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Revision of the Morphocryptic, Caribbean *Mayaguana* Species Subcluster in the *Drosophila repleta* Group (Diptera: Drosophilidae)

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ABSTRACT

Two new species are described from the Caribbean: *Drosophila* (*D.*) *straubae,* from Cuba, Hispaniola, and Navassa Island (west of the Haitian peninsula); and *D. parisiena,* from Cuba, Hispaniola, and Jamaica. It is possible that at least one of the Jamaican populations of *D. parisiena* is another, more cryptic, species. *Drosophila mayaguana* Vilela has been found to occur not only on Mayaguana Island (Bahamas), but also on Conception, Little San Salvador, Exumas and Great Inagua Islands (Bahamas); and on Grand Cayman (U.K.), Cuba, Hispaniola, Jamaica, and Tortola (British Virgin Islands). These species form a group of closely related sympatric species, based on the morphology of male genitalia and polytene chromosomal work still in progress. Diagnostic features separating the species were found using larval, pupal, adult female, and adult male characters, and the host cactus species that serve as breeding sites. *Drosophila straubae* and *D. parisiena* are most similar morphologically and chromosomally, which agrees with previous electrophoretic studies. The larvae of *D. mayaguana* and *D. straubae* breed in the rotting cladodes of *Opuntia stricta* cactus, and the decaying arms of several species of *Cephalocereus. D. mayaguana* also uses decaying leaves of *Agave* while *D. straubae* also uses *Opuntia moniliformis. Drosophila parisiena* is restricted to *Stenocereus hystrix.*

INTRODUCTION

Vilela (1983) published a major revision of the *Drosophila repleta* group, in which he included 76 species, 13 of them new. About eight species have been added to the *repleta* group since then by various authors. The discovery of the two new species described here is a result of several expeditions which surveyed the Caribbean for members of the pre-

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TABLE 1
Drosophila parisiena

Strain/origin	1	2	3	4	5	6	7
951.55: Barahona, Dom. Rep.	13 11–14 (N = 4)	35 μm – (1)	210 μm – (1)	95 μm – (1)	2.21 – (2)	19 17–21 (4)	13 13–14 (2)
940.10: Monte Cristi, D.R.	13 12–15 (3)	38 – (1)	200 – (1)	95 – (1)	2.10 – (1)	19 18–21 (5)	13 12–14 (5)
ORV-4: Hatillo, DR	13 12–14 (10)					17 15–18 (18)	13 11–15 (7)
ORV-33: CUBA	12 11–14 (4)	35 – (2)	192 185–200 (2)	72 55–90 (2)	2.66 – (2)	18 17–19 (6)	15 13–17 (3)
ORV-23: Palisades, JAM	12 11–12 (4)	37 37–38 (2)	183 180–187 (2)	62 60–65 (2)	2.95 – (2)	19 17–21 (16)	18 16–23 (14)
ORV-24: Port Hend., JAM	13 11–14 (6)	38 35–41 (2)	215 – (2)	103 100–105 (2)	2.08 – (2)	22 21–23 (7)	21 20–25 (7)
ORV-2: Gonaives, HAITI	13 11–15 (9)					16 15–17 (12)	14 12–16 (8)

1 = Number of marginal pegs on oviscapt; 2 = endophallus thickness; 3 = aedeagus length; 4 = length of aedeagal apodeme; 5 = ratio: length of aedeagus/aedeagus apodeme; 6 = number of teeth on surstylus; 7 = number of setae on ventral epandrial lobe.

dominantly Neotropical *Drosophila repleta* species group and their natural breeding sites. The expeditions took place on cruises CF-8205 and CF-8314 of the NSF Ocean Research Vessel (ORV) Cape Florida.

Drosophila straubae, n. sp. and *D. parisiena,* n. sp. were originally recognized by polytene chromosome inversion differences. Morphological details were then found that distinguish the three species in the *mayaguana* subcluster. The polytene chromosomes are described elsewhere by Dr. Marvin Wasserman. A comprehensive electrophoretic comparison of allozymes was made of the same species and cultures that were studied here morphologically (Heed et al., 1990); the results of that study will be discussed at the end of this paper.

In *Drosophila* taxonomy, the taxonomic unit of major importance is the species group. For larger, well-studied species groups there are lower hierarchical ranks; for species within the *repleta* group these are subgroups, complexes, and clusters (in descending order), with subcategories for the complexes and clusters. The *mayaguana* subcluster belongs to the *mulleri* cluster of species, and the *mulleri* cluster belongs to the larger *mulleri* complex in the *mulleri* subgroup. The taxonomy of *repleta* group relationships as summarized by Wasserman (1982a, 1982b) is based on polytene chromosomes; Heed et al. (1990) reviewed the *mulleri* complex.

The morphological terminology used in Vilela (1983), which was derived from McAlpine (1981), is used here with several exceptions. Vilela's "gonopods," a pair of lobes immediately ventrolateral to the aedeagus, are actually the paramere sensu McAlpine (paraphysis according to Grimaldi [1987]), and his "concha of hypandrium" is the gonopod. Also, what Vilela terms the primary and secondary teeth are called here prensisetae, after McAlpine (1981) and subsequently Grimaldi (1987). The departure of drosophilists from the standard terms to the use of those of McAlpine ("clasper" instead of surstylus; "genital arch" instead of epandrium) is necessary in order to make statements concerning homologous structures among various Diptera, as well as to standardize terminology for dipterists. Since the study material is derived from laboratory cultures, we were able to compare features rarely used in field-captured *repleta* group specimens, namely, several internal morphological structures, immature features, and female genitalia. Traditionally, female genitalia have not been used in the identification and classification of *repleta* group flies (e.g., Vilela, 1983), because of the difficulty of associating wild-caught males and females. Thus, it is interesting to note that the oviscapt ("ovipositor") can be diagnostic in two species that are otherwise morphologically very similar.

Collectors for most of the cultures (except types) are not listed since a team of eight scientists participated in the trip; among them were William B. Heed, Marvin Wasserman, and William T. Starmer. Islands that were surveyed in the expeditions but which yielded no *mayaguana* subcluster flies were the following: Cayman Brac and Little Cayman Islands, Montserrat (northern Lesser Antilles), and Virgin Gorda (British Virgin Islands). Microsocope slide preparation of the genitalia involved the glycerine jelly technique discussed in Grimaldi (1987), which insures a consistent orientation when viewing particular structures and drawing them with a camera lucida. To measure the lengths of the curved filaments on the anterior spiracles of the pupa, a compound microscope was used to project a camera lucida image at 100× magnification; a string was laid along the image, then straightened, measured, and the length converted to microns. Types and all other pinned and slide-mounted specimens are in the American Museum of Natural History.

Acknowledgments

Peling Fong gave assistance with the scanning electron microscopy, Toby Schuh loaned his stage micrometer, and Marvin Wasserman and Wayne Mathis provided comments on the manuscript. André Lachance, University of Western Ontario, provided valuable material from the Bahamas. This research was supported by NSF Grant DEB-8207056 to WBH.

TAXONOMY

Drosophila parisiena Heed and Grimaldi, new species

Figures 1–5,16,17,24–27,40,41–44, 59,60,62,65,66, Table 1

Drosophila SB-5: Heed et al., 1990.

DIAGNOSIS: Distinguished mostly on the basis of male genitalia: surstylus strongly crescentic, with row of 15–21 prensisetae pegs along medial margin (mean of 18); aedeagus slightly longer (mean of 200 μm) than in *D. straubae* (mean of 192 μm); distiphallus with apical tooth slightly more prominent (in lateral view) than in *D. straubae*; male genitalia otherwise indistinguishable from those of *D. straubae*. Ventral margin of ventral epandrial lobe oblique (males). Females: apex of oviscapt narrower in lateral view than in *D. straubae*. Pupa: trunk of anterior spiracle much shorter than in *D. straubae* (about same length as longest spiracular filaments). Larva: hooked portion of mandible deeper in lateral view than in *D. straubae*.

