 but not preserved); 33 wild-caught δ, ♀, same date and collection site.

Diagnosis. Aedeagus bearing 2 subapical, serrate, lateral, ear-shaped expansions which, in ventral view, are noticeably narrower than those present in D. cuaso sp. nov. and slightly longer than those present in D. mediosignata as in Fig. 6 (see also Vilela & Bächli, 1990: 255–257, figs 98–100). See additional differences under the diagnosis of D. mediosignata.

Redescription (n_max = 21). See also Vilela & Bächli (1990: 102). Frontal length 0.30 (0.27–0.32) mm, frontal index 0.76 (0.70–0.83), top to bottom width ratio 1.24 (1.18–1.32). Postocellar setae strongly convergent or crossed. Length ratio of anterior to posterior orbital seta 0.68 (0.63–0.85), of mid to anterior orbital 0.33 (0.25–0.46); poc 0.66x (0.56–0.76), oc 0.85x (0.67–0.95) frontal length; vt index
Fig. 6. Aedeagus and aedeagal apodeme, left lateral (at left) and ventral (at right) views: A, B, *Drosophila mediosignata*, paratype; C, D, *D. paraguayensis*, São Paulo, 173F170, generation F1; E, F, idem, Praia Grande, V.1943; G, H, *D. cuaso* sp. nov., holotype; I, J, idem, Bucaramanga.

1.12 (1.05–1.21); vibrissal index 0.54 (0.42–0.90). Cheek index about 12. Eye index 1.22 (1.18–1.27). First flagellomere brownish; length to width ratio 1.70 (1.67–1.80). Arista with 5–7 upper and 2–4 lower long branches, plus terminal fork.
Drosophila mediosignata

Fig. 7. Left (A, C, E) and right (B, D, F) oviscapt valves, lateral view: A, B, Drosophila mediosignata, paratype; C, D, D. paraguayensis, São Paulo, 173F170, generation F; E, F, idem, Praia Grande, V.1943.

Thorax length 1.27 (1.12–1.45) mm; h index 1.02 (0.92–1.18); dc index 0.61 (0.59–0.77); scut index 1.05 (0.70–1.16); sterno index 0.57 (0.50–0.68), mid katepisternal seta 0.71x (0.57–0.93) length of the anterior one. Tarsomere 1 of hind leg with short yellow basal-ventral setae. Preapical setae on tibia I (small), 2 and 3, apical setae on tibia 2.

Wing (Fig. 1) hyaline, crossvein dM-Cu distinctly clouded; length 2.52 (2.24–3.10) mm; length to width ratio 2.36 (2.20–2.50). Indices: C, 4.66 (3.50–5.33); ac, 1.70 (1.50–2.00); hb, 0.39 (0.22–0.50); 4c, 0.53 (0.46–0.73); 4v, 1.45 (1.30–1.57); 5x, 1.07 (0.80–1.29); M, 0.37 (0.32–0.44); prox. X, 0.46 (0.39–0.68).

Abdomen (Figs 11A, B; 12A–H; 13A–H) brownish yellow, t II–t IV usually with a more or less distinct, medially interrupted marginal band, t VI usually with a faint median spot which is not darker than the marginal bands (Figs 11A, B; 12A–H). See also item “conclusions”.

♂ Terminalia (Figs 3B, C; 4B, C; 5B, C; 6C–F). Anterodorsal margin (remnant of tergite VIII according to several authors; see Salles, 1947 for discussion)
of the epandrium (tergite IX) is, in lateral view, conspicuously well developed, dor-sally pointed and projected anteriad (see VILELA & BACHLI, 1990: 255, fig.98A, although not exactly in lateral view), being wider than the epandrium itself (twice as wide in aged specimens) whereas in D. cuaso sp. nov. and in D. mediSIGNAta (revaluated) it is of the normal size of most species of Drosophila belonging to the triPunctata group. Ventral lobe of epandrium distally finger-shaped bearing ca. six setae: hypandrium, gonopods and paraphyses as in Figs 5B, C; distoventral mem-branous area of aedeagus somewhat U-shaped, as seen with the method by SPAssKY (1957) in anesthetized living specimens under stereomicroscope.

