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Morphological and ecological notes on the two species of
Drosophila belonging to the subgenus *Siphlodora* PATTERSON &
MAINLAND, 1944 (Diptera, Drosophilidae)

CARLOS R. VILELA¹ & GERHARD BÄCHLI²

Drosophila (*Siphlodora*) *flexa* LOEW, 1866, and *D. (Siphlodora) sigmoides* LOEW, 1872, are redescribed and new distribution records, based upon museum specimens label data, are added. In total 6 type and 327 pinned non-type specimens were analyzed. An updated diagnosis for this American subgenus they belong to is given. Photomicrographs of inner spermathecal capsules, oviscapt valves, aedeagi, and right wings, as well as line drawings of the oviscapt valves and male terminalia are provided. A total of 288 specimens of *D. flexa* were aspirated from tassels and 3 from ears of maize (*Zea mays* L.) in three collections made in late 1992 and early 1993 at Chácara Santa Mônica, Santa Isabel, state of São Paulo, Brazil. Moreover, 376 imagines emerged in the laboratory from a total of 16 maize tassels sampled at the same place and dates. The larvae of the Neotropical *D. flexa* apparently feed on pollen of maize. Similarly, as reported in the literature, the larvae of its close relative, the Nearctic *D. sigmoides*, feed on pollen of the staminate florets of *Tripsacum dactyloides* L., a relative of maize.

Keywords: Breeding sites, *Drosophila flexa*, *Drosophila sigmoides*, ecology, pollen, *Siphlodora*, *Zea mays*, revision.

INTRODUCTION

The subgenus *Siphlodora* was proposed by PATTERSON & MAINLAND (1944) to include the following three species of *Drosophila*: *D. flexa* LOEW, 1866, *D. sigmoides* LOEW, 1872, and *D. subsigmoides* PATTERSON & MAINLAND, 1944. Later on, *Drosophila subsigmoides* was considered to be a junior synonym of *D. flexa* (WHEELER, 1957). Hence only two species are currently included in the subgenus *Siphlodora*: *D. flexa*, widespread in the Neotropical region (from Mexico to Argentina), Caribbean islands included, and *D. sigmoides*, endemic to the Nearctic region (from Texas to the eastern United States).

These two species are usually not attracted to fruit-baited traps and have only occasionally been collected by such a method. For instance, only 35 specimens belonging to *D. sigmoides* were identified among 849,997 drosophilids collected by baiting in 21 states of the United States of America (PATTERSON, 1943) and only 16 *D. flexa* (cited as *D. subsigmoides*) were present among 76,911 drosophilids collected by baiting in 17 states of Mexico (PATTERSON & MAINLAND, 1944). However, collections made from July to October in the Great Smoky Mountains, Tennessee (CARPENTER & GIORDANO, 1955) using the same methods yielded proportionally more specimens of *D. sigmoides* (15 specimens, all collected only in October, out of 26,741 flies sampled).

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According to BUTLER & METTLER (1963), adults of *D. sigmoides* have been observed flying near or resting on *Tripsacum dactyloides* (Poaceae), a relative of maize, at Raleigh, North Carolina, USA. The staminate portion of the bisexual inflorescence is the site of egg deposition and the larvae feed upon the anthers until they pupariate. As a similar breeding site was to be expected for its close relative, the Neotropical *D. flexa*, particular attention was given by one of us (CRV), in the early nineties, to the observation in the Neotropical region of the staminate spikelets of plants belonging to the Poaceae, as part of an extensive research project on drosophilid breeding sites. The preliminary outcome of this study prompted this report.

The present paper has a double purpose: to redescribe the two poorly known species of *Drosophila* belonging to the American subgenus *Siphlodora*, namely *D. flexa* and *D. sigmoides*, including the redescription of male and female terminalia, and to present the results of the quest for the natural breeding site of *D. flexa*.

MATERIAL AND METHODS

The taxonomic accounts have been based on the analysis of 6 type specimens in addition to 327 non-type specimens as detailed under the item “material examined” accompanying each redescription.

Label data attached to each type 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). Countries are printed in **BOLD CAPITAL LETTERS** and states or equivalents, whenever known, are in *bold italics*.

Preparations of microscope slides were made following WHEELER & KAMBYSELLIS (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. Before cutting the distal half of the abdomen with microscissors the specimens were softened in a wet chamber for ca. 9 h. Before softening, the right wing of each dissected specimen was removed, kept in xylene for ca. 5–15 min (to reduce the bubbles inside the veins), mounted in Canada Balsam between two microslides (cover glasses of 11 x 11 mm) glued to a punched cardboard whose free side was attached (below the labels) to the pin of the respective specimen.

Illustrations were drawn using a microscope with an objective 20x and a camera lucida (1.8x). Eight drawings of the ♂ terminalia were made for both species as follows: Posterior and oblique posterior views of epandrium and associated structures, posterior view of hypandrium and five views (from dorsal through ventral) of the aedeagus and associated structures. Photomicrographs were taken of the following structures: right wing, aedeagus in dorsal and left lateral views, outer lateral view of oviscapt valves and lateral view of the inner spermathecal capsules. Whenever in the same plate, all figures were drawn to the same scale and all photomicrographs were taken and enlarged to the same magnification.

For measurements and indices see VILELA & BÄCHLI (1990). Averages are followed by ranges (in parentheses). Morphological terminology also follows VILELA & BÄCHLI (1990) with the following modifications (in parentheses the former terms) adopted by BÄCHLI (1998), MERZ & HAENNI (2000), and in part by GRIMALDI (1990): seta (bristle), setula (hair), microtrichose (micropubescent or microsetose), post-ocellar seta (postvertical), vibrissa (oral bristle), basal scutellar seta (anterior scutellar), apical scutellar seta (posterior scutellar), katapisternal setae (sternopleural bristles), R₂₊₃ (second longitudinal), R₄₊₅ (third longitudinal), M₁ (fourth longitudi-

nal), CuA (fifth longitudinal), R-M (anterior crossvein), dM-Cu (posterior crossvein), prenisetae (primary teeth), outer setae of surstylus (secondary teeth), inner setae of surstylus (marginal bristles), paraphyses (parameres), oviscapt valves (ovipositor plates), marginal ovisensilla (marginal teeth of ovipositor), discal ovisensilla (discal teeth of ovipositor), inner spermathecal capsule (spermatheca) and introvert (duct of spermatheca).

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.

The studied specimens are deposited in the following collections: American Museum of Natural History, New York (AMNH); Museu de Zoologia, Universidade de São Paulo, São Paulo (MZSP); National Museum of Natural History, Washington, D.C. (USNM); The Natural History Museum, London (BMNH); Zoologisches Museum, Universität Zürich-Irchel, Zurich (ZMUZ).

RESULTS

1 - TAXONOMIC ACCOUNTS

Subgenus *Siphlodora* PATTERSON & MAINLAND, 1944: 25.

THROCKMORTON, 1975: 449, 461 (figs 4, 6, phylogeny); GRIMALDI, 1991: 93 (fig. 1, cladogram).
Type species: *Drosophila sigmoides* LOEW, 1872

The most striking feature shared by the species of *Drosophila* belonging to the subgenus *Siphlodora* is the presence of the sigmoid-shaped dM-Cu crossvein in the wings (Fig. 1).

According to PATTERSON & MAINLAND (1944) the subgenus *Siphlodora* is diagnosed as follows: yellowish-brown species; arista with 8 branches; acrostichal hairs in 6 rows; prescutellar bristles well developed; abdomen dull brown; posterior crossveins distinctly sinuate; testes coiled; ventral receptacle loosely coiled or looped; and 2 egg-filaments. We propose that the rather wide oviscapt (sternite VIII), besides other features, be included in the diagnosis of the subgenus *Siphlodora*. So, to update the diagnosis cited above we mention the following features:

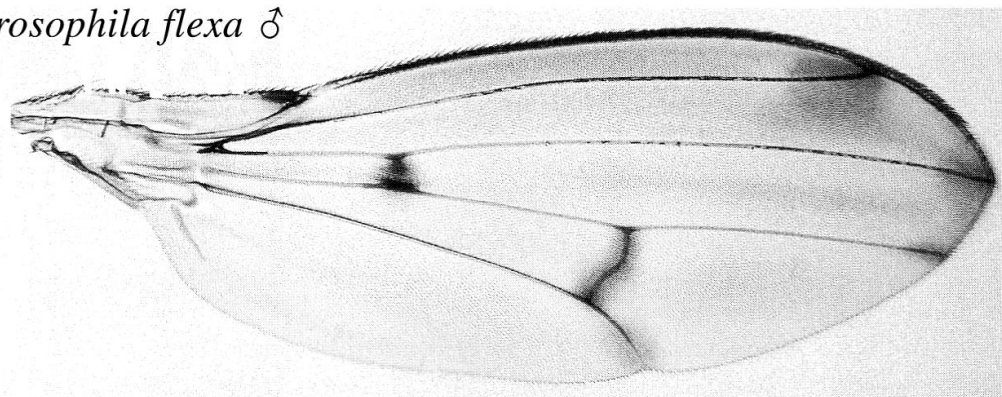
- 1) Valves of oviscapt remarkably wide and bearing trichoid ovisensilla instead of the usual pegs present in most species of *Drosophila* (Figs 7, 8A, B, D, E); introvert very short.
- 2) proclinate orbital seta as long as posterior reclinate seta;
- 3) scutum with a diffuse, slightly silvery median stripe;
- 4) abdomen with a diffuse darker brown median stripe.

***Drosophila flexa* LOEW, 1866**

(Figs 1A, B, 3, 5A–E, 6A, B, 7A, 8A–C)

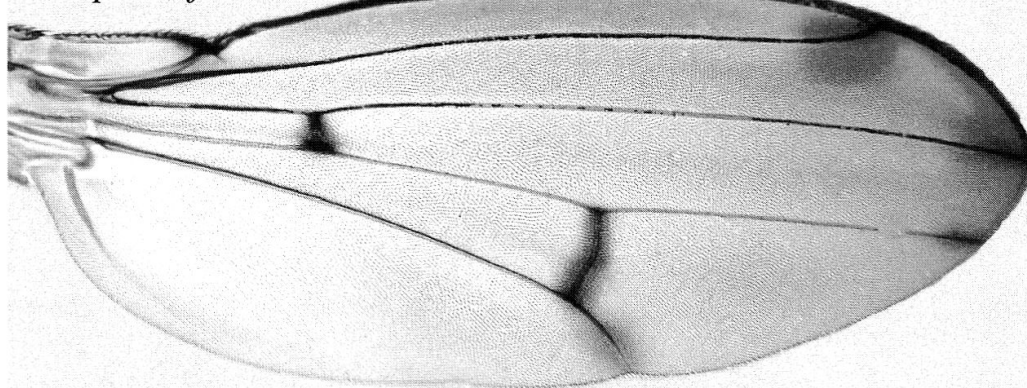
Drosophila flexa LOEW, 1866:182; ALDRICH, 1905: 642 (catalogue); STURTEVANT, 1921: 68 (key), 71 (redescription, distribution, ecology); DUDA, 1925: 198 (copy of description), 202 (key); DUDA, 1927: 115 (fig. 28, oviscapt; fig. 29, right wing), 133 (key), unnumbered page referring to figures captions (distribution); STURTEVANT, 1942: 44 (key); BÄCHLI, 1988: 137 (collection list).
Type locality: Cuba.