DESCRIPTION: **Adult:** Head: eyes red-brown, with dense, short pile. Frontal-orbital plate yellow, frontal vitta light brown (both approximately equal in width). Edges of ocellar triangle yellow, dark brown between ocelli. Face mostly yellow except these light brown areas: down the medial portion of the anterior surface of the carina, anterodorsal portion of pedicel and flagellomere I. Tiny flagellomere II yellow, arista dark brown. Gena yellow. Inner vertical and outer vertical setae about equal in length, both distinctly longer than postocellars. Postocellars convergent, ends touching. Ocellars extended to slightly past bases of proclinates. Posterior reclinate slightly longer than proclinate. Anterior reclinate ca. one-half the length of post. reclinate; closer to proclinate than to post. reclinate, and slightly lateral to the line connecting post. reclinate and proclinate. 6 or 7 orbital setulae anterior to and in line with ipsilateral reclinates. Row of 4 or 5 interfrontal setulae in middle of frontal vitta. Flagellomere 3 (arista) with 3 dorsal plus 2 ventral branches (excluding terminal fork) and 4 or 5 minute medial branches. Proboscis entirely yellow. Vibrissa subtended by 5 smaller, subvibrissal setulae which point anteriad, 5 smaller, subvibrissal setulae pointed dorsad. 2 genal setae.

Thorax: Ground color of mesonotum light brown, with a small, dark brown spot at the base of each seta and setula. Postpronotal lobe yellow; dorsal surface of scutellum mostly dark brown, with a yellow rim. Postnotum, dorsal portions of anepisternum and anepimeron, and ventral portion of katetergite dark brown. Halter knob entirely yellow, halter stem light brown. Ventral edge of posterior spiracle with dark brown rim. Legs uniformly light yellow, mid and hind tibiae with light brown band on proximal end. Acrostichals in 8 rows. No prescutellars. Anterior dorsocentral slightly more than one-half length of posterior dorsocentral. 2 humeral, 2 notopleural, 2 supralars, and 2 long, subequal katepisternal setae present. Katepisternum with 5 or 6 minute setulae in vertical row, 5 others. Anterior scutellars slightly convergent, posterior scutellars cruciate for ca. one-third their length. Wing hyaline. Measurements: Costal Index = 4.26 (males), 4.07 (females) (N = 5 each, for all material cited hereafter), 4-V index = 2.31 (M), 2.18 (F). Thorax length = 0.95 (M), 1.05 (F).

Abdomen and terminalia: Posterior half to two-thirds of tergites dark brown, medial portion entirely interrupted, forming yellow stripes down middle of tergites. Each band widened to full width of tergite on lateral surface. Sternites, epandrium, cerci, epi- and hypoproct, and oviscapt, yellow. Epandial lobe with oblique ventral margin in lateral view, usually concave outline (but not concave in Jamaican specimens). Epandrial lobe with 13–17 (mean of 14) setae in all populations except Jamaica; with 16–25 setae in Jamaican populations (mean of 19). Aedeagus crescentic in lateral view, distiphallus with brush of fine spicules on distal half of ventral surface; distiphallal shape triangular in dorsoventral view. Lateroventral edges of distiphallus produced into flaps, bearing fine scales. Fewer and less prominent spicules and scales occur in the Jamaican populations. Prominent spine at apex of dorsal margin. Phallosomal index means = 2.08–2.95. Medial margin of surstylus strongly crescentic, bearing 15–21 (mean of 18) prensisetae pegs. Testis of living fly lemon yellow, becoming slightly darker with age. Oviscapt with 11–15 (mean of 13) ovisensilla pegs on outer margin, 2 on lateral surface. Apex of oviscapt abruptly narrowed into terminal point. Spermathecal capsule dome-shaped, distal half slightly wrinkled, sometimes finely papillate; introvert extended three-fourths into capsule.

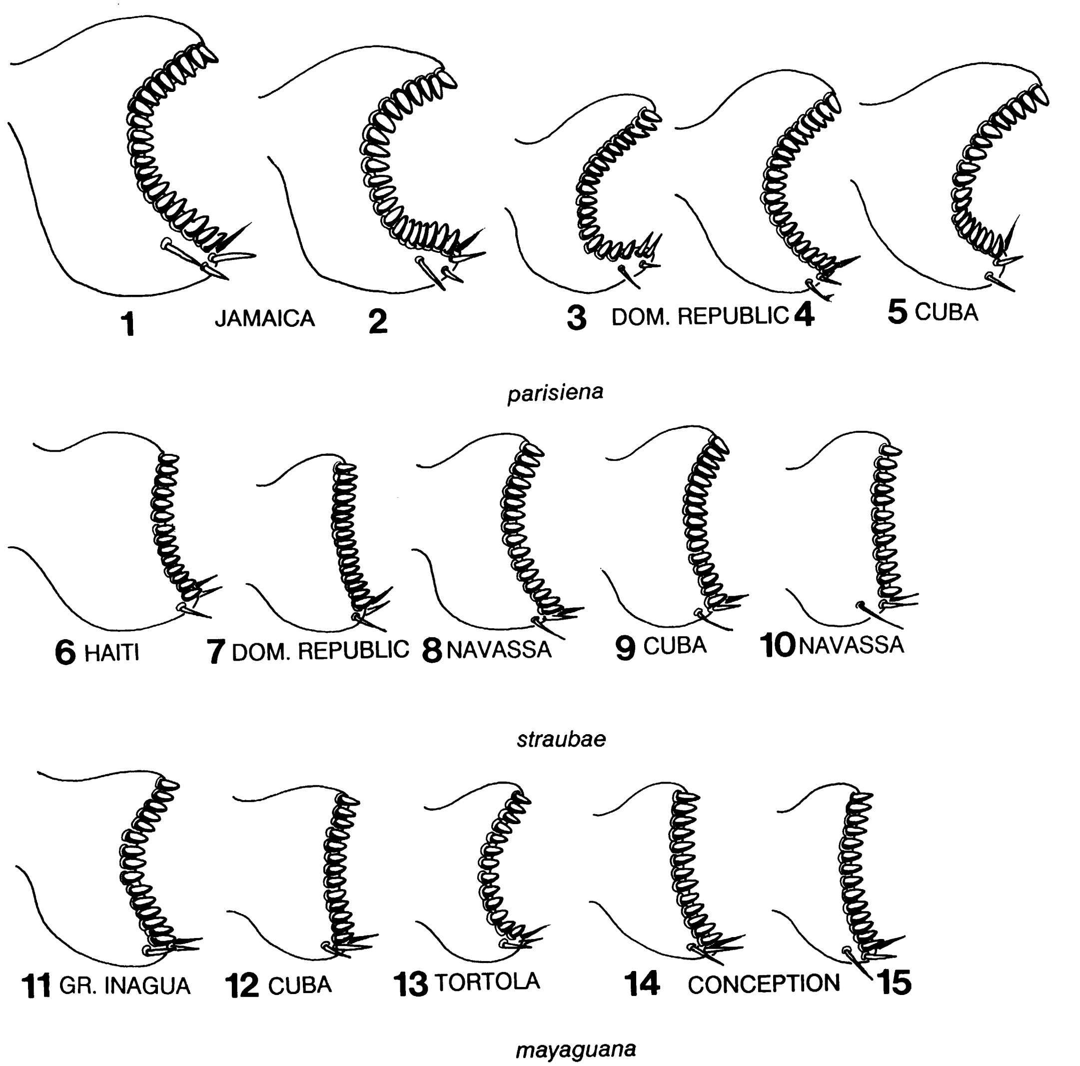
Pupa: Trunk length of anterior spiracle from 310 to 380 μm in lab reared specimens (mean of 350 μm); length of longest spiracular filament 410–450 (mean of 430 μm) (N = 4). Anterior spiracles with 8–10 filaments. Ratio of longest filament length/trunk length = 1.24 (1.08–1.42). Larva: Hooked portion of mandible deeper in lateral view than in *Drosophila straubae*. Egg: 0.5 mm long, with 0.7 mm long filaments; posterior filaments slightly longer than anterior filaments.