2 Terminalia (Figs 7C–F; 9B, C; 10B). Valves of oviscapt as in Figs 7C–F, with about 20 marginal and 7 discal peg ovisessilla. Spermathecal capsule some-what oval as in Figs 9B, C, sclerotized; spermathecal duct within the introvert long, as wide as the base of capsule. We want to point out that the median dilatation of the spermathecal duct within the introvert as figured by Frota-Pessoa (1954; plate XVIII, fig. 65) for D. medionotata was not observed in the specimens we dissected (Fig. 10B).

Ecology. Larval breeding sites. PipKIN et al. (1966) bred D. paraguayensis (cited as D. medionotata) from living flowers of Centropogon coccarneus [Campa-nulaceae, in Cerro La Campana], Erythrina berteroaena [Fabaceae, in Cerro La Cam-pana], Helianthus sp. [Asteraceae, in the base of Cerro Campana] and Costus villosissimus [Zingiberaceae, in Ft. Sherman Reservation, Canal Zone] in Panama. They considered this species a polyphagous ground-feeder that only occasionally uses some species of living flowers as breeding sites. SAAVEDRA et al. (1995) bred D. paraguayensis [D. mediSIGNAta and/or D. cuaso sp. nov. might be included or could be the species that really emerged] from rotten [fallen] fruits of Arecastrum romanZoffianum [currently SyagrUS romanZoffiana] (Arecaaceae), in Guafba (state of Rio Grande do Sul, Brazil).

Adult feeding sites. Collected over fruits of Randia armata (Rutaceae) in Turvo and of SyagrUS romanZoffiana (Arecaaceae) in Turvo and Guafba (both in state of Rio Grande do Sul, Brazil) (SAAVEDRA et al., 1995; see comments under larval breeding sites).

Distribution. Honduras ? (La Lima), El Salvador (San Salvador ?, La Palma, Lago de Coatepeque ?, Lago Pichichuela ?), Panama (Canal Zone, Cerro La Cam-pana), Colombia, Brazil (Minas Gerais, Rio de Janeiro, São Paulo and Rio Grande do Sul ?). This species is probably widespread from Panama to meridional South America and sympatric with Drosophila cuaso sp. nov. The question marks following some localities were quoted from the paper of Clayton & WASSERMAN (1957) who were in doubt regarding to the species identification of the strains they used.

Notes. DUDA (1927) based his description of D. paraguayensis upon only two type specimens. After having analyzed both flies it became quite clear to us that the male lectotype (from Petrópolis, Rio de Janeiro, Brazil) and the female paralecto-type (from Hohenau, Paraguay, Figs 14A–C) of D. paraguayensis do not belong to the same species. As the original description was based mainly on the female paralectotype it should be regarded as inappropriate for the current concept of this species (as shown in the present paper). However, the redescriptions of the external features (but not the internal ones) made by VILELA & BACHLI (1990) was based only on the lectotype. The female paralectotype most probably belongs to an as yet unde-
scribed species which was redescribed by FROTA-PESSOA (1954: 278), based on specimens collected in three Brazilian states, as *D. angustibucca* (misidentification, not *D. angustibucca* DUDA, 1925 described from Costa Rica). This undescribed species, as previously suspected by WHEELER (1963: 53), will be described in a forthcoming paper by the second author (CRV) together with some colleagues from Porto Alegre (Brazil) working at the Universidade Federal do Rio Grande do Sul. Therefore, it seems now quite clear why DUDA (1927) mentions that he was not sure whether his description of *Drosophila paraguayensis* referred to an undescribed species or to just a variety of *D. angustibucca* from Costa Rica (DUDA, 1925: 218). Indeed, as previously mentioned, the female paralectotype of *D. paraguayensis* apparently belongs to the above cited undescribed species which seems to be a sibling of *D. angustibucca* from Costa Rica. In short, we currently regard *D. paraguayensis* DUDA, 1927 as a senior synonym of *D. medionotata* FROTA-PESSOA, 1954, based on its male lectotype, but not on its female paralectotype. See VAL (1982) for comments on the type series of *D. medionotata*.

As previously mentioned under the item additional specimens, we have checked five specimens which were probably used by DOBZHANSKY & PAVAN (1943) to redescribe *D. prosimilis* DUDA; they all appear to belong to the nominal species *D. paraguayensis* (see also notes under *D. prosimilis*).