Drosophila flexa ♂



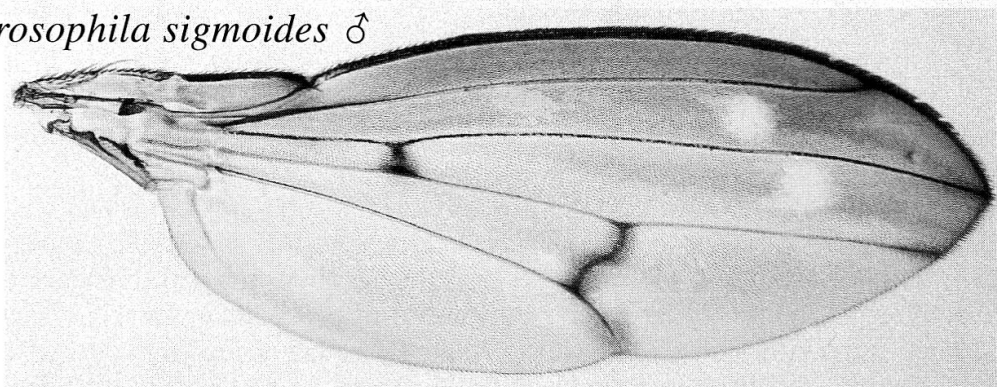
A

Drosophila flexa ♀



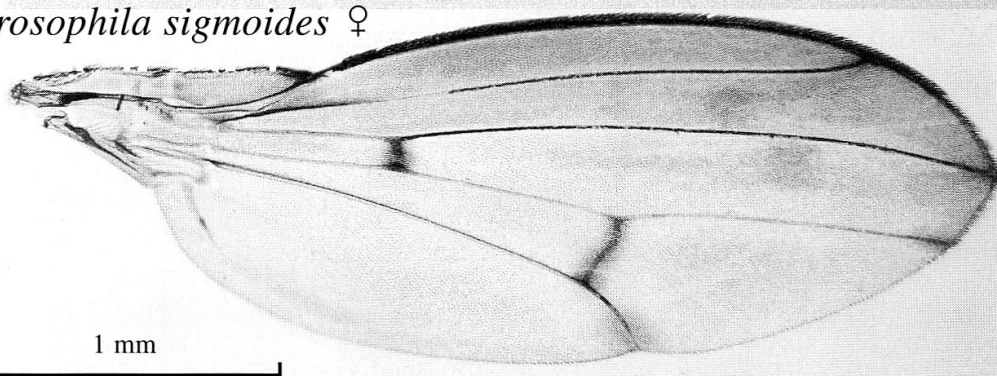
B

Drosophila sigmoides ♂



C

Drosophila sigmoides ♀

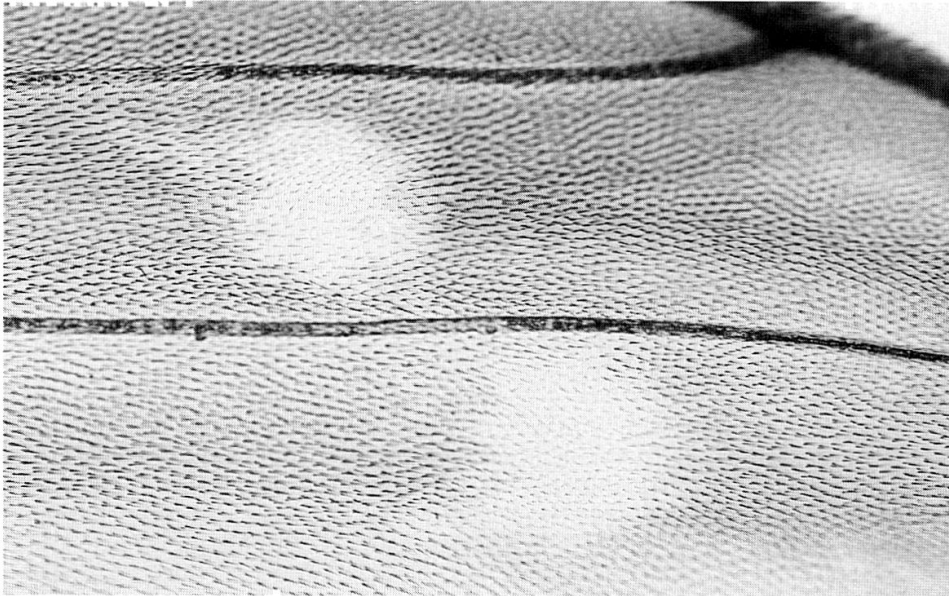


D

1 mm

Fig. 1. Right wings (dorsal views) of: – A, *Drosophila flexa* LOEW (non-type ♂, Chácara Santa Mônica, Santa Isabel, state of São Paulo, Brazil, 25.I.1993, C.R. VILELA coll., aspirated from maize tassel [code: F81]); – B, *D. flexa* Loew (non-type ♀: Chácara Santa Mônica, Santa Isabel, state of São Paulo, Brazil, 25.XII.1992, C.R. VILELA coll., aspirated from maize tassel [code: F75]); – C, *D. sigmoides* Loew (non-type ♂, Myrtle Beach S.P., South Carolina, USA, Aug. 1961, M. LEVITAN coll.); – D, *D. sigmoides* Loew (non-type ♀: Myrtle Beach S.P., South Carolina, USA, Aug. 1961, M. LEVITAN coll.).

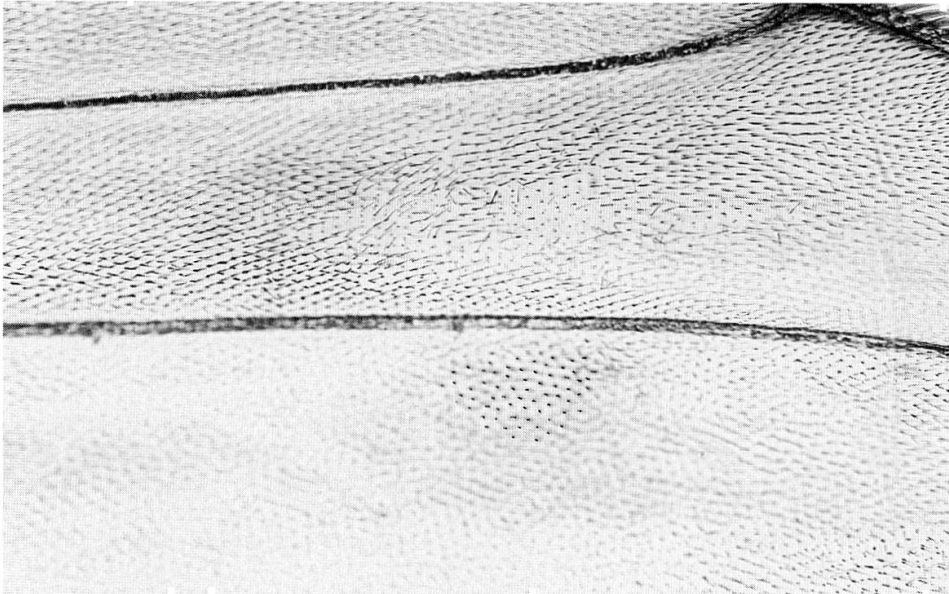
Drosophila sigmoides ♂



A

0.25 mm

Drosophila sigmoides ♀



B

Fig. 2. *Drosophila sigmoides*, details on the spots of the wings (same specimens as in Fig. 1C and 1D, respectively): A, ♂ (note that the microtrichia on the hyaline spots are thinner and shorter than those in the surrounding areas); B, ♀.

Drosophila (Siphlodora) flexa LOEW; PATTERSON & MAINLAND, 1944: 25 (subgenus description); PATTERSON & WHEELER, 1949: 221 (catalogue); DE CASTRO, 1953: 366 (fig. 10, median tarsus); WHEELER, 1957:80 (distribution); THROCKMORTON, 1962: 465 (chromatographic pattern); WHEELER, 1981a: 59 (catalogue); GRIMALDI, 1990:90 (fig. 488, aedeagus, hypandrium and paraphyses), 94 (fig. 519, oviscapt), 102 (fig. 544, cladogram).

Drosophila subsigmoides PATTERSON & MAINLAND, 1944:26 (synonymized by WHEELER, 1957:79); HSU, 1949: 93 (♂ terminalia description), 129 (plate V, fig. 4, external ♂ terminalia); PATTER-

SON & WHEELER, 1949: 228 (catalogue); PATTERSON & STONE, 1952: 50 (map); HEED, 1956: 62 (distribution); WHEELER, 1959: 198 (catalogue).
Type locality: Distrito Federal, Mexico (WHEELER, 1957).

Material examined. Type specimens (1 ♂, 3 ♀♀): Holotype ♂ of *Drosophila flexa* LOEW, 1865: "LOEW Coll. / *flexa* / Type 13419 [red] *Drosophila flexa* ♂ VILELA & BÄCHLI det. 1999 / Holotype", deposited in MCZH; holotype ♀ and two ♀♀ paratypes of the junior synonym *Drosophila subsigmoides* PATTERSON & MAINLAND, 1944, the first one labelled: "D.F. Mexico, 8-43, 1407.4 ♀, G.B. MAINLAND / Holotype subsigmoides [pink] / Type No. 101,021 U.S.N.M [red]", in USNM, the latter two labelled: "MEXICO: Distrito Federal VIII/18-VIII/19/43 G.B. MAINLAND ♀ [in just one] 1407.4 / PARATYPE *subsigmoides* [yellow]", in AMNH.