Metaphase chromosomes: 5 pairs of rods, 1 pair of dots. The X chromosome is the longest rod, the Y chromosome is three-quarters the length of the X and is J-shaped. From culture ORV-4, Hatillo, Dominican Republic.

ETYMOLOGY: For the type locality of the species, Fond Parisien, Haiti.

HOLOTYPE: Male, from laboratory culture no. ORV-1 collected by W. B. Heed and M. Wasserman 7/V/82 in Haiti: Ouest Province, Fond Parisien, east of Port-au-Prince. 10 male and 10 female paratypes from this same culture have been designated. All types in the AMNH.

MATERIAL EXAMINED: Numerous males and females from cultures established at the following localities: **CUBA:** Guantánamo Province, Guantánamo Bay U.S. Naval Reserve, culture ORV-33 started with material collected IX/18/88. **HISPANIOLA: DOMINICAN REPUBLIC:** Azua Province, Hatillo, culture ORV-4 started with material collected 12/V/82; Barahona Province, culture 951.55; Monte Cristi Province, near Monte Cristi, cultures 940.10 and 950.25; **HAITI:** Artibonite Province, 5 km N Gonaives, cultures 902.9 started with material collected 9/V/82. Ouest Province: between Port-au-Prince and Mirebelais, culture 903.7, started

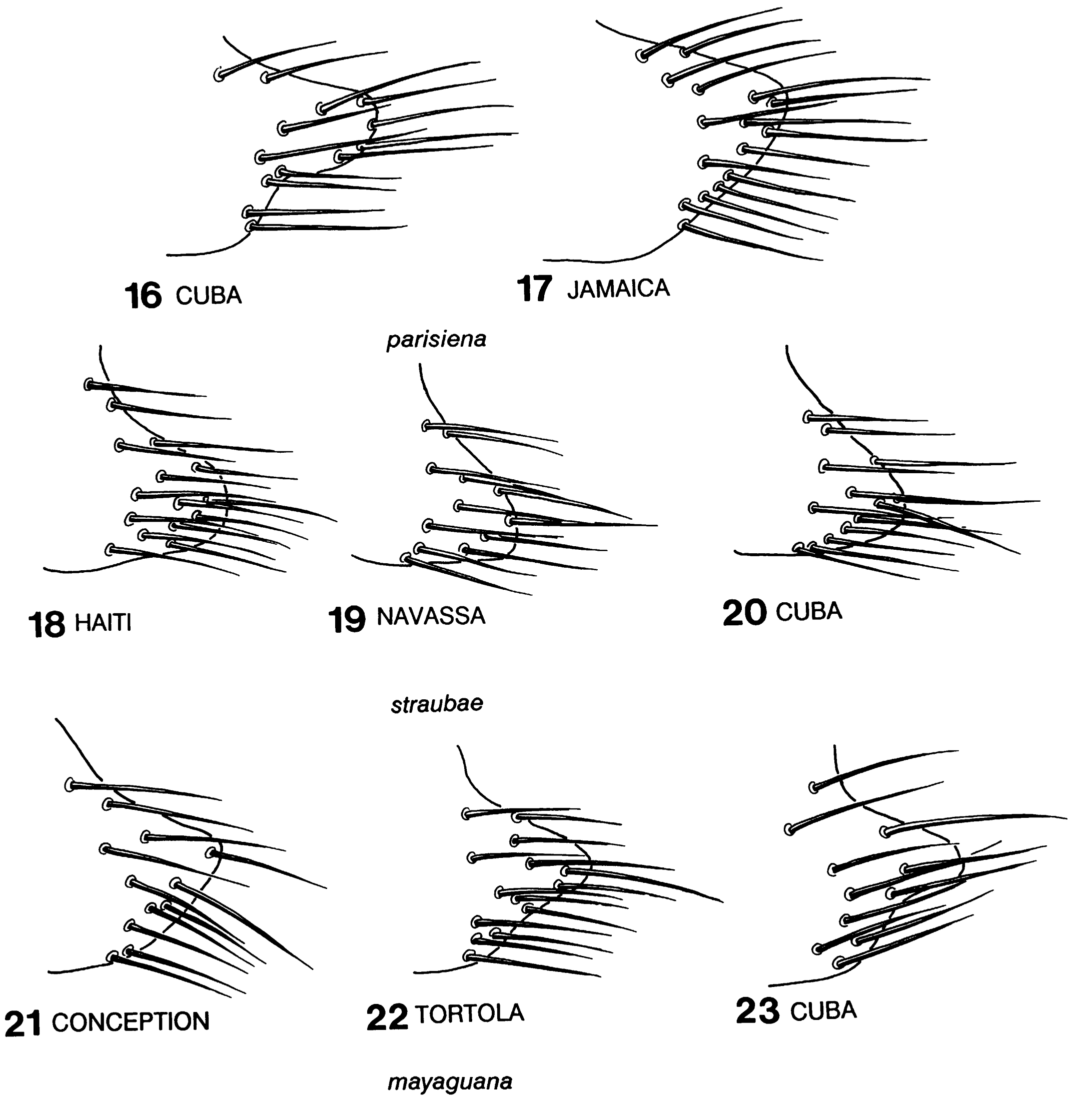


Figs. 1–15. Intra- and interspecific variation in surstyli.

with material reared 8/V/82 from a *Stenocereus* cactus rot. **JAMAICA:** Palisades Airport and Port Henderson, near Kingston, cultures ORV-23 and ORV-24 started with material collected 24–25/XI/83.

HOSTS: 1948 specimens of *D. parisiena* were reared from rot pockets in the cactus *Stenocereus hystrix.* The numbers and localities of reared specimens are the following: Cuba: Guantánamo Bay (780). Dominican Republic: Azua (84), and Hatillo (28). Haiti: Fond Parisien (720), Gonaives (251), Pont Beudet (80), Galeon (5). Several species of *Opuntia* and *Cephalocereus* were surveyed in collecting areas where *D. parisiena* was found, but this species did not occur in these cacti. In fact, the larvae of this fly do not coexist with other *Drosophila,* which suggests that perhaps nutritional and/or chemical defenses are responsible for the monophagy.