The following differences, regarded as intraspecific variation by us, were observed between the specimens sampled from the isofemale line 173F170 (São Paulo City, state of São Paulo) and the following specimens: those (from Vila Atlântica [located in Mongaguá] also in state of São Paulo) belonging to the type series of *D. medionotata* as well as the drawings presented by FROTA-PESSOA (1954: 256) for this species, in addition to the 5 specimens (MZSP) also collected at Praia Grande (near Vila Atlântica, then belonging to Itanhaém) and used by DOBZHANSKY & PAVAN in their redescription (misidentification) of *D. prosimilis*:

1) The ventral lobe of epandrium bears about 6 setae in the specimens from São Paulo City and about 3 setae in those from Vila Atlântica and Praia Grande (Figs 4B, C).
2) The aedeagus (in profile) is slightly narrower proximally in the specimens from São Paulo City than in those from Vila Atlântica and Praia Grande (Figs 6C, E).
3) The aedeagus (in ventral view) is slightly narrower distally in the specimens from São Paulo City than in those from Vila Atlântica and Praia Grande (Figs 6D, F).

*D. paraguayensis* is kept in the subgroup II of FROTA-PESSOA (1954: 256) as proposed by VILELA & BÄCHLI (1990: 103), although its female paralectotype belongs to subgroup I. According to VILELA (1984: 247) there are some similarities between the male terminalia of *D. paraguayensis* (cited as *D. medionotata*) and those of *D. albirostris*, although they are included in different subgroups.

**Drosophila cuaso sp. nov.**

(Figs 2, 3D, E; 4D, E; 5D, E; 6G–J; 8; 9C, D; 10C, D; 11C, D; 12I–P; 13I–P)


Type locality: Cidade Universitária “Armando de Salles Oliveira”, São Paulo City, state of São Paulo, Brazil.
**Drosophila cuaso**

![Fig. 8. *Drosophila cuaso* sp. nov., left (A, C) and right (B, D) oviscap valves: A, B, allotype; C, D, Bucaramanga.](image)

**Material examined.** Holotype ♂ (dissected, right wing removed), labelled “BRASIL SP São Paulo Cid. Universitária / Isofemale line IBUSP 176F16 / RATCOV & VILELA leg. 15–17.IX.1998 / * 24.XII.98–13.I.99, † 26.II.99 / generation F₁ / Drosophila cuaso BÄCHLI, VILELA & RATCOV det. 1999”. 1 allotype ♀ (dissected, right wing removed): same labels as holotype, except generation (= F₂). 62 paratypes (30 ♂♂ and 32 ♀♀, one ♀ dissected): same isofemale line as holotype, but only some of them were sampled from the same generation as the holotype and they are as follows: 1 wild-caught ♀ who gave origin to the isofemale line I76F16, 3 ♂♂ and 2 ♀♀ of the generation F₁ (emerged 24.XI.98–13.1.99, killed and pinned on 26.II.99), 1 ♂ and 3 ♀♀ (emerged 29.XI.98–22.1.99, killed and pinned on 26.II.99), and 26 ♂♂ and 26 ♀♀ from undetermined generation (emerged 12–19.IX.99, killed and pinned on 11.X.99); all deposited in MZSP. Additional specimens which are not being considered as type specimens: abdomens of 8 ♂♂ and 8 ♀♀ taken randomly from the isofemale line I73F170 were photographed on 29.IX.1999 but not preserved; (MZSP) 12 ♂♂, 13 ♀♀: same site and collection date but Isofemale line IBUSP 176F15. (AMNH) 4 ♂♂, 3 ♀♀ [1 ♂ and 1 ♀ dissected]; “Bucaramanga Colombia Sept. 1956 / HLCARSON, MWASSERMAN / 181.28”; 1 ♂: “Colombia: Medellin Facultad de Agronomía Antioquia 5000’ H91.14 XII/13– XII/15/55 W.B. HEED / Drosophila cuaso BÄCHLI, VILELA & RATCOV det. 1999”.