Additional specimens (124 ♂♂, 129 ♀♀, 2 ?): **CUBA. Oriente:** Santiago de Cuba "CUBA M BREUER Ja-Fb '56 / Puerto Boniato Santiago de Cuba / [terminalia in microvial, previously dissected]" [1 ♂, AMNH]; "Santiago CUBA M BREUER Ja-Fb '56 / 2388.3" [1 ♀, AMNH]. **JAMAICA.** Montego Bay "Montego Bay Jamaica BWI / Jul-Aug 1957 WBHEED" [1 ♀, AMNH]. **HAITI.** Kenscoff "Haiti WBHEED / Kenscoff 4000 ft / Feb 1956" [1 ♂, AMNH]; Petionville "HAITI / Petionville 1000 ft / WBHEED HLCARSON Jun Jul 1959" [1 ♀, AMNH]. **PUERTO RICO.** Mayaguez "Puerto Rico Mayaguez / Jul-Aug 1957 WBHEED" [1 ♂, AMNH]; San Juan Puerto Rico 21.VIII.1953 / BBSUGARMAN fruitfly trap 54-2592" [1 ♀, NMNH]; Cidral "Cidral P.R. II-19-32 / Coll. S.T. DANFORTH" [1 ♂, AMNH]. **TRINIDAD & TOBAGO. St. Andrew:** Valencia "TRINIDAD W.I. 4 MI E. Valencin [Valencia ?] II-16-1964 J.G. ROZEN" [1 ♀, AMNH]. **MEXICO. Tepic:** Nayarit "Tepec, Mex. Nayarit Sept. 2-24 1947 B. MALKIN" [1 ♂, median and hind legs missing, AMNH]; *Hidalgo:* Chapulhuacan "MEXICO: S. Chapulhuacan, Hidalgo 2257.14 VI/16/52 W.B. HEED / M. WASSERMAN" [1 ♀, AMNH]; *Veracruz:* Xalapa "MEXICO Veracruz Xalapa (= Jalapa) Bot. Garden 20.II.98 B. MERZ" [1 ♂, ZMUZ]; *Puebla:* Atlixco "MEXICO: 1 mi S. Atlixco, Puebla, IX/5/47 1802.11 ♂ M.R. WHEELER / F.A. COWAN" [1 ♂, 2 ♀♀, AMNH], Huachinango "Huachinango Puebla MEX / Dec 1958 A. FABERGE" [1 ♂, 1 ♀, AMNH]; *Oaxaca:* Oaxaca "MEXICO: 60mi S. Oaxaca Oaxaca ♂ IX/6 - IX/7/47 1808.17 M.R. WHEELER / F.A. COWAN" [1 ♂, right wing missing, 2 ♀♀, AMNH]; "maíz / km 554 MEXICO-TEHUANTEPEC, OAX. Mexico 1570 m 22-V-1951 / ANA MARIA DE BUEN., Colector" [1 ♂, previously dissected, terminalia in microvial, AMNH]; Huipulco "Huipulco Mex. Aug 21 1922 / EGSMYTH Coll" [1 ♀, USNM], Peña de Gato "MEXICO: 10 mi W. Rio Frio, Peña de Gato IX/4/47 1800.19 ♂ M.R. WHEELER / F.A. COWAN" [1 ♂, AMNH]. **GUATEMALA.** Yepocapa "Yepocapa Guatemala 1948-1949 / HTDALMAT Collector" [2 ♀♀, USNM]; idem except date (April 1948) [1 ♂, USNM]; Peten "GUATEMALA Peten: Santa Elena, 120-160 m., August, 1976 / N.L.H. KRAUSS" [1 ♂, AMNH]; El Amparo "GUATEMALA: El Amparo Dep. Chimaltenango Oct. 4 1944" [1 ♀, AMNH]. **EL SALVADOR.** Nueva San Salvador [ex Santa Tecla] "Santa Tecla 12 Klm NW 46.32 / Rep. de EL SALVADOR / May 9 [Apr 23 in ♂, head missing] '54 WBHEED" [1 ♂, 2 ♀♀, AMNH]; La Palma "Rep. de El Salvador [except for one ♀] La Palma 3200 Ft. [62.63 in one ♀] / Rep. de EL SALVADOR / Aug 1954 W B HEED" [1 ♂, 3 ♀♀, AMNH]; San Salvador "San Salvador / Rep. de EL SALVADOR / W.B.HEED Sept. 1955" [2 ♀♀, AMNH]; San Salvador "Oct 13 1953 WBHEED / Rep. de EL SALVADOR / 9.1 SAN SALVADOR" [1 ♀, AMNH]; San Salvador "San Salvador / San Salvador 37.56 / Rep. de EL SALVADOR / Jan 20 1954 WBHEED" [1 ♂, AMNH]; "San Salvador 35.47 / Rep. de EL SALVADOR / Dez 1953 WBHEED" [1 ♀, AMNH]; Volcan Santa Ana "Volcan Santa Ana 5670 ft 60.30 [26.39 in ♀] / Jul 1954 [Nov-53 in ♀] WBHEED / Rep de El Salvador" [1 ♂, 1 ♀, AMNH]; Laguna Alegria "Laguna Alegria 100 Klm SE of San Salvador / Rep. de EL SALVADOR / 59.10 Jul 1954 WBHEED" [1 ♀, AMNH]; Volcan Boqueron "Volcan Boqueron 4500 ft 41.40 Jul 1954 WBHEED / Rep. de EL SALVADOR" [1 ♂, AMNH]; Santa Ana "EL SALVADOR: Santa Ana 600-700 m., July 16, 1975 N.L.H. KRAUSS" [1 ♂, 1 ♀, AMNH]. **NICARAGUA.** San Marcos "San Marcos, Nicaragua coll. BAKER / *Drosophila flexa* LOEW Sttt.[SURTEVANT]" [1 ♂, USNM]. **COSTA RICA.** San Jose "San Jose C[osta]R[ica] VII [= July] [no year stated] / HSCHMIDT coll." [2 ♂♂, 6 ♀♀, USNM]; idem except date [X] [1 ♀, USNM]; San Jose "San Jose Costa Rica 3000 ft. / WBHEED HLCARSON MWASSERMAN Jy-Aug 1956 [WBHEED Oct. 1955 in one ♂ and in the ♀]" [2 ♂♂, 1 ♀ headless, AMNH]. Suiza de Turrialba "*Drosophila flexa* Lw / COSTA RICA / La Suiza April 1922 / Pab SCHILD / ALMELANDER Collection 1961" [1 ♀, USNM]; San Mateo "Higuito San Mateo, CR / PabloSCHILD Coll" [2 ♂♂, 4 ♀♀, 1 ?, USNM]; Cartago "20 mi S Cartago Costa Rica / WBHEED HLCARSON MWASSERMAN Jy-Aug 1956" [2 ♂♂, AMNH]; "COSTA RICA: Cartago X-1953 / Collector N.L.H.KRAUSS" [1 ♂, 2 ♀♀, AMNH]; Orosi "COSTA RICA: Orosi X-1953 / Collector N.L.H.KRAUSS" [1 ♂, AMNH]; **PANAMA.** Chiriqui "Panama Chiriqui / Bambito Volcan / NLH-KRAUSS Col'n Dec. 46 / *Drosophila flexa* Lw. Det. 1957 MRWHEELER" [1 ♀, USNM]; Pacora "Pacora Pan[ama] 27Jan1953 / FSBLANTON Collector" [1 ♀, USNM]; Tabernilla "Tabernilla C[anal]Z[one] Pan / Aug. BUSCK Collector" [1 ♂, USNM]; Barro Colorado Island "Barro Colorado Island [Isl. in one ♀], C.Z. VIII-IX.1936 / Ex fruit fly traps - Z - 3748 [or 3749] / *Drosophila flexa* Lw. Det. 196

[blank] MRWHEELER [missing in one ♀] [2 ♀♀, USNM]; Chiriqui "PANAMA: Chiriqui Cerro Punta 6000 ft. X-1953 / N.L.H. KRAUSS Collector [only in one ♀]" [1 ♂, 2 ♀♀, AMNH]. **COLOMBIA.** *Antioquia*: Medellín "COLOMBIA S.A.WBHEED Nov. 1955 / Medellín coffee finca 5000 ft." [1 ♂, 1 ♀, AMNH]; Sonson "Sonson, Ant. Colombia 16 [17 in one ♀]-XI-1955, Alt. 2500 mts. / L. POSADA / *Solanum andigenum* / 4 [it varies from 3 to 6] / e / *Drosophila flexa* Lw. det. WWIRTH '59 [not in all specimens]" [3 ♂♂, 5 ♀♀, USNM]; Bello "Bello Ant. 5.I.55 / A. UNIGARRO [?] Maiz 4332 [or 4324, or 4327 to 4330] / *Drosophila flexa* LOEW Det. 1959 M.R. WHEELER [only in one ♀]" [1 ♂, 5 ♀♀, AMNH]; "Bello Ant. 27.V.55 C. RIOS / Maíz / 5395 [5404 in one ♂, head glued to thorax]" [2 ♂♂, AMNH]; "Bello. Ant. 2-VII-55 / C. RIOS Frijol / 6411 [6410 in one]" [2 ♀♀, AMNH]; idem "Bello Ant. 27-VII-55 / C. CARMONA Soya / 5875" [1 ♂, AMNH]; "Bello Ant. VII-16-55 / C. RIOS Frijol / 6811" [1 ♂, AMNH]; "Bello Ant. 11-XII-54 / A. UMIGARRO Maiz [Frijol in one ♂] / 3624 [3614 in ♀, 3578 in ♂]" [1 ♂, 1 ♀, 1 ? (without abdomen), AMNH]; "Bello Ant. 1-9-56 / L. SALAS MAIZ" [1 ♀, headless, AMNH]; "Bello Ant. 1-10-56 / L. SALAS Frijol / 8254" [1 ♀, AMNH]; "Bello Ant. 15-V-56 / A. SILDARRIAGA Frijol" [1 ♂, AMNH]; "Bello Ant. 1-11-56 / L. SALAS Leguminosas / 8284" [1 ♂, AMNH]; La Ceja "La Ceja Ant. 2-IX-54 / O. SANCHEZ Papa [?] / 3073" [1 ♂, AMNH]; "La Ceja Ant. 6-VIII-54 / A. SILDARRIAGA Maiz / 2626 [or 2615, 2627]" [3 ♂♂ (one headless), AMNH]; Rio Negro "Rio Negro A VIII-19-55 / C. CARMONA B. B. ARRACHAY Frijol / 8041" [1 ♂, AMNH]; *Valle*: Palmira "Palmira (V.) XII-3-54 / E. CARDONA Frijol" [2 ♂♂ (right wing missing in one), 3 ♀♀, AMNH]; "Palmira Valle II-27-56 [21-VI-54 in one ♂] / C. CARMONA Maiz 8705 [or 8703, 8708, 8687, 8694, 2802]" [3 ♂♂, 3 ♀♀, AMNH]; Palmira "COLOMBIA WBHEED Nov. 1955 / Palmira nr Cali 3300 ft" [7 ♂♂ (one headless, one lacking the right wing), 1 ♀, AMNH]. **VENEZUELA.** *Mérida*: "Tovar Merida 7 Aug 1943 / PANDUZE Collector / *Drosophila flexa* LOEW Det. 1956 MRWHEELER" [1 ♂, USNM]; *Aragua*: Rancho Grande "Venezuela Rancho Grande near Maracay / M. WASSERMAN Oct-Nov 1956" [1 ♂, AMNH]; Rancho Grande "VENEZUELA: Ar.[?] Rancho Gr[ande] 9 aug 1967 R.W. POOLE 1100 m CPDd [Critical Point Dried ?] from alcohol" [2 ♂♂, AMNH]. **ECUADOR.** *Chimborazo*: Linje Chimborazo "ECUADOR Linje Chimborazo July 1955 / Collr. LEVI-CASTILLO" [1 ♂, AMNH]; "ECUADOR Chimborazo July 1955 / Bubna [?] / LEVICASTILLO Collector" [1 ♂, AMNH]; Pomasqui "Potato vines, Pomasqui Ecuad. X.16.53 HRYUST. [?] 143 53-12735 / *Drosophila flexa* LOEW det. WWIRTH '53" [1 ♀, right wing missing, USNM]. **PERU.** Lima "Lima Peru D. BRNCIC April 1956" [1 ♂, AMNH]; "Lima PERU 15 May 1920 / Cornell Univ. Expedition Lot. 607 Sub 49" [1 ♂, left wing missing, AMNH]. **BRAZIL.** *Rio Grande do Norte*: Natal "BRAZIL: Natal St., RGN IV/56" [1 ♀, AMNH]. *São Paulo*: Itaquaquecetuba "Itaquaquecetuba São Paulo Brazil / CHTTOWNSEND Collr. III-9" [1 ♂, 2 ♀♀]; Santa Isabel "BRAZIL SP / 11 km NE of Santa Isabel, Chácara Santa Mônica (23° 17' S, 46° 12'), C.R. VILELA coll. / aspirated from maize tassels [except three from maize ears] / *Drosophila flexa* C.R. VILELA det." [MZSP = 21 ♂♂ and 10 ♀♀ (25.II.1992), 5 ♂♂ and 5 ♀♀ (23.I.1993), 5 ♂♂ and 5 ♀♀ (25.I.1993)]; same locality but emerged on 3-6.II.1993 from maize tassels collected on 23.I.1993 = 3 ♂♂, 6 ♀♀ [of these 2 ♂♂ each with its puparium glued to a cardpoint between imago and labels, MZSP]; same locality but emerged on 5-11.II.1993 from maize tassels collected on 25.I.1993 = 14 ♂♂ and 13 ♀♀ [of these, 9 ♂♂ and 8 ♀♀ each with its puparium glued to a point between the imago and labels, MZSP]; São Sebastião "Brasilien, S.P. / L.635 / São Sebastião [Centro de Biologia Marinha, USP] 19-20.III.1986, v[on]. TSCHIRNHAUS leg. / ♀ / *Drosophila flexa* LOEW G. BÄCHLI det." [1 ♀, ZMUZ], "Brasilien, S.P. / L.633 / São Sebastião P. Mares. [Praia Maresias] 18.III.1986, v. TSCHIRNHAUS leg. / *Drosophila flexa* LOEW G. BÄCHLI det." [1 ♀, ZMUZ]; São Lourenço da Serra "Brasilien, S.P. / L.553 / São Lourenço da Serra [camping site at highway BR 116, km 319], 19.II.1986, v. TSCHIRNHAUS leg. / ♀ / *Drosophila flexa* LOEW G. BÄCHLI det." [1 ♀, ZMUZ]. *Goiás*: Brasilien Goiás Barra do Garças [SE of; on highway BR158; rice field], 12.III.1986 / L.627 / v. TSCHIRNHAUS leg. / ♂ / *Drosophila flexa* LOEW G. BÄCHLI det." [1 ♂, ZMUZ]. *Rio de Janeiro*: "*D. flexa* ♂ Rio [de Janeiro], II.54 / 504 [505 in one ♂]" [2 ♂♂ (previously dissected, parts in microscope slides), ZMUZ]. **BOLIVIA.** Cochabamba "Bolivia Cocha Bamba / MRWASSERMAN April 1958 / 345.19" [1 ♀, AMNH]. **ARGENTINA.** *Salta*: "Max KISLUK Coll. No. 684 May 14 1927 / Salta Argentina swept in grove" [7 ♂♂, 6 ♀♀, USNM].