DISCUSSION: The phenotypic limits of this species are not especially clear because of the differences seen between the Jamaican specimens and those from the other localities. In particular, the Jamaican specimens have significantly more prensisetae on the surstylus (means of 19 [range 17–21] and 22 [21–23]) (vs. mean of 18 [range 15–21] for other lo-

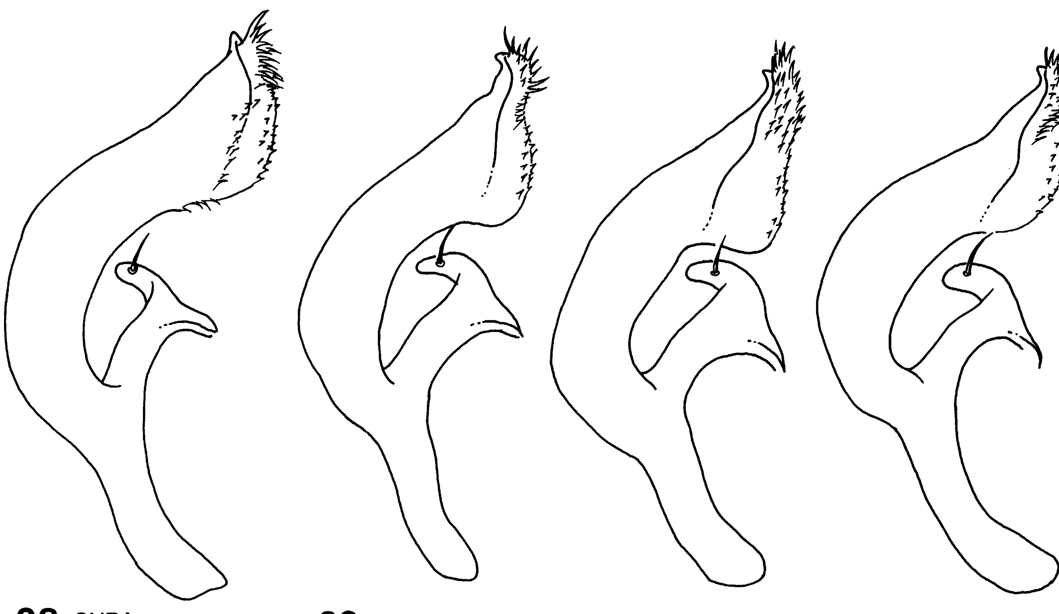


Figs. 16–23. Intra- and interspecific variation in the ventral margin and setation of epandrial lobes.

calities), and a corresponding higher number of setae on the ventral lobe of the epandrium (means of 18 and 21) (vs. mean of 14 for other islands). In addition, the ventral margin of the epandrial lobe is not indented as in *D. parisiena* specimens from other localities, the surstylus is noticeably larger, and the distiphallus possesses smaller and fewer apical spicules and membrane scales. No differences were found with female or immature characters, but the uniqueness of the Jamaican populations corresponds well with the electrophoretic evidence and hybridization. Regardless of how the electrophoretic tree is rooted, or the computer algorithm used, the two Jamaican populations of *D. parisiena* always show up as a monophyletic sister group to the rest of the *D. parisiena* populations (Heed et al., 1990). Also, the cross between Jamaican *parisiena* with any strain of *D. straubae* is the only one to produce infertile males; all other *straubae* × *parisiena* crosses produce fertile males (M. Wasserman, personal commun.). In lieu of data on morphometrics and mating preference, and any consistent differences in immature and female