**Diagnosis.** Aedeagus bearing 2 subapical, serrate, lateral, ear-shaped expansions which, in ventral view, are noticeably wider than those present in *D. mediosignata* and *D. paraguayensis* as in Fig. 6 (see also VILELA & BÄCHLI, 1990: 255–257, figs 98–100)

**Description** ($n_{max} = 20$). Characters as in *D. paraguayensis* except: Frontal length 0.31 (0.29–0.35) mm, frontal index 0.79 (0.71–0.87), top to bottom width ratio 1.25 (1.18–1.32). Length ratio of anterior to posterior orbital seta 0.71 (0.62–0.85), of mid to anterior orbital seta 0.37 (0.30–0.50); poc 0.67x (0.52–0.94), oc 0.82x (0.67–0.94) frontal length; vt index 1.18 (1.00–1.33); vibrissal index 0.49 (0.36–0.61). Cheek index about 11. Eye index 1.17 (1.11–1.22). Arista with 6–8 upper and 3–4 lower branches, plus terminal fork, inner branches short. Proboscis and palpi yellow.
Fig. 9. Inner spermathecal capsules (some are accidentally deformed): A, *Drosophila mediosignata*, paratype; B, *D. paraguayensis*, São Paulo, 173F170, generation F2; C, idem, Praia Grande, V.1943; D, *D. cuaso* sp. nov., allotype; E, idem, Bucaramanga.

Thorax length 1.23 (1.02–1.58) mm; h index 1.02 (0.92–1.17); dc index 0.67 (0.56–0.80); scut index 1.04 (0.96–1.15); sterno index 0.56 (0.48–0.64), mid katepisternal seta 0.78x (0.39–0.93) length of the anterior one. Halteres and legs yellow.

Wing (Fig. 2) length 2.49 (2.14–2.77) mm; length to width ratio 2.37 (2.26–2.61). Indices: C, 4.09 (3.46–5.00); ac, 2.04 (1.50–2.60); hb, 0.42 (0.38–0.57); 4c, 0.61 (0.48–0.68); 4v, 1.51 (1.17–1.71); 5x, 1.11 (0.89–1.29); M, 0.38 (0.32–0.45); prox. X, 0.52 (0.31–0.57).

Abdomen (Figs 11C, D; 12I–P; 13I–P): in many specimens the inner border of the marginal bands is broader on t III and t IV, sometimes forming a median stripe. On t VI there is a large median spot which is much darker than the other abdominal markings (Figs 11C, D; 12I–P, 13I–P). See also item “conclusions”.

♂ *Terminalia* (Figs 3D, E; 4D, E; 5D, E; 6G–J). Anterodorsal margin of the epandrium, in lateral view, blunt and not extremely developed, but projected anteriad (see VILELA & BÄCHLI, 1990: 255, fig. 98A, although not exactly in lateral view), in aged specimens being as wide as the epandrium itself. Ventral lobe of epandrium apically somewhat squared bearing about six setae; membranous distoventral area of aedeagus somewhat V-shaped, as seen in anesthetized living specimens under stereomicroscope.
Drosophila mediosignata  Drosophila paraguayensis

Fig. 10. Inner spermathecal capsules, enlarged (some are accidentally deformed): A, Drosophila mediosignata, paratype; B, D. paraguayensis, São Paulo, 173F170, generation F5; C, D. cuaso sp. nov., paratype; D, idem, Bucaramanga.

♀ Terminalia (Figs 8; 9C, D; 10C, D). Oviscapt valves as in Figs 8A, D, with about 15 marginal and 7 discal peg ovisensilla. Spermathecal capsule somewhat cylindrical as is Figs 10C, D, recalling that of D. mesostigma as figured by FrOTa-
Pessoa (1954, plate XVIII, fig. 44), sclerotized, bearing (not as in other Drosophila species) about 5 uneven short spines around the centroidal area which is subtly invaginated (the specimen from Bucaramanga has much more spines, see Figs 10C, d); introvert long but clearly narrower (ca. half the width of) than the base of capsule; distal half of spermathecal duct within the introvert slightly narrower than the proximal half.

Etymology. The species epithet cuaso is a noun in apposition referring to the acronym of the type locality Cidade Universitária “Armando de Salles Oliveira”.

Notes. Although relatively abundant in the forest reserve of the Cidade Universitária “Armando de Salles Oliveira” during the 24 months survey, D. cuaso sp. nov. was mostly collected in lower numbers than its sibling D. paraguayensis. However, the samples identified by Ratcov & Vilela (1997) as D. paraguayensis will be reanalyzed in the near future in order to check their species identities, as D. mediosignata (revalidated) may be also present in the surveyed area. D. cuaso sp. nov. is reared with much more difficulty in powdered milk-agar medium than D. paraguayensis (at least during the first generation) and does not seem to breed at all in banana-agar medium.