Note. The label "*Drosophila flexa* [♂ or ♀] VILELA & BÄCHLI det. 1999" was added to every specimen.

Diagnosis: *D. flexa* may be distinguished from *D. sigmoides* by the following combination of characters (mostly seen with the naked eye): wings not darker on anterior half (noticeably infuscated anteriorly and paler posteriorly in *D. sigmoides*); areas of wing cells at the tips of all longitudinal veins sharply darkened, the one around R₂₊₃ is conspicuously roundish (oblong in *D. sigmoides*) and the largest, while the remaining ones are diffuse and somewhat triangular; wing cells r₂₊₃ and r₄₊₅ without any contrasting roundish darker or lighter areas in both sexes (in *D. sig-*

moides, each of these cells bears in its subdistal portion one roundish, colorless and better defined spot in males and a darker and not so well defined area in females, contrasting with the cloudy infuscation of the background); oviscapt valves triangular (dorsally prominent and more roundish in *D. sigmoides*); inner spermathecal capsule heart-shaped (spherical in *D. sigmoides*), and egg filaments fine, short and about 1/10 (about 4/10 in *D. sigmoides*) length of egg.

Redescription ($n_{\max.} = 32$). Head mainly brownish-yellow. Frontal length 0.35 (0.32–0.40) mm, frontal index 0.92 (0.83–0.96), top to bottom width ratio 1.20 (1.12–1.32). Frontal triangle slightly whitish, about 0.85x frontal length; ocellar triangle darker, about 0.25x frontal length. Frontorbital plates narrow; slightly diverging from eye margin, slightly whitish, about 0.85x frontal length. Orbital setae subequidistant, in a line, distance of posterior orbital to anterior one about 0.75x that to inner vertical. Postocellar setae convergent, rarely crossing. Length ratio of anterior to posterior orbital seta 1.06 (0.92–1.25), of mid to anterior orbital seta 0.48 (0.31–0.58); poc 0.43x (0.35–0.52), oc 0.81x (0.70–0.91) frontal length; vt index 1.10 (0.84–1.23); vibrissal index 0.43 (0.40–0.47). Cheek index about 12. Eye index 1.31 (1.23–1.41). First flagellomere brownish; length to width ratio 1.85 (1.60–2.00). Arista with 3–5 upper and 2 lower long branches, plus terminal fork; inner branches relatively short. Proboscis and palpi yellow. Carina dilated in lower part, longitudinally slightly grooved.

Thorax brownish-yellow; length about 1.43 (1.22–1.62) mm; h index 1.04 (0.95–1.14); six rows of acrostichal setulae. Scutum subshiny, without pattern but with a faint silvery shining stripe (visible at a certain angle), mostly between the dorsocentral rows, more noticeable in anterior third. Transverse distance of dorsocentral setae about 2.5x longitudinal distance; dc index 0.67 (0.55–0.77). Scutellum apically rounded, paler than scutum; one pair of prescutellar setae which are in some specimens indistinguishable from the acrostichal setulae nearby; scutellar setae nearly equidistant, basal ones more or less parallel; scut index 1.02 (0.83–1.11); sterno index 0.67 (0.61–0.81), mid katapisternal seta 0.53x length of the anterior one. Halteres and legs yellow; dorsal preapical setae on all tibiae, ventral apical setae on mid and hind tibiae.

Wing (Figs 1A, B) slightly brownish tinged in costal half, crossvein dM-Cu distinctly curved, both crossveins and the tips of all longitudinal veins with brown markings, darkest at wing margin, fading towards wing base, the marking at R_{2+3} roundish; length 2.98 (2.77–3.56) mm; length to width ratio 2.42 (2.27–2.64). Indices: C, 3.30 (2.65–4.25); ac, 1.96 (1.70–2.22); hb, 0.55 (0.33–0.67); 4c, 0.72 (0.53–0.90); 4v, 1.32 (0.94–1.48); 5x, 1.01 (0.90–1.25); M, 0.38 (0.29–0.50); prox. X, 0.80 (0.59–1.00).

Abdomen pale yellowish, subshiny, with a median, broad brown longitudinal stripe, mostly diffuse at base, darker towards apex.

♂ *Terminalia*. (Figs 3, 5A–E, 6A, B). Epandrium with about 14 lower, 5 median and 3 upper setae; ventral lobe anteriorly finger-shaped. Cerci anteriorly fused to epandrium. Surstylus not micropubescent, with about 10 long, rod-shaped prenisetae and 9 long inner setae. Decasternum as in Figs 3A, B. Hypandrium shorter than epandrium; bow absent, gonopod laterally incised at the middle of the inner margin, slightly microtrichose, bearing one large submedian seta, linked to paraphysis by membranous tissue; paraphysis straight anteriorly, roundish posteriorly, bearing a subapical seta. Aedeagus slightly curved, ventrally expanded and marginally serrate at tip, dorsoapically covered with tiny spines, ventral margins serrate at dis-

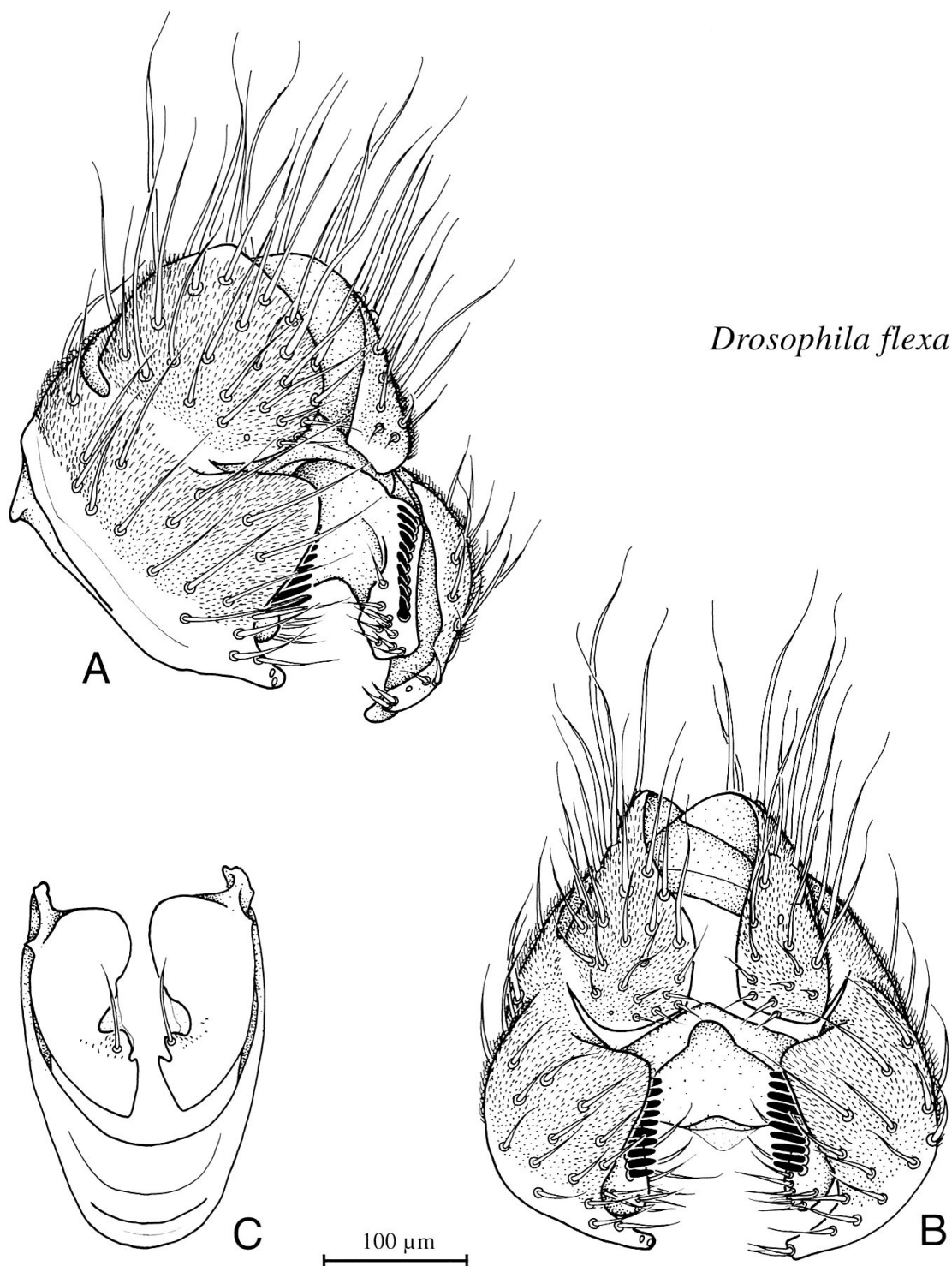


Fig. 3. *Drosophila flexa* LOEW, non-type ♂ (Chácara Santa Mônica, Santa Isabel, state of São Paulo, Brazil, 23.I.1993, C.R. VILELA coll., aspirated from maize tassel, code: F78). – A, epandrium, cerci, surstyli and decasternum; oblique posterior view. – B, idem; posterior view. – C, hyandrium and gonopods; posterior view.

tal half. Aedeagal apodeme shorter than aedeagus, laterally flattened. Ventral rod shorter than paraphyses.