24 JAMAICA **25** JAMAICA **26** CUBA **27** DOM. REPUBLIC

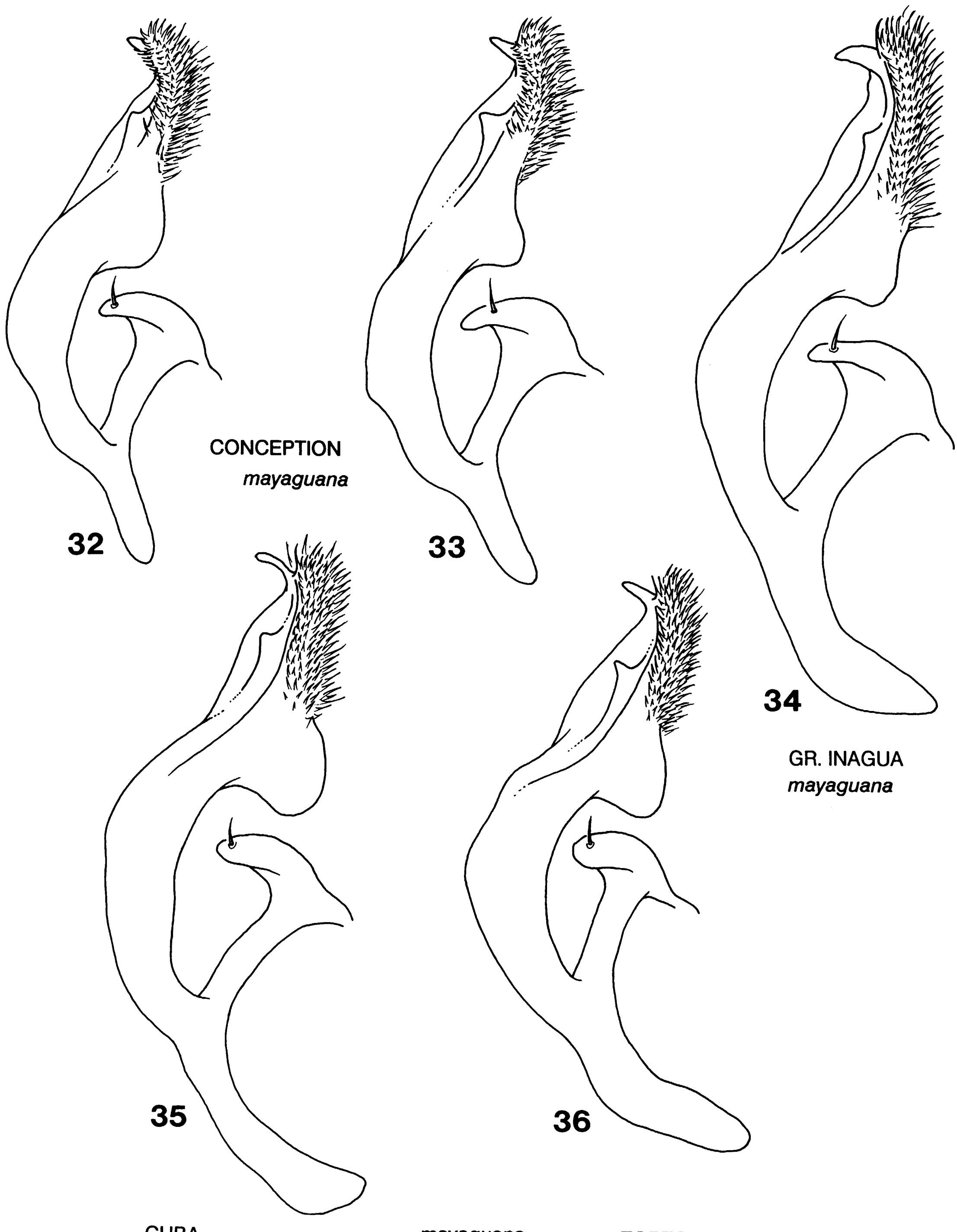
parisiena



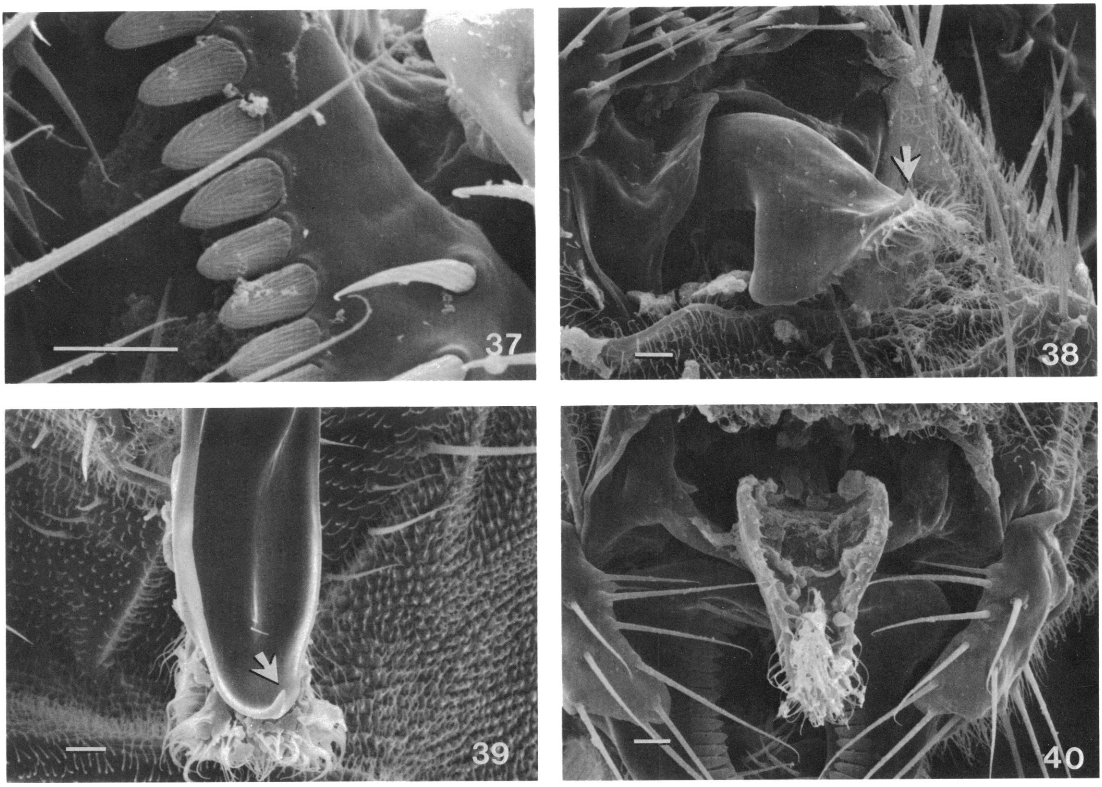
28 CUBA **29** HAITI **30** NAVASSA **31** DOM. REPUBLIC

straubae

Figs. 24–36. Intra- and interspecific variation in aedeagi and aedeagal apodemes (lateral views).



Figs. 24–36 (*Continued*)



Figs. 37–40. Scanning electron micrographs of male genitalia. **37, 38.** *Drosophila straubae,* n. sp. **37.** Detail of prensisetae. **38.** Oblique apical view of distiphallus, showing lateral flanges, spicules, and dorsal-apical tooth (arrow). **39.** *Drosophila mayaguana* Vilela, dorsal view of distiphallus; arrow points to dorsal-apical tooth. **40.** *Drosophila parisiena,* n. sp.; ventral view showing epandrial lobes, portion of surstyli, and distiphallus (center). Scale bars = 10 μm.

characters, we believe it is prudent to retain the Jamaican populations within *D. parisiena.*

Drosophila straubae
Heed and Grimaldi,
new species
Figures 6–10,18–20,28–31,37,38, 47–49,55–57,61,64,Table 2

DROSOPHILA SB+: Heed et al., 1990.

DIAGNOSIS: This species is best distinguished from *D. parisiena* by the following features: Males: Inner (toothed) margin of surstylus barely crescentic, almost straight; surstylus with row of generally 15 to 16 prensisetae pegs along medial margin [compared to a mean of 18 in *D. parisiena*]; ventral margin of epandrial lobe with straight, not oblique, margin; tooth on dorsoapical surface of distiphallus minute, or barely evident. Females: oviscapt has a more rounded apex in lateral view. Pupa: trunk of anterior spiracle long, about same length as longest spiracular filament. Larva: hooked portion of mandible shallower in lateral view.

DESCRIPTION: **Adult:** The species agrees in most characteristics with those given under the description for *D. parisiena,* and so the diagnosis above is most informative for the unique features. Measurements: Costal index = 4.45 (M), 4.17 (F); 4-V index = 2.06 (M), 1.99 (F). Thorax length = 0.988 (M), 1.059 (F). For other measurements see table 2.

Pupa: Trunk length of anterior spiracle in lab reared material 490–520 μm (mean of 370); length of longest spiracular filament 300–390 μm (mean of 370) (N = 4). Anterior spiracles with 8–10 filaments. Ratio of long-

TABLE 2
Drosophila straubae

Strain/origin	1	2	3	4	5	6	7
941.1: Barahona, D.R.	13	39 μm	183 μm	92 μm	1.99	16	14
	12–14	35–40	180–185	85–100	—	15–17	13–14
	(4)	(2)	(2)	(2)	(2)	(6)	(2)
ORV-1: F. Parisien, HAITI	14	37	191	79	2.42	15	13
	13–16	37–38	190–192	70–88	—	13–19	10–16
	(6)	(2)	(2)	(2)	(2)	(19)	(16)
ORV-34: CUBA	14	39	197	86	2.29	15	13
	13–16	37–41	190–210	80–100	—	14–16	11–14
	(4)	(4)	(4)	(3)	(3)	(12)	(7)
922: NAVASSA I.	13	38	197	82	2.14	16	12
	12–16	38–39	190–205	80–85	—	14–17	12–13
	(10)	(2)	(2)	(2)	—	(7)	(4)

For measurements 1–7, see table 1.

est filament length/trunk length = 0.72–1.13 (mean of 0.88). Larva: mandible as stated in diagnosis. Egg: as in *D. parisiena.*

Metaphase chromosomes: Not examined.

ETYMOLOGY: patronym, for Jean Straub Russell, co-investigator with W. B. Heed for many years.

HOLOTYPE: Male, from laboratory culture no. ORV-1 collected by W. B. Heed and M. W. Wasserman 7/V/82 in Haiti: Ouest Province, Fond Parisien, east of Port-au-Prince. 10 male and 10 female paratypes from this same culture have been designated. All types in the AMNH. This is a locality sympatric for *parisiena* and *straubae.*

MATERIAL EXAMINED: Numerous males and females from cultures established at the following localities: **CUBA:** Guantánamo Province, Guantánamo Bay U.S. Naval Reserve, cultures ORV-34 and ORV-30 started with material collected XI/18/83. **HISPANIOLA: DOMINICAN REPUBLIC:** Barahona Province, 25 km N Barahona, from laboratory cultures 951.5 L2 and 941.1, started with material collected 22/VII/85. **NAVASSA ISLAND:** Culture 922.2, started with material collected 21/XI/83 on *Opuntia* cactus. Navassa is a tiny island, ca. 2 mi long, in possession by the USA, lying between Haiti and Jamaica.

HOSTS: 2238 specimens were reared from the following three cactus hosts in the localities indicated: *Opuntia moniliformis*: Fond Parisien, Haiti (1542); Azua, Dominican Republic (2); Guantánamo Bay, Cuba (28). *Opuntia stricta*: Navassa Island (195). *Cephalocereus* sp.: Guantánamo Bay, Cuba (471). The larvae were found to coexist in the cactus rots with *Drosophila mulleri* Sturtevant in Hispaniola and with *Drosophila stalkeri* Wheeler in Cuba.