Drosophila proximilis Duda, 1927

Drosophila proximilis Duda, 1927: 194 (tentatively as a variant of D. similis Williston, 1896); Dobzhansky & Pavan, 1943: 23 (misidentification, not Drosophila proximilis Duda, 1927); Frota-Pessoa, 1954: 285 (comparison with D. medionotata); Vilela & Bächli, 1990: 103 (redescription, holotype), 291 (fig. 134F, left oviscapte valve, holotype), 324 (fig. 167I, inner spermathecal capsules, holotype).

Material examined (SMTD). ♀ holotype (head and wings missing; for labels see Vilela & Bächli, 1990:103); two ♂ and two ♀ cited by Duda (1927) in the redescription of D. similis Williston (cardini group) under which he first used the binomial D. proximilis. His comparison between these two forms, in addition to the holotype of D. proximilis, was probably based on these specimens (as supposedly belonging to D. similis) and has been considered as the original description of D. proximilis, although Duda had not described it formally. They are labelled as follows: one ♀ (head and right wing missing): “Bolivia-Mapiri, 22.II.03, S. Antonio 1000 [green with two red stripes] / D. similis Will. ♂ [♀, DET. Dr. O. Duda / Staat Museum für Tierekunde Dresden / Drosophila polymorpha D. & P. G. Bächli det. 1988]”, 1 ♂, 1 ♀ (head missing): “Bolivia-Mapiri, III.03 [♂, 7.II.03, ♂], Sarampioni 700 m [green with two red stripes] / D. similis Will. ♂ [♀ or ♂] / D. DUDA [DET. Dr. O. Duda in ?] / Staat Museum für Tierekunde Dresden / Drosophila polymorpha D. & P. G. Bächli det. 1988”; 1 ♂ (right wing and part of left wing missing, dissected): “Peru-Urubambafi, 14.9.03, Umahuankilia [green] / D. similis Will. ♂ [♀, DET. Dr. O. DUDA / Staat Museum für Tierekunde Dresden / Drosophila polymorpha D. & P. G. Bächli det. 1988 / D. neocardiin ♂ Bächli, Vilela & Ratcov det. 1999”.

Notes. In the four specimens cited above, Duda added question marks in his determination labels, except for the last one. This fact could indicate that the latter specimen (undoubtedly D. neocardini, undescribed at that time) whose aedeagus is depicted in Fig. 14E represents the concept of Duda for D. similis Williston. The first three specimens, although not dissected, clearly belong to D. polymorpha (also undescribed in 1927) and apparently were tentatively identified by him as D. similis. The surstyli of the specimen collected at Sarampioni are visible even without dissection and bear their outer peg-like setae arranged in an ellipse-shaped row (see Val, 1982: 326, figs 5a, b) that so far seems to occur only in D. polymorpha Dobzhansky & Pavan, 1943.

We have found in the MZSP collection five pinned specimens collectively labelled D. proximilis which were collected at Praia Grande, state of São Paulo, Brazil, and were probably among those used by Dobzhansky & Pavan (1943) to rede-
scribe *D. prosimilis* DUDA; as we believe they all belong to the nominal species *D. paraguayensis*, they are listed under this species in the item additional specimens. The lectotype of *D. paraguayensis*, dissected and designated by VILELA & BACHLI (1990: 102), is a male and was collected at Petrópolis, state of Rio de Janeiro, Brazil, and there are no doubts regarding its status.

At present, we are unable to identify females of many species of the *D. tripunctata* group with certainty and the data we have got (VILELA & BACHLI, 1990) from the female holotype of *D. prosimilis* do not allow any decision regarding its identity, except that it seems to belong to the *tripunctata* group. In the holotype of *D. prosimilis*, dissected and photographed by VILELA & BACHLI (1990, figs 134F, 1671), the spermathecal capsule is nearly spherical, recalling that of *D. albescens* as figured by FROTA-PESSOA (1954, plate XVIII, fig. 60), but in *D. prosimilis* the part of the spermathecal duct within the introvert (see THROCKMORTON, 1962: 260, for discussion) clearly has a terminal expansion following a median constriction. The outline of its oviscapte valve also recalls that of *D. albescens* although it seems to be much less setose.

Hence, until one male specimen can be associated to the female holotype, *D. prosimilis* remains a nomen dubium within the *tripunctata* group. Anyway, it seems to be different from the three species discussed above: *D. mediosignata*, *D. paraguayensis* and *D. cuaso*, sp. nov.