♀ *Terminalia* (Figs 7A, 8A–C). Valves of oviscapt ventrally straight, distally unusually blunt-edged, somewhat triangular, with about 8 marginal and 8 discal tri-

choid ovisensilla; the subterminal ovisensillum (missing in Figs 7A, 8A, B) could be indistinguishable from the marginal ones; additionally there are three smaller, distally positioned ovisensilla which are present in the species of the subgenus *Drosophila* (see VILELA & BÄCHLI, 1990, for details). Inner spermathecal capsule (Fig. 8C) heart-shaped, sclerotized; introvert very short.

Puparia (n = 16). Length (without horn) about 3.3 mm. Horn-index about 16; each anterior spiracle with 5.6 (4-7) branches.

Eggs. White, bearing two fine and short filaments about 0.10x length of egg.

Ecology. After the emergence of imagoes from vials containing branches of maize tassels we searched for egg cases and puparia of *D. flexa*. It was observed that the females layed their eggs (or slightly glued them) mostly over the outer, hairy and somewhat hard surface of both the outer and the inner glume of the male spikelet, but some of the eggs were found inserted into the space where the two glumes overlap. In two of the analyzed spikelets we found 6 rather closely positioned egg cases. The puparia were found among the sand grains as well as inside unopened spikelets. In the latter case the puparia were mostly found with their aperture slightly protruding from the tip of the unopened spikelet. Some parasitoids (micro-hymenopterans) died during the emergence and in such cases only their emerged heads were seen outside the unopened spikelets. Samples of spikelets with eggs or parasitized as well as unparasitized puparia were glued to points on pins and some puparia could be even mounted together with their respective imagoes on the same pin as they had previously been individualized in vials; they are preserved in the MZSP collection.

Distribution: Mexico (San Luis Potosí [northernmost record], Tepic, Hidalgo, Vera Cruz, Distrito Federal, Morelos, Puebla and Oaxaca), Guatemala, El Salvador, Nicaragua, Costa Rica, Panama, Colombia (Antioquia, Valle), Venezuela (Aragua, Mérida), Ecuador (Chimborazo), Peru, Bolivia [**New Record**], Brazil (Rio Grande do Norte [**New Record**], Goiás [**New Record**], São Paulo [**New Record**], Paraná and Rio de Janeiro), Argentina (Salta) [southernmost record] [**New Record**], Cuba, Jamaica [**New Record**], Haiti, Trinidad [**New Record**] and Puerto Rico (DUDA, 1927; WHEELER, 1957; WASSERMAN, 1967, and new records based on labels of museum specimens).

Note. This species has not yet been recorded in Chile (see BRNCIC, 1987) where maize has been intensively cultivated since pre-Columbian times. Additionally, it should be pointed out that PILARES & VASQUEZ (1977) overlooked the paper of WHEELER (1957) and did not include *D. flexa* in their list of 67 species of *Drosophila* occurring in Peru. However, if *D. flexa* is really associated with the Indian Corn it is expected to occur in most areas of the Andes as well as in the Guianas, Paraguay, Uruguay (no record in GOÑI *et al.*, 1998) and all the Caribbean Islands, where maize fields are often present. Its apparent absence might be mostly due to a lack of collections (mainly by sweeping). If *D. flexa* is a warm-adapted species its distribution could also be limited to the lower latitudes of America as well as the lower altitudes of the Andes.

Drosophila sigmoides LOEW, 1872

(Figs 1C, D, 2, 4, 5F-J, 6C, D, 7B, 8D-F)

Drosophila sigmoides LOEW, 1872:103; ALDRICH, 1905: 643 (catalogue); AINSLIE, 1906: 44 (misidentification, see STURTEVANT, 1918: 443); STURTEVANT, 1918: 443 (key); 1921:67 (key), 70,71 (redescription, ecology, distribution); MALLOCH & MCATEE, 1924: 34 (key); DUDA, 1927: 114

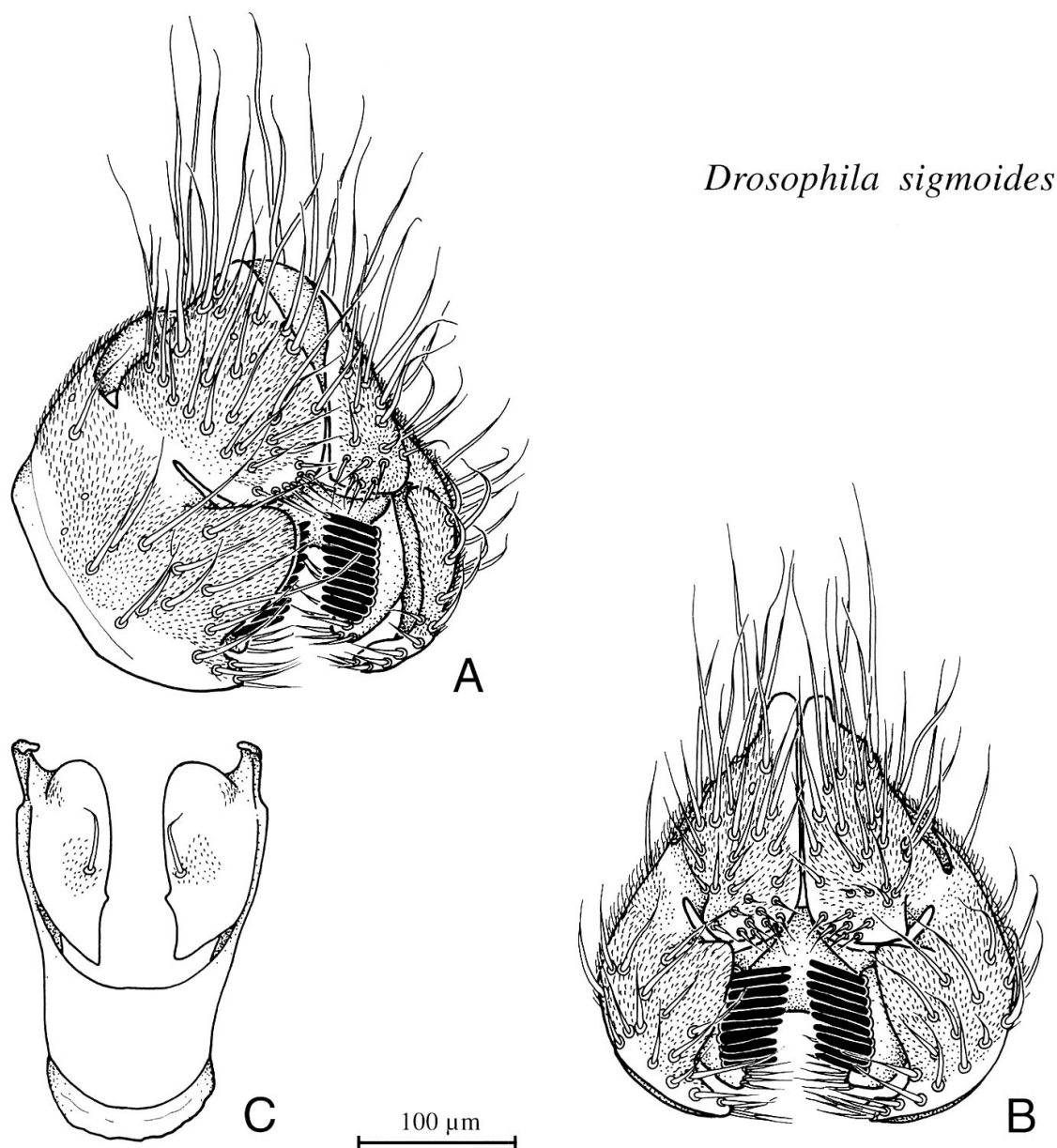


Fig. 4. *Drosophila sigmoides* LOEW, (non-type ♂, same specimen as in Fig. 1C). – A, epandrium, cerci, surstyli and decasternum; oblique posterior view. – B, idem; posterior view. – C, hypandrium and gonopods; posterior view.

(copy of description), 133 (key); BRIMLEY, 1938: 388 (collection list with dates); STURTEVANT, 1942: 44 (key); PATTERSON, 1943: 191 (redescription), 192 (fig. 65 = ♂ and ♀ reproductive systems, egg, puparium; misplaced in the subgenus *Sophophora*) plate III (habitus ♂); PATTERSON & WAGNER, 1943: 239 (map 16, distribution).

Type locality: Plano, Texas, USA.

Drosophila (*Siphodora*) *sigmoides* LOEW, 1872; PATTERSON & MAINLAND, 1944: 18 (key), 25 (type species of the subgenus); HSU, 1949: 92 (♂ terminalia), 129 (plate V, fig. 5, external ♂ terminalia); PATTERSON & WHEELER, 1949: 227 (catalogue); PATTERSON & STONE, 1952: 14 (fig. 4, egg, ♂ and ♀ reproductive systems); WHEELER & TAKADA, 1971: 232 (fig. 12, ♂ terminalia); WHEELER, 1981a: 59 (catalogue); GRIMALDI, 1990: 91 (fig. 497, right surstylus).

Material examined. Type specimens (2 ♀♀): Lectotype ♀ (by present designation): "Texas LOFR. / LOEW Coll. / *sigmoides* Lw. Cent. / Type 13418 / *Drosophila sigmoides* ♀ VILELA & BÄCHLI det. 1999