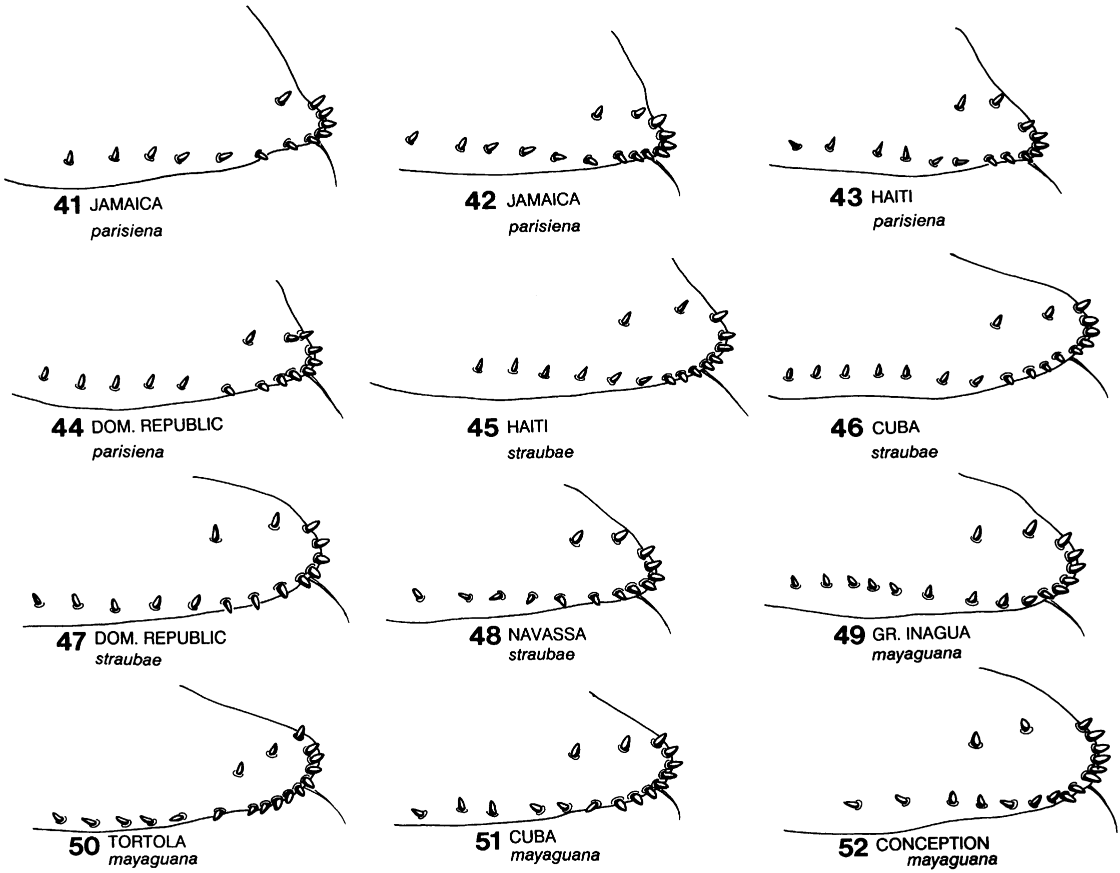
Drosophila mayaguana

Figures 11–15, 21, 23, 32–36, 39, 49–52, 53, 54, 63, 67, Table 3

Vilela, 1983: 98. Type locality: Mayaguana Island, Bahamas. Holotype: Male, genitalia dissected and figured (fig. 82, p. 99); in American Museum of Natural History.

DIAGNOSIS: This species is easily distinguished from *D. parisiena,* n. sp. and *D. straubae,* n. sp. based on the following genitalic features: dorsoapical tooth on distiphallus large; distiphallus laterally with pair of dorsal teeth and flanges; ventroapical half of distiphallus with dense, long spicules; oviscapt (female) with 15–16 marginal pegs (instead of 12–14 in *straubae* and *parisiena*). Pupa: Anterior spiracles: ratio of longest filament/trunk length = 0.48:0.75; trunk about same length as in *D. straubae,* but filaments slightly shorter.

DESCRIPTION: **Adult.** Mean length of aedeagus 245 μm (range 230–265); phallosomal index = 1.97–2.87 (reported as 1.7 by Vilela [1983]). Ground color of thorax is brown in all populations of *mayaguana* except ones from the Bahamas islands, which are tan to light brown.

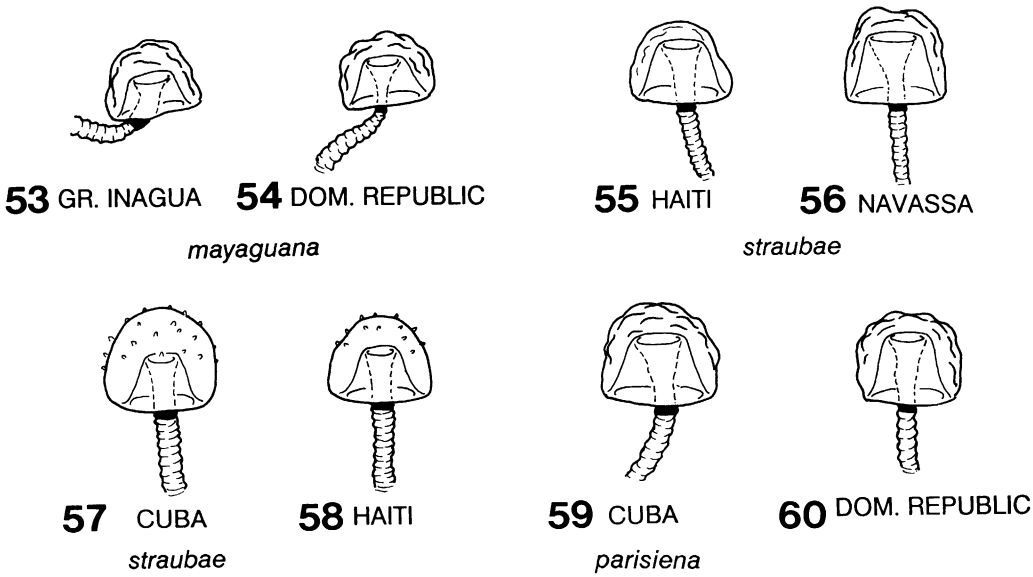


Figs. 41–52. Intra- and interspecific variation in oviscapts (lateral views).