PATTERSON & WHEELER (1949: 226) included *D. prosimilis* in the cardini group. However, FROTA-PESSOA (1954: 263), stating that *D. prosimilis* has none of the diagnostic characters of the cardini group, transferred it to the *tripunctata* group, although the limits between those two groups of species are not well defined.

CONCLUSIONS

Etherized imagoes (and sometimes pinned specimens as well) of *D. cuaso* sp. nov. and *D. paraguayensis* (now excluding its no longer junior synonym *D. mediosignata*, revalidated) can distinguished as follows:

1) *D. cuaso* sp. nov. always bears, in both sexes, one black or coffee brown, remarkably shining, well outlined and relatively large spot on the middle area of t VI. In females this spot never reaches the anterior or posterior margin (in males apparently reaches the anterior one) and contrasts noticeably with the posterior bands of the remaining tergites which are light brown in color. In addition, t V may also be spotted in males, in which case the spot is not as dark and shining as that of t VI. Tergite VI of both sexes of *D. paraguayensis* may be completely unspotted, and whenever one middle spot is present it is relatively small, light brown (as the posterior bands of the remaining tergites) and poorly outlined. In addition t V of *D. paraguayensis* is always unspotted.

2) In *D. cuaso* sp. nov. sternite V never covers the surstyli (as seen both in profile and ventral views in anesthetized living specimens under the stereomicroscope) whereas they are conspicuously covered by the distal region of sternite V in *D. paraguayensis*.

3) In *D. cuaso* sp. nov., the general body color (light yellow) is usually relatively lighter, contrasting more effectively with the brown bands of the tergites. The general body color (yellowish) of *D. paraguayensis* is slightly darker and more uniform in relation to the tergite bands.

4) In *D. cuaso* sp. nov., the anterolateral margins of the ventral membranous area of the aedeagus is, in ventral view, somewhat V-shaped and the inner area seems
Fig. 11. Male (left) and female (right) abdominal spotting pattern (non-type specimens): A, B, *Drosophila paraguayensis*, isofemale line I73F170 (São Paulo City, state of São Paulo, Brazil, undetermined generation, emerged 28.VIII–21.IX.1999); C, D, *D. cuaso* sp. nov., isofemale line I76F16 (São Paulo City, state of São Paulo, Brazil, undetermined generation, emerged 28.VIII–3.IX.1999).
Fig. 12. Samples (non-type specimens) of variation of abdominal spotting patterns in eight males of *Drosophila paraguayensis* (A–H), isofemale line 173F170 (São Paulo City, state of São Paulo, Brazil, undetermined generation, emerged 28.VIII–2.IX.1999) and in eight males of *D. cuaso* sp. nov. (I–P), isofemale line 176F16 (São Paulo City, state of São Paulo, Brazil, undetermined generation, emerged 28.VIII–2.IX.1999).
Fig. 13. Samples (non-type specimens) of variation of abdominal spotting patterns in eight females of *Drosophila paraguayensis* (A–H), isofemale line 173F170 (São Paulo City, state of São Paulo, Brazil, undetermined generation, emerged 28.VIII–2.IX.1999) and in eight females of *D. cuaso* sp. nov (I–P), isofemale line 176F16 (São Paulo City, state of São Paulo, Brazil, undetermined generation, emerged 28.VIII–2.IX.1999).
to be relatively longer than wide as can be seen (when the aedagus is not yet completely extruded) in living specimens by gently pressing the abdominal tip with the aid of a pair of entomological pins. In *D. paraguayensis* the anterolateral margins of the ventral membranous area of the aedagus are, in ventral view, somewhat U-shaped and the inner area seems to be relatively wider than long (Figs 6D, F) (see also Vilela & Bächli, 1990: 255, fig. 98H; 257, fig. 100D) than in *D. cuaso* sp. nov. (Figs 6H, J).

5) In males of *D. cuaso* sp. nov. the marginal setae of tergite VI are as strong as the marginal setae of the previous tergites whereas in males of *D. paraguayensis* they are noticeably thinner.

We did not analyze an isofemale line of *Drosophila mediosignata* (revalidated). However, the reappraisal of the type material and of the illustrations presented by Vilela & Bächli (1990: 256) permit to distinguish it from its two siblings species, namely *D. cuaso* sp. nov. and *D. paraguayensis*, as follows:

1) The spots on the t VI, whenever present, are virtually of the same variation as in *D. paraguayensis*, but clearly not so different in color compared to the bands of the preceding tergites as in *D. cuaso* sp. nov.