/ Lectotype"; 1 ♀ paralectotype (by present designation): "Texas LOFR. / LOEW Coll. / Type 13418 / *Drosophila sigmoides* ♀ VILELA & BÄCHLI det. 1999 / Paralectotype", both deposited in MCZH. Additional specimens (27 ♂♂, 46 ♀♀): **UNITED STATES. Texas:** Plano "Plano Texas May dusk [?] 1907 / E.S. TUCKER / In Oat field / 423 [in ♀] / *Drosophila sigmoides* Lw. [in ♀]" [2 ♂♂, 1 ♀, USNM]. **Mississippi:** Oxford "Oxford Miss. Oct.11 [Oct 4, ♂, right wing missing and head partially eaten] 1941 / F.M. HULL Collector / *Drosophila sigmoides* Lw d. STEYSKAL '45 [last label missing in ♂]" [1 ♂, 1 ♀, USNM]; Agricultural College Mississippi "Agr. Col Miss. Oct12 1922 / 133 / A.H. STURTEVANT Collection 1970" [1 ♀, head missing, USNM]. **Alabama:** Florence "Florence Ala. Sept.20 1946 Polio study trap PHS-F1 1026" [1 ♀, USNM]; Kushla "Kushla Ala., IV.9.15 [VIII '18 in one ♂, right wing missing, and IV.4.15 in another] A.H. STURTEVANT [absent in one ♂] / sigm. ? [just in one ♂] / A.H. STURTEVANT Collection 1970" [3 ♂♂, wings missing in one, USNM]; Gulf Crest "Gulf Crest Ala. XI.4.16 / A.H. STURTEVANT Collection 1970 [1 ♂, USNM]; Montgomery "Pickett Springs Montgomery Ala. Aug. 5-6 '16 Ac. 4849 / *Drosophila sigmoides* LOEW STURT.[just in ♂]" [1 ♂, 1 ♀, AMNH]. **Georgia:** Stone Mountains "Stone Mt. Ga. 10-26-47 P.W. FATTIG / *Drosophila sigmoides* LOEW det WWIRTH '53 [last label only in one ♂]" [2 ♂♂, 2 ♀♀, USNM]; Dekalb Co. "Dekalb Co. [also Stone Mt.] Ga. XI.11.53 DODGE [& SEAGO, in one ♂]" [4 ♂♂, 2 ♀♀, USNM]. **South Carolina:** Clemson "GGAINSLE Collector / Clemson Col SC / WEBSTER No. 4863" [2 ♀♀, USNM]; Myrtle Beach "Myrtle Beach S.P. South Carolina Aug. 1961 M. LEVITAN" [2 ♂♂, 15 ♀♀ (left wing missing in one; 1 ♂ and 1 ♀ dissected, right wing removed), AMNH]. **Arkansas:** Dewitt "Dewitt. Ark. XII.20.1917 / A.WETMORE Collector" [1 ♀, USNM]. **Tennessee:** Hamilton Co. "Hamilton Co. Tenn. 20/III/39 Wild Honeysuckle / TURNER # 13310 / Lot No. 39-7520" [1 ♀, USNM]; Sv. Elmo "Sv. Elmo Tenn. / VIII.10.16 / A.H. STURTEVANT Collection 1970" [1 ♂, USNM]; Great Smoky National Park "TENNESSEE: Great Smoky Nat. Park. ♂ IX/10 - IX/13/41 1272.16 G.B. MAINLAND / WAGENER" [2 ♂♂, 1 ♀, AMNH]; Coal Creek "Coal Creek Tenn Aug 30.1916 W.S. ADKINS / ac. 5300 / *Drosophila sigmoides* LOEW STURT." [1 ♀, AMNH]. **North Carolina:** Raleigh "Raleigh N.C. Early Aug. F.SHERMAN / 265" [1 ♂, USNM]; Idem "Raleigh N.C. Late Jun C.S. BRIMLEY / 253" [1 ♀, USNM]; "NC" [just as NC and no additional label] [1 ♀, USNM]. **Virginia:** Chain Bridge "Chain Bridge Sept 10 1922 [12.IX.13, ♀, Sept 11 1921, ♂ and Sept 18 1921, 2 ♂♂] Va / JRMALLOCH Collector [except in two ♀♀; a third ♀ labelled RCSHANNON Coll.] / ALMELANDER Collection 1961 [only in one ♂ and one ♀] *Drosophila sigmoides* Lw. Det. J.R.MALLOCH [only in one ♀] / Pres.[ented] by J.R. MALLOCH B.[ritish] M.[useum] 1925-344 [only in the ♀ in BMNH]" [2 ♂♂, 5 ♀♀, USNM; 1 ♀, BMNH]; Scotts Run "Scotts Run Va. Oct. 23 1921 / Stubblefields Falls / On *Pinus virginiana* / JRMALLOCH Collector" [1 ♂, head missing, USNM]; Falls Church "Falls Church IX.11.17 Va / GMGREENE collector *Drosophila sigmoides* " [1 ♀, USNM]. **Maryland:** Plummers Island "Plummers I / 26-X-06 Md / AKFISHER Collector" [1 ♀, USNM]; Chain Bridge "Chain Bridg[e] 12.IX.13 Md / RCSHANON Coll / *Drosophila sigmoides* Lw. ST [STURTEVANT]" [1 ♀, USNM]. **Washington D.C.:** "14-X-56 / WLMCATEE Collector / *Drosophila sigmoides* LOEW" [1 ♂, right wing missing, USNM]. **Missouri:** "Missouri: Webster Groves IX/50 H.D. STALKER / *D. sigmoides* LOEW" [1 ♀, AMNH]. **Illinois:** Algonquin "Algonquin 10.5.95-134 [♂ as 10.3.95-100 / *Drosophila sigmoides* Lw" [1 ♂, 1 ♀, USNM]. **New York:** Long Island "Cold Spring Harbor L.I. / A.H. STURTEVANT Collection 1970 / *Drosophila sigmoides* LOEW STTT. [STURTEVANT]" [1 ♂, USNM]; New York "New York N.Y. X.20.21 [X.31.21 in ♀] A.H. STURTEVANT / A.H. STURTEVANT Collection 1970" [1 ♂, 1 ♀, USNM]. **New Jersey:** Fort Lee "Ft. Lee N.J. X.6.21 A.H. STURTEVANT / A.H. STURTEVANT Collection 1970" [1 ♂, right half of head and thorax missing, USNM]; NEW JERSEY: Bass River State Park "Bass Riv St. Pk. X/21/81 D.A. GRIMALDI ex. *Sarracenia* pitchers" [1 ♀, AMNH]

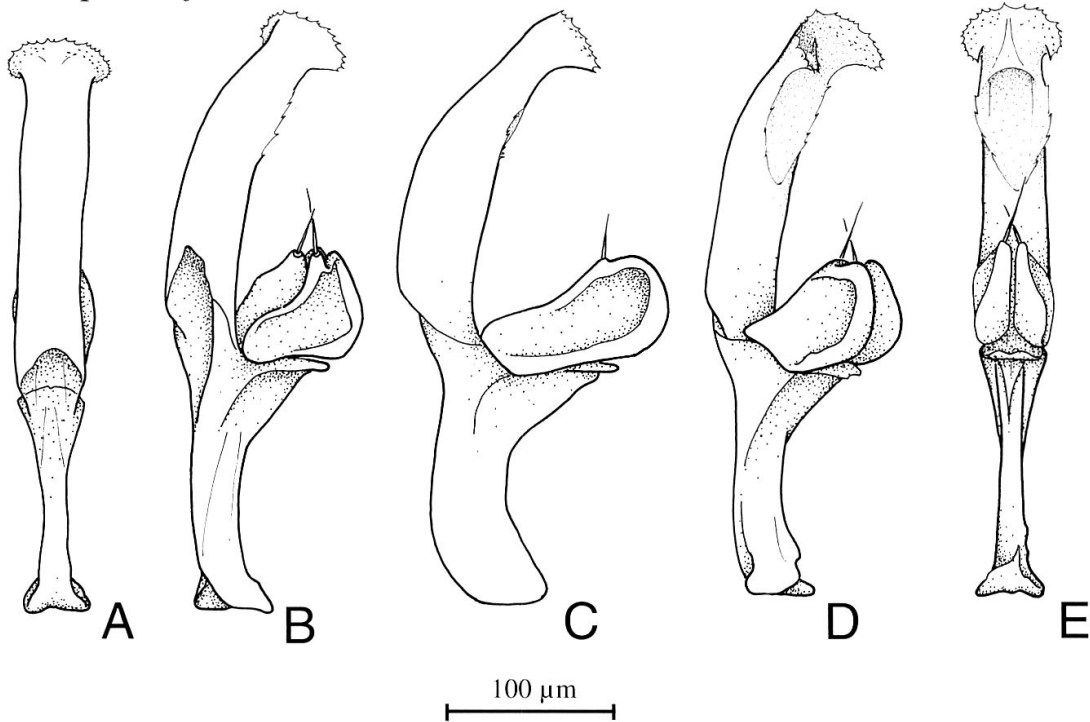
Note. The label "*Drosophila sigmoides* [♂ or ♀] VILELA & BÄCHLI det. 1999 " was added to every specimen.

Diagnosis: See the comparative diagnosis under *D. flexa*.

Redescription ($n_{\max.} = 30$). Characters as in *D. flexa* except: Frontal length 0.34 (0.30–0.39) mm, frontal index 0.92 (0.79–1.05), top to bottom width ratio 1.19 (1.12–1.39). Length ratio of anterior to posterior orbital seta 1.08 (0.90–1.30), of mid to anterior orbital seta 0.47 (0.33–0.60); poc 0.40x (0.33–0.48), oc 0.80x (0.67–1.05) frontal length; vt index 1.07 (0.89–1.31); vibrissal index 0.43 (0.36–0.57). Cheek index about 11. Eye index 1.32 (1.21–1.52). Arista with 3–4 upper and 2–4 lower branches, plus terminal fork.

Thorax length about 1.28 (1.12–1.48) mm; h index 1.06 (0.88–1.31); six rows of acrostichal setulae. dc index 0.66 (0.56–0.86). scut index 1.00 (0.85–1.12); sterno

Drosophila flexa



Drosophila sigmoides

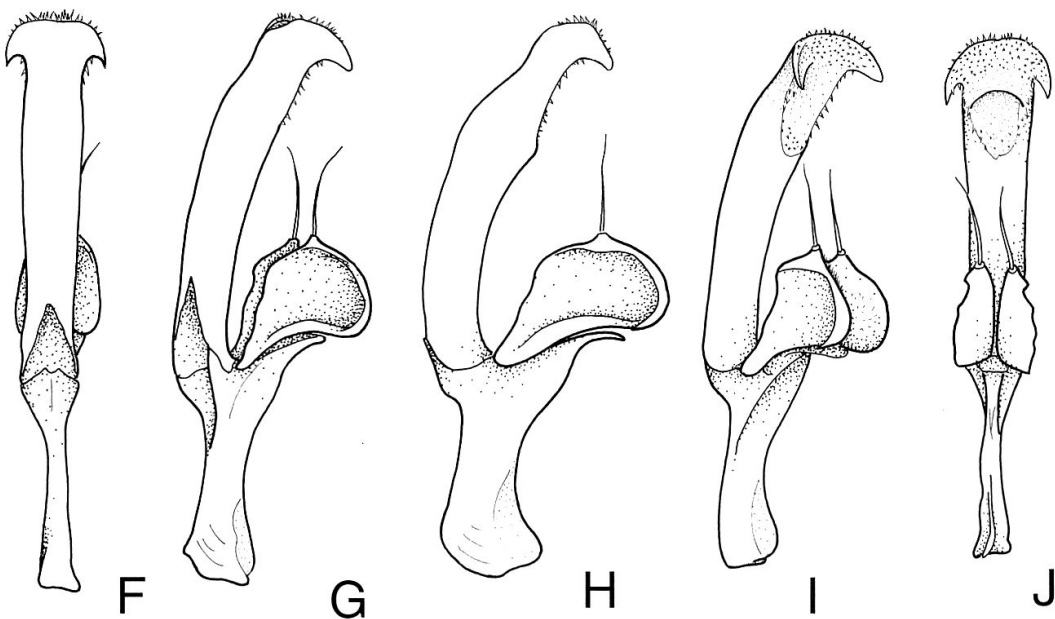


Fig. 5. *Drosophila flexa* LOEW (non-type ♂, same specimen as in Fig. 3): A–E, aedeagus, aedeagal apodeme and paraphyses; several views from dorsal through ventral. – *Drosophila sigmoides* LOEW (non-type ♂, same specimen as in Fig. 4): F–J, aedeagus, aedeagal apodeme and paraphyses; several views from dorsal through ventral.

index 0.73 (0.64–0.78), mid katepisternal seta about 0.41x length of the anterior one.