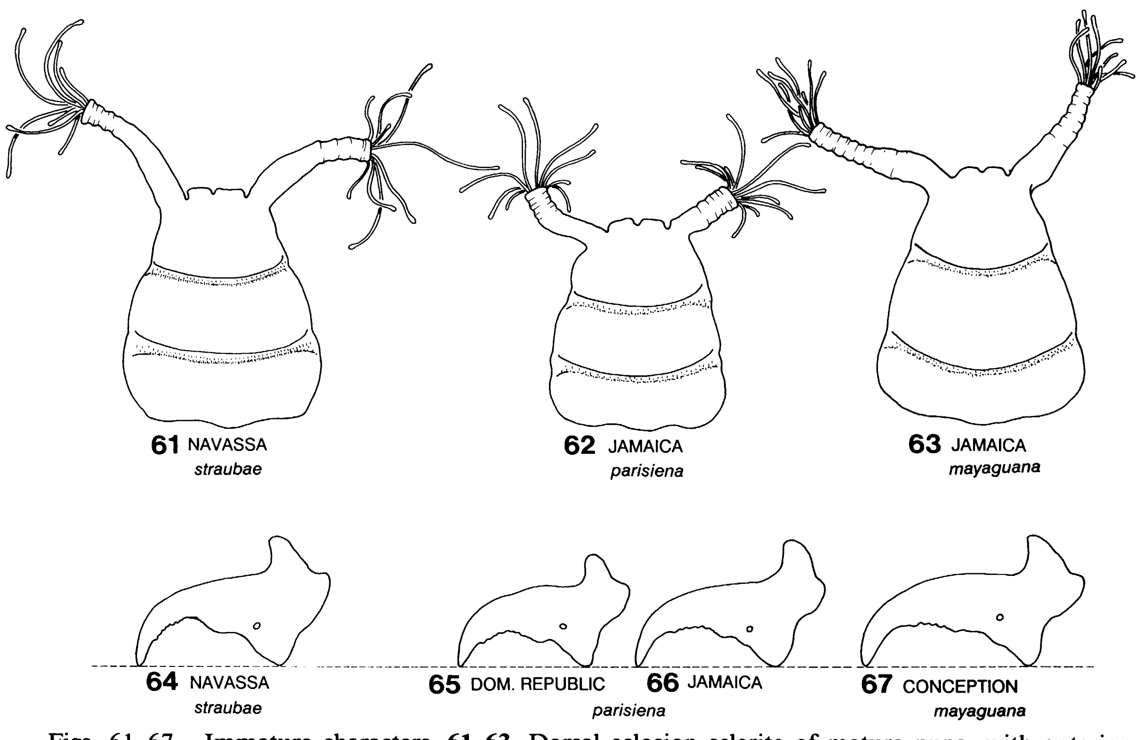
TABLE 3
Drosophila mayaguana

Strain/origin	1	2	3	4	5	6	7
ORV-21: Gr. Inagua. I., BAHAMAS	14 13–15 (2)	38 μm — (2)	260 μm — (2)	132 μm 125–140 (2)	1.97 — (2)	14 14–15 (2)	13 12–14 (2)
ORV-33: CUBA	16 — (1)	39 30–45 (3)	246 230–265 (3)	127 123–132 (2)	1.94 — (3)	13 12–15 (5)	12 10–14 (4)
ORV-24: Port Hend., JAM	15 13–18 (6)	30 — (1)	230 — (1)	80 — (1)	2.87 — (1)	12 12–13 (6)	12 10–14 (6)
ORV-8: Tortola I., BVI	16 15–18 (4)	37 35–40 (3)	246 240–255 (3)	110 — (3)	2.24 — (3)	13 12–15 (6)	12 12–13 (2)
ORV-20: Conception I., BAHAMAS	15 14–16 (3)	35 — (3)	235 230–245 (3)	56 50–65 (3)	4.19 — (3)	14 13–15 (5)	12 12–13 (5)

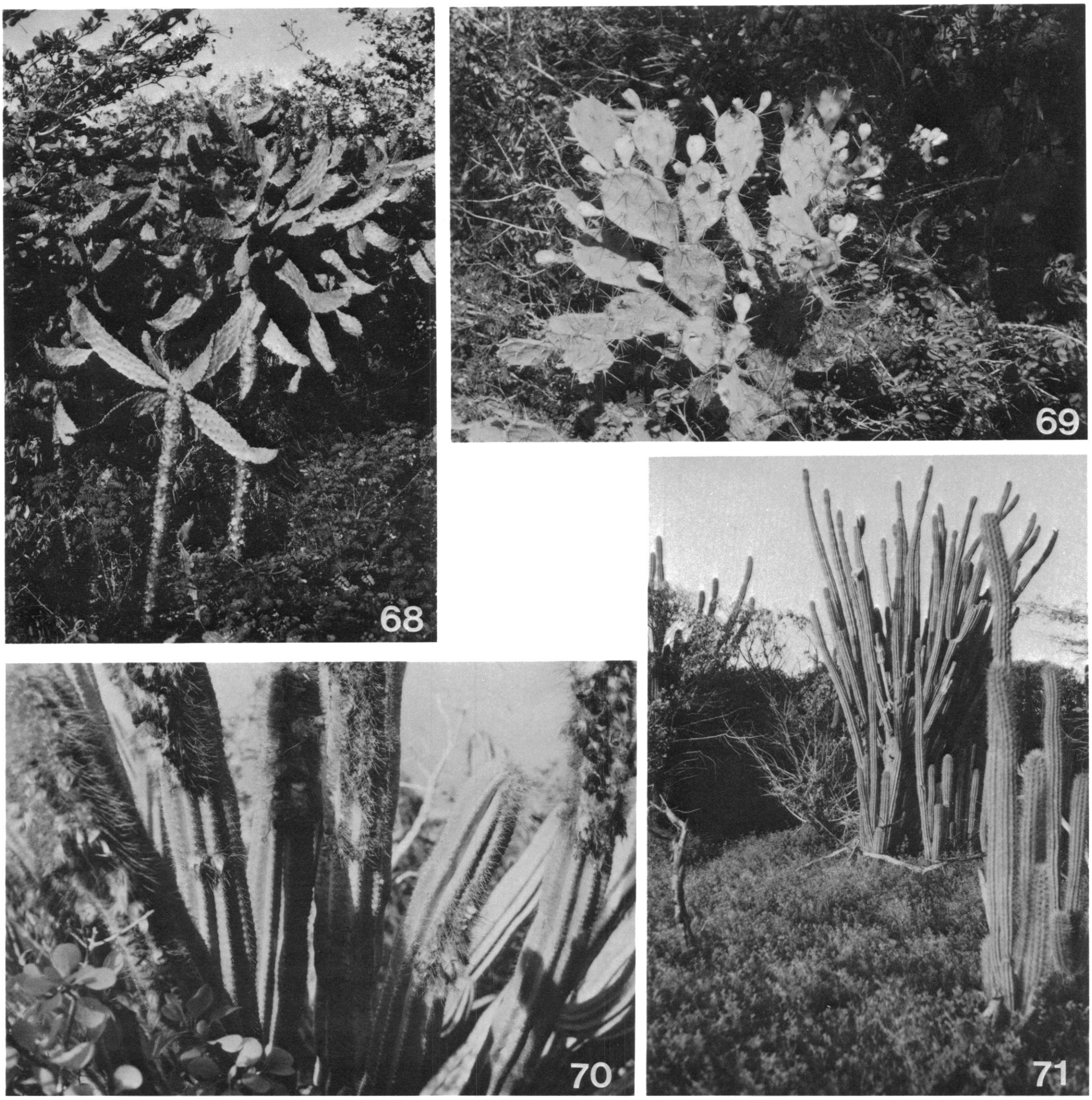
For measurements 1–7, see table 1.



Figs. 53–60. Intra- and interspecific variation in spermathecal capsules.



Figs. 61–67. Immature characters. **61-63.** Dorsal eclosion sclerite of mature pupa, with anterior spiracles. **64-67.** Third instar mandibles (lateral views).

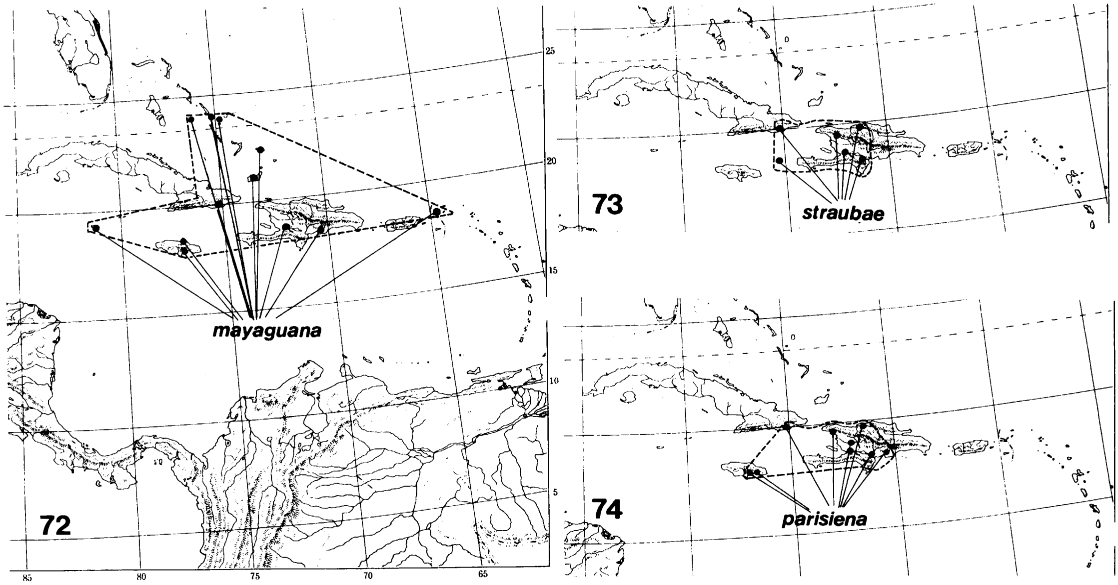


Figs. 68–71. Host cacti of *mayaguana* subcluster flies in the West Indies. **68.** *Opuntia moniliformis,* Great Inagua. **69.** *Opuntia stricta,* Great Inagua. **70.** *Cephalocereus* sp., Great Inagua. **71.** *Stenocereus hystrix,* Jamaica.