2) Whereas in aged specimens of *D. cuaso* sp. nov. and *D. mediosignata* the anterodorsal margin of the epandrium is of the normal size of most species of *Drosophila* belonging the *tripunctata* group, in *D. paraguayensis* this supposed remnant of t VIII is twice as wide as the epandrium itself (t IX) (see Vilela & Bächli, 1990: 255, fig. 98A, although they were not depicted exactly in lateral view).

3) The lower inner corner (tip) of the cerci of *D. paraguayensis* (see Vilela & Bächli, 1990: 255, fig. 98A; 257, figs 100A, B) and *D. cuaso* sp. nov. shows two or three small setae which are completely absent in *D. mediosignata* (see Vilela & Bächli, 1990: 256, figs 99A, B).

4) The ventral lobe of epandrium is apically slightly concave, somewhat right-angled dorsally and roundish ventrally in *D. cuaso* sp. nov. and finger-shaped in *D. paraguayensis* (see also Vilela & Bächli, 1990: 255, fig. 98A; 257, figs 100A, B), while in *D. mediosignata* (see also Vilela & Bächli, 1990: 256, figs 99A, B) it is slightly concave apically, obtuse-angled dorsally and somewhat roundish ventrally, being intermediate in shape between that of *D. paraguayensis* and *D. cuaso* sp. nov.

5) The prensisetae of the surstyli are arranged in a neat sigmoid-shaped row in *D. mediosignata* and a hook-shaped row (sometimes also slightly sigmoid-shaped) in *D. paraguayensis* and *D. cuaso* sp. nov.

6) In *D. cuaso* sp. nov. the aedeagus (in lateral profile) is remarkably thinner than those of the other two species and bears a pair of much wider, marginally serrate, ear-shaped, lateral subdistal expansions, as seen in ventral and dorsal views. The aedeagus of *D. mediosignata* is somewhat elliptical in lateral profile while in *D. paraguayensis* it is somewhat triangular.

7) The inner spermathecal capsules of *D. mediosignata* are pear-shaped and most distinct from those of the other two species. The proximal aperture of the capsule is larger in *D. paraguayensis* than in *D. cuaso* sp. nov. The distal surface of the inner spermathecal capsule of *D. cuaso* sp. nov. is slightly invaginated and conspicuously covered with tiny spines (absent in the other two species).

Many of the differences between *D. mediosignata* and *D. paraguayensis* listed above have been pointed out previously by Frota-Pessoa (1954: 287–288) but were regarded as intraspecific variation by Vilela & Bächli (1990).
Fig. 14. A–D: Drosophila paraguayensis Duda, 1927, paralectotype ♀, SMTD (Hohenau, Paraguay, 06.X. 1907) (undescribed Drosophila species, different from male lectotype). A, left wing, dorsal view; B, left oviscapt valve; C, right oviscapt valve; D, inner spermathecal capsules. E, D. neocardinii Streisgung, 1946, SMTD (Peru, Urubamba River, Umahuankilia, 14.IX.1903), aedeagus and aedeagal apodeme, left lateral view.

The information found in the literature regarding distribution, ecology and other aspects of D. mediosignata (revalidated), and D. paraguayensis as proposed in the present paper are to be regarded with caution as they may refer to different biological species. It is likely that they have also been confused with their sibling D. cuaso sp. nov.

The only paper in the literature known to us that has probably used the binomial D. paraguayensis as we currently understand it is that by Vilela & Mori (1999). Males and females belonging to one isofemale line (184F47) from Serra do Cipó (state of Minas Gerais, Brazil) and maintained in IBUSP were analyzed regard-
ing both their external and internal morphology, which mostly agree with the diag-
osing traits proposed in the present paper. It should be noted that the ventral lobe of
their epandrium seems to be more similar to that found in specimens from the
isosexual line I73F170 (São Paulo City) than to that from the specimens collected
at Praia Grande in May, 1943 (Figs 4B, C). However, the 53 other specimens identi-
fied by them (VILELA & MORI, 1999: 323) as D. paraguayensis were not analyzed as regards to the terminalia. Hence, for the time being we cannot state that D. medio-
SIGNATA (revalidated) is not included in that sample, but based on the analysis of
their abdominal banding and spotting pattern it can be said that none of the 54 spe-
cimens belong to D. cuaso sp. nov.

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