Wing (Figs 1C, D, 2) hyaline in posterior half, becoming brownish towards costal margin, crossvein dM-Cu distinctly curved (s-shaped), both crossveins and

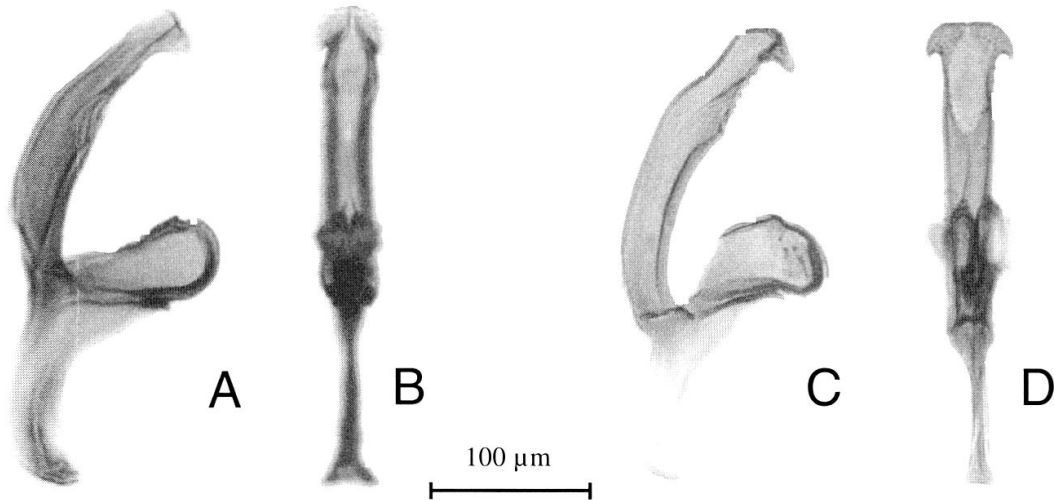
*Drosophila flexa**Drosophila sigmoides*

Fig. 6. *Drosophila flexa* LOEW (non-type ♂, same specimen as in Fig. 3): A–B, aedeagus, aedeagal apodeme and paraphyses; left lateral and dorsal views. – *Drosophila sigmoides* LOEW (non-type ♂, same specimen as in Fig. 4): C–D, aedeagus, aedeagal apodeme and paraphyses; left lateral and dorsal views.

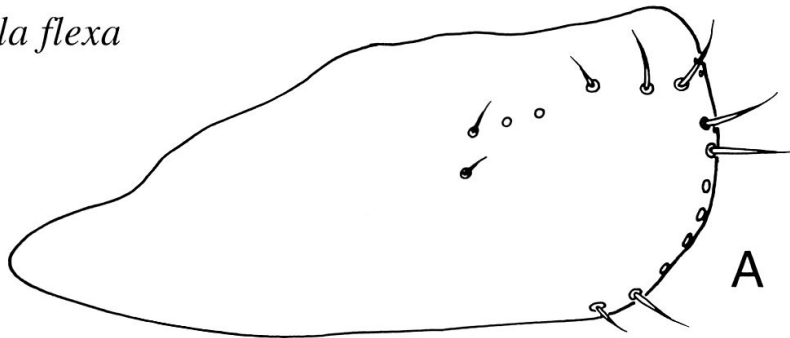
the tips of all longitudinal veins with brown markings, darkest at wing margin, fading towards wing base, the marking at R_{2+3} small; in males two whitish (hyaline) roundish spots are visible, one in cell r_{2+3} , the other one in cell r_{4+5} , not close to the wing margin. The microtrichia of these hyaline spots (Fig. 2A) are markedly thinner and shorter than those of the clouded surrounding areas both in the dorsal and ventral membrane of the wing. In females, these areas are not hyaline but darker brown than the surrounding wing area, and the microtrichia of these spots are apparently slightly thicker than those nearby. Length 2.76 (2.29–3.18) mm; length to width ratio 2.31 (2.00–2.45). Indices: C, 3.33 (2.88–4.23); ac, 1.83 (1.44–2.12); hb, 0.53 (0.42–0.65); 4c, 0.74 (0.59–0.95); 4v, 1.40 (1.23–1.75); 5x, 1.08 (0.70–1.38); M, 0.39 (0.31–0.50); prox. X, 0.79 (0.62–1.00).

Abdomen pale yellowish, with a median, brown longitudinal stripe, mostly diffuse at base, darker towards apex.

♂ *Terminalia* (Figs 4, 5F–J, 6C, D). Epandrium with about 15 lower, 2 median and 3 upper setae; ventral lobe anteriorly finger-shaped. Cerci anteriorly fused to hypandrium. Surstylus not micropubescent, with about 10 long, rod-shaped prenisetae and 8 long inner setae. Decasternum as in Figs 4A, B. Hypandrium shorter than epandrium; bow absent, gonopod not incised at the inner margin, slightly micropubescent, medianly bearing one large seta, linked to paraphysis by membranous tissue; paraphysis anteriorly pointed, posteriorly roundish, bearing a long subapical seta. Aedeagus slightly curved, subapically narrowed in profile, ventrally expanded and pointed at tip, ventroapically covered with tiny spines, ventral margins subapically bearing a row of spines. Aedeagal apodeme shorter than aedeagus, laterally flattened. Ventral rod shorter than paraphyses.

♀ *Terminalia* (Figs 7B, 8D–F). Valves of oviscapt ventrally convex, distally somewhat blunt-edged, but more roundish and dorsally more prominent than in *D. flexa*, with about 12 marginal and 5 discal trichoid ovisensilla; the subterminal ovisensillum is longer (Fig. 8D) than the marginal ones; in addition there are three smaller, distally positioned ovisensilla which are present in the species of the subgenus *Drosophila*. Inner spermathecal capsule (Fig. 8F) spherical, sclerotized; introvert very short.

Drosophila flexa



Drosophila sigmoides

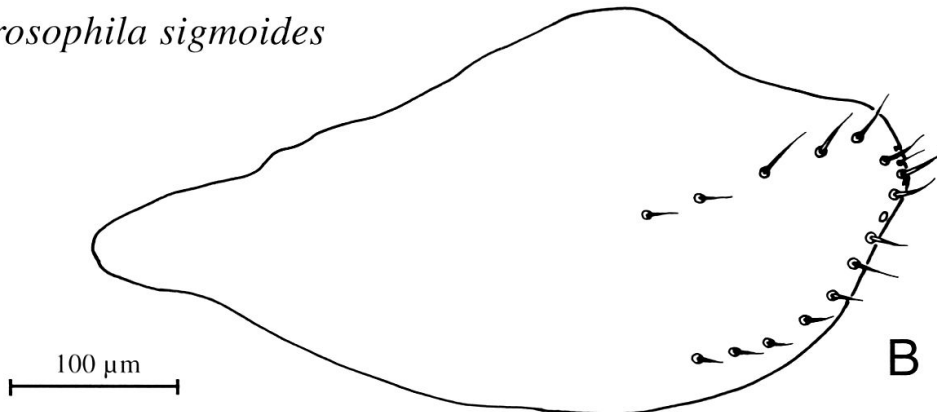


Fig. 7. Left oviscapt valves of: A, *Drosophila flexa* LOEW (same specimen as Fig. 1A); – B, *D. sigmoides* LOEW (same specimen as Fig. 1D).

Distribution: Central (Texas [westernmost record]) and Eastern United States of America (Mississippi [New record], Alabama [southernmost record], Georgia [New record], South Carolina [New record], Arkansas [New record], Tennessee, North Carolina, Virginia, Maryland, Washington, D.C. [New record], Missouri, Illinois, Indiana [New record], West Virginia, New Jersey [New record], New York, Massachusetts [northernmost and easternmost record]) (PATTERSON & WAGNER, 1943; CARSON & STALKER, 1951; SPIESS, 1951; DORSEY & CARSON, 1956, and new records based on labels attached to museum specimens).

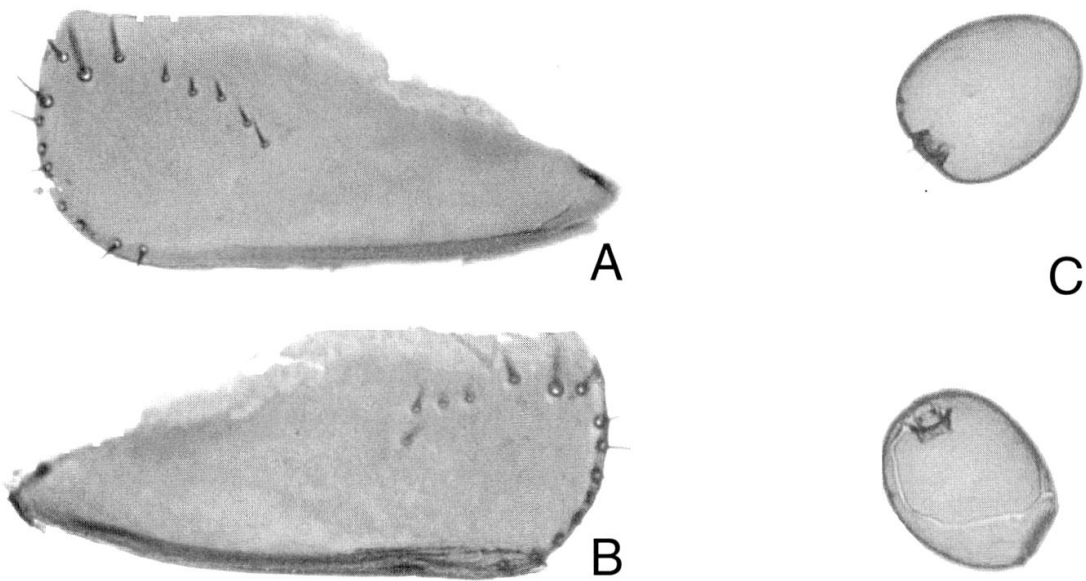
2 - ECOLOGICAL ACCOUNTS

Before detailing our own observations, it seems worthwhile to quote some ecological and distributional data available in the literature on the two species of the subgenus *Siphlodora*.

STURTEVANT (1921: 72) stated: “Dr. Metz and I have collected this species [*Drosophila flexa*] in Cuba by sweeping. It has not been found about fruit, and we have been unable to get it to breed on fruit in the laboratory, though the adults are quite hardy”.