Pupa: Anterior spiracle trunk length 530–690 μm (mean 610 μm), length of longest filament 320–445 μm (mean 343); mean ratio of filament/trunk length = 0.56 μm (0.48–0.66) (N = 5). Anterior spiracle with 9–11 filaments.

Metaphase chromosomes: Very similar to *parisiena,* except that the Y is two-thirds the length of X. Examined in specimens from culture ORV-1 (Fond Parisien, Haiti).

MATERIAL EXAMINED: Numerous males and females from cultures established at the following localities. **BAHAMAS:** Conception Island, culture ORV-20 started with 4 flies bred from *Opuntia stricta* (this was the only cactus that yielded *Drosophila* on Conception); Exuma Islands, near Allan's Cay, M. A. Lachance; Great Inagua Island, culture ORV-21 started with material collected IX/19/83; Little San Salvador Is., 2 M, 1F, M.



Figs. 72–74. Distribution of *mayaguana* subcluster species.

A. Lachance. **BRITISH VIRGIN ISLANDS:** Tortola Island, strain ORV-8. **CUBA:** Guantánamo Province, Guantánamo Bay U.S. Naval Reserve, culture ORV-33-1, started with material collected IX/18/88. **GRAND CAYMAN ISLAND:** Culture ORV-29 started with material collected IX/27-28/83. **HISPANIOLA:** Haiti, Ouest Province, Fond Parisien, east of Port-au-Prince, culture ORV-1 started with material collected V/7/82.

HOSTS: 150 specimens were reared from the following hosts: *Opuntia stricta*: Great Inagua Is. (48), Conception Is. (4). *Cephalocereus* sp.: Great Inagua (88). *Agave* leaf: Tortola, BVI (10). The larvae coexist with *Drosophila mulleri* on Great Inagua Island in *Opuntia stricta*.

DISCUSSION: This species was recently described from a single specimen collected on the island of Mayaguana, Bahamas. Vilela was not able to place *D. mayaguana* into one of the existing species subgroups, so he kept it incertae sedis. *Drosophila mayaguana* exhibits a color polytypism in that the cultures from Great Inagua and Conception have a light brown to tan thorax, compared to cultures from all other localities which have a darker gray-brown thorax. The polytypism is genetically determined.

DISCUSSION

Figures 72–74 show the distributions of the three species in the *mayaguana* subcluster.

Heed et al. (1990) recently completed an extensive electrophoretic survey of 14 populations and 55 alleles using 15 allozymes, for the species treated here. They computed Rogers' genetic distances to produce distance Wagner trees and a PAUP analysis (on 56 electromorphs and chromosomal inversions). The two approaches yielded trees of similar topologies. They found *D. mayaguana* from Conception Island to be the sister group to other populations of *mayaguana,* and *straubae* (SB+ in their paper) to be either the sister species to *parisiena* (SB-5 in their paper), or paraphyletic to it. In addition, Jamaican populations of *parisiena* were found to be a sister group to the rest of *D. parisiena.* These results correspond very well with the morphological results presented above.

The Conception Island population of *mayaguana* is morphologically more variable than on other islands. In particular, the lengths of the aedeagal apodeme relative to the aedeagus are quite variable here: in some specimens the aedeagal apodeme is quite short (cf., figs. 32–33, 34–36). This result may explain the very large genetic distances among *may-*

aguana populations (including Conception Is.) relative to *straubae* and *parisiena* reported by Heed et al. (1990). It is interesting that *D. mayaguana* is chromosomally homosequential with other *mulleri* cluster flies, but not with *straubae* or *parisiena. Drosophila straubae,* in particular, has accrued a remarkable suite of chromosomal inversions, to be reported on elsewhere (M. Wasserman, personal commun.).

Even more intriguing is the *straubae* + *parisiena* clade. As Heed et al. (1990) questioned, is *D. straubae* indeed a paraphyletic species? We found here that it can be diagnosed by few morphological characters that are *derived* with respect to *parisiena* (the latter actually does appear to be monophyletic: it has many apomorphies). Yet, on a gross morphological level the populations of *D. straubae* are indistinguishable. Paraphyly of *D. straubae* perhaps explains the chromosomal heterogeneity of this "species." *Drosophila parisiena* also deserves closer and more detailed scrutiny; as we have shown, it is quite likely that the Jamaican populations of this "species" are consistently different morphologically (e.g., distiphallus vestiture, surstylus tooth number, epandrial lobe setae), chromosomally (M. Wasserman, personal commun.), electrophoretically (fixation of several unique alleles [Heed et al., 1990]), and in terms of hybrid breakdown (M. Wasserman, personal commun.). These contrasting differences and similarities may be typical of differentiation among islands.

Our criteria for circumscribing and diagnosing species lie in *consistency* of differences, at various phenotypic levels, albeit some of these differences are rather subtle. Work in progress examines the degree of hybridization (postmating isolation) and mating preferences (premating isolation) among species and strains. We predict that the results of that work, the chromosomal work by Wasserman, and hopefully some morphometric studies, will corroborate the phylogenetic patterns discerned here and previously (Heed et al., 1990). Such an integrated set of comparisons illustrates the value of *Drosophila* in defining the phenotypic limits of species as a phylogenetic unit.

REFERENCES

Grimaldi, D. A.
1987. Phylogenetics and taxonomy of *Zygothrica* (Diptera: Drosophilidae). Bull. Am. Mus. Nat. Hist. 186: 103–268.
1988. Relicts in the Drosophilidae (Diptera). *In* J.K. Liebherr (ed.), Zoogeography of Caribbean insects, Ithaca, N.Y.: Cornell University Press, pp. 183–213.

Heed, W.B., A. Sánchez, R. Armengol, and A. Fontedvila
1990. Genetic differentiation among island populations and species of cactophilic *Drosophila* in the West Indies. *In* J. S. F. Barker, R. MacIntyre, and W. T. Starmer (eds.), Monogr. Evol. Biol., New York: Plenum. In press.

McAlpine, J. F.
1981. Morphology and terminology—adults. *In* J. F. McAlpine (ed.), Manual of Nearctic Diptera, vol. 1, pp. 9–64. Research Branch Agriculture Canada monogr. 27. Ottawa: Minister of Supply and Services Canada.

Vilela, C. R.
1983. A revision of the *Drosophila repleta* species group (Diptera, Drosophilidae). Rev. Brasil. Entomol. 27: 1–114.

Wasserman, M.
1982a. Evolution of the *repleta* group. *In* M. Ashburner, H. L. Carson, and J. N. Thompson, Jr., The genetics and biology of *Drosophila* 3b: 61–139. London: Academic Press.
1982b. Cytological evolution in the *Drosophila repleta* species group. *In* J. F. Barker and W. Starmer, Ecological genetics and evolution, pp. 49–64. Sydney: Academic Press.