PATTERSON & STONE (1952: 50) mention that *D. flexa* [cited as *D. subsigmoides*] has been collected in both the Nearctic and Neotropical regions of Mexico, while *D. sigmoides* apparently is restricted to the Nearctic region. However, WHEE-

Drosophila flexa



Drosophila sigmoides

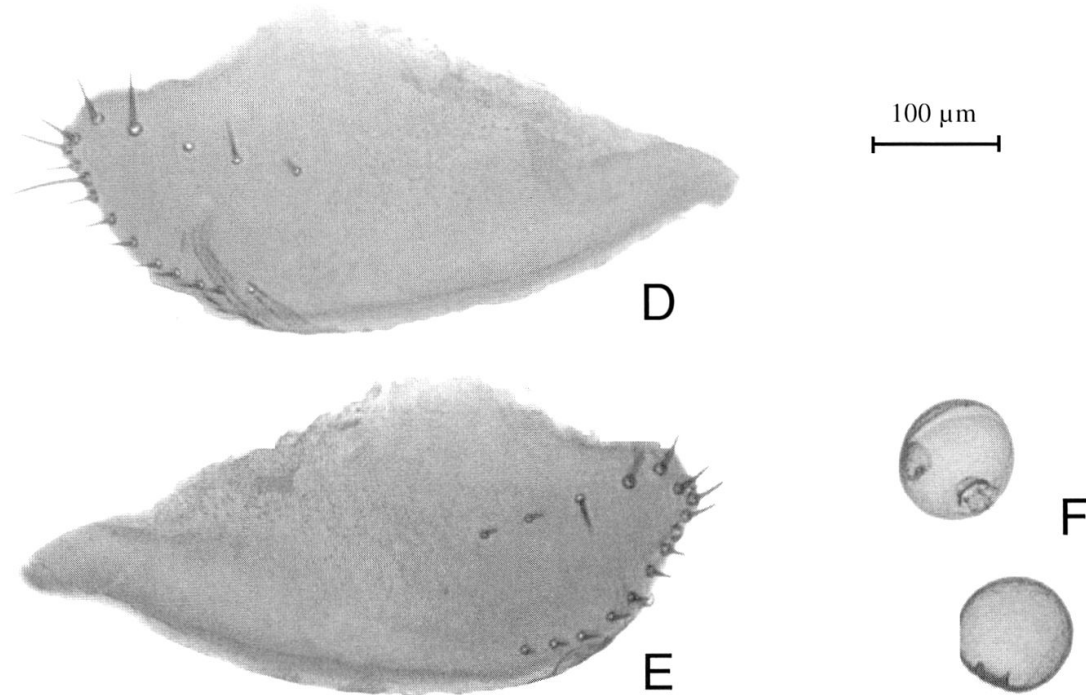


Fig. 8. *Drosophila flexa* LOEW (same specimen as in Fig. 7A): A, right oviscapt valve; B, left oviscapt valve; C, inner spermathecal capsules. – *D. sigmoides* LOEW (same specimen as Fig. 1D): D, right oviscapt valve; E, left oviscapt valve; F, inner spermathecal capsules.

LER (1981b: 110) stated “The two species of *Drosophila*, subgenus *Siphlodora*, present an unusual situation: *sigmoides* is clearly a Nearctic endemic whereas its only known relative, *flexa*, is just as clearly a Neotropical endemic.” He also mentioned

the difficulty in determining the Nearctic-Neotropical status of species which occur in the highlands of central Mexico. On p. 111, he stated "In this area of mountains, dissected by valleys and fringed by lowlands, the boundary between the two realms is almost imperceptible". In agreement with WHEELER'S (1981b) arguments we regard *D. sigmoides* as a Nearctic species and *D. flexa* as occurring, so far, only in the Neotropics as its known northernmost records are located in the realms' boundary of central Mexico.

Drosophila flexa

The first observation of a putative breeding site for *D. flexa* was made by one of us (CRV) on 19.XII.1992 in a maize field at Chácara Santa Mônica (a country house), 11 km NE of Santa Isabel, state of São Paulo, Brazil. The maize plants were about 2 m high and in early bloom. It was a cloudy day and at noon no fly was observed; however, dozens of imagoes were spotted swarming near or resting on several tassels of maize at 4:45 p.m. It was noted that the flies, mainly those apparently resting on the spikelets, had the peculiar behavior of rapidly vibrating the wings for several seconds.

No collecting material was available at that time, hence no fly was captured. However, three collections were made at the same maize field in the subsequent week and later on, as follows:

The first sampling of flies (collection coded F75) and tassels (coded F76) was made on 25.XII.92. Among the drosophilids captured those belonging to the genus *Drosophila* (21 males, 10 females) were mainly resting (18 males, 10 females) on the staminate spikelets of tassels and were individually aspirated. The three remaining males were aspirated from the ears. Only three females belonging to the genus *Drosophila* emerged in the laboratory from 4 tassels collected and kept in 1/4 liter vials with some wet sand at the bottom. All specimens of *Drosophila* were later identified as belonging to *D. flexa*. Moreover, 8 parasitoid hymenopterans also emerged from the tassels and two female chloropids and a single male of an as yet undetermined dipteran were aspirated from the tassels. Four undetermined dipterans were additionally aspirated from other portions of the maize plants: one male and two females from the ears and one female from one leaf (they are not included in Tab. 1).

A second collection was made ca. one month later, on 23.I.93, late in the afternoon (5-6 p.m.). A total of 84 *D. flexa* (44 males, 40 females) were aspirated (coded F78) from the maize tassels and 88 imagines (sex undetermined) belonging to the same species emerged (coded F80) in the laboratory from 4 randomly collected maize tassels, which were kept in plugged vials over wet sand. Moreover, three female syrphids and 3 parasitoid hymenopterans also emerged from the tassels. Two out of these four already loosened and spread out tassels bore only unexserted anthers, and no flies emerged from one of them.

The last and largest sampling was made two days later on 25.I.93, also late in the afternoon (5-6 p.m.). A total of 176 *D. flexa* (103 males, 73 females) were aspirated (coded F81) from the tassels and 285 adults of the same species emerged (coded F82) in the laboratory (25-28 °C) from 8 collected maize tassels, selected among those most attractive to the flies during sampling time, as recognized by the large number of flies swarming near or resting on them. Additionally two female chloropids, one male tephritid and one undetermined male dipteran were also aspirated and one chloropid, one undetermined dipteran and 13 parasitoid hymenopterans emerged from the tassels. Six out of these eight collected tassels bore only

unexserted anthers, and no flies emerged from two of them. In fact, two out of the eight tassels had not loosened and spread out their branches yet and could have been too immature and unsuitable for oviposition; unfortunately there is no way of knowing if they were those that yielded no flies, as the vials were not labelled with regard to this aspect. The collected branch number/tassel varied from 7 to 29; the number of spikelets per lateral branch, counted only for one seven-branched tassel out of the 8 collected ones, varied from 59 to 87 in addition to the 289 spikelets present in the central rachis. There was an overlap between the emergence dates for *D. flexa* (2 to 14.II.93) and for the parasitoid hymenopterans (10 to 15.II.93).

The results of the three collections are summarized in Tab. 1, including 12 dipterans unidentified to genus or species level as well as 24 parasitoid hymenopterans that emerged mostly, if not all, from pupae of *D. flexa*. The dipterans other than *D. flexa* are as follows: emerged = 3 syrphids, 1 chloropid, 1 undetermined dipteran; aspirated = 4 chloropids, 1 tephritid and 2 dipteran of undetermined family. In addition, 4 unidentified dipterans were aspirated (3 from ears and a single one from leaf). Samples of *D. flexa* collected on or emerged from the maize tassels, the remaining dipterans, except for the syrphids, and most of the parasitoids as well are housed in the MZSP, São Paulo, Brazil. The emerged syrphid flies stuck in the culture medium and were too damaged to be preserved.

No attempts were made to analyze the intestines of the larvae, hence we are not quite sure if they are really pollen-feeders.

Later analysis of the sand and of the remains of the tassels kept in the vials from where flies emerged revealed that some larvae pupariate inside the male spikelets and some in the surrounding sand. Samples of maize spikelets containing empty and partially exserted puparia of *D. flexa* as well as samples of puparia from which parasitoids emerged were glued to points on pins and are preserved in the MZUSP.

Tab. 1. Numbers of dipterans and hymenopteran parasitoids aspirated and/or emerged from maize tassels [except for three males of *D. flexa* from the collection code F75, which were aspirated from maize ears] in three collections made in late 1992 and early 1993 at Chácara Santa Mônica, 11 km NE of Santa Isabel, state of São Paulo, Brazil.

collection date method	25.XII.1992		23.I.1993		25.I.1993		total
	aspirated	emerged from 4 tassels	aspirated	emerged from 4 tassels	aspirated	emerged from 8 tassels	
code	F75	F76	F78	F80	F81	F82	
<i>Drosophila flexa</i> ♂	21	0	44	*	103	*	*
<i>Drosophila flexa</i> ♀	10	3	40	*	73	*	*
Total of <i>Drosophila flexa</i>	31	3	84	88	176	285	667
chloropids	2	0	0	0	2	1	5
syrphids	0	0	0	3	0	0	3
tephritids	0	0	0	0	1	0	1
undetermined Diptera	1	0	0	0	1	1	3
hymenopteran parasitoids	0	8	0	3	0	13	24
Total of other insects	3	8	0	6	4	15	36

* = identified with regard to the species (*Drosophila flexa*) but not to the sex.

Drosophila sigmoides

STURTEVANT (1921: 70) states: "I have collected this form [*D. sigmoides*] in southern Alabama by sweeping grass and weeds. Attempts to get it to breed on fruit have not been successful. It was not attracted to fruit that was exposed for several days in a small patch of young plants of *Solidago canadensis* [goldenrod, Asteraceae] from which *D. sigmoides* could be swept at any time. The specimen from New York, however, was collected by Dr. Metz on windfall apples".

According to BUTLER & METTLER (1963), the females of *D. sigmoides* lay their eggs in the spikelets of the host plant (*Tripsacum dactyloides*) before the anthers reach their full size.

DISCUSSION

Some putative host plants

The probable association between imagoes of *D. sigmoides* and plants of one species of goldenrod (*Solidago canadensis*) in Alabama, as observed by STURTEVANT (1921), deserves further analysis. According to him adults of *D. sigmoides* could be swept at any time around the plant. This fact could be an indication that the flies were using the plant either as a feeding or a breeding site, or even for both purposes. If the larvae of *D. sigmoides* are exclusively pollen-feeders and also use goldenrods as a host plant, it would be expected to find them swarming around the plant during the blooming season. However, that does not seem to be the case as STURTEVANT (1921) states that they were young plants.

Several additional data probably related to the ecology of *D. flexa* were found on the labels of museum specimens. Most probably they refer to the substrate where the adult flies were perched when collected. As stressed by CARSON & STALKER (1951), the conspicuous congregation of flies around a natural material does not necessarily indicate that the species is breeding there. They also state that "a species may not necessarily congregate about its breeding site, nor are the latter always suitable for oviposition over extended periods of time". The following label data were found attached to pinned *D. flexa*. In specimens from Colombia = coffee finca; frijol [bean]; soya [soy bean], leguminosas [Leguminosae]; maíz [maize]; *Solanum andigenum* [Solanaceae]. In specimens from Ecuador = potato vines. With regard to several specimens of *D. flexa* collected in Colombia bearing a label "frijol", it seems interesting to note that in Latin America farmers frequently sow beans and maize in alternating rows, so that the bean vines can use the maize stalks for climbing.

Known host plants

According to HEISER (1973) and BEADLE (1980) at the time the first Europeans arrived in the Americas, maize (*Zea mays* L.) was the most widely grown plant in the continent, extending from southern Canada (mouth of The Saint Lawrence River) to southern South America (central Chile). However, little maize grew in the prairie that was to become the great corn belt of the United States and for many years much of it was to continue to be dominated by wild grasses and American bisons. Among the grasses *Tripsacum dactyloides* which is found either as a diploid (2x; 2n = 36) or as a tetraploid (4x; 2n = 72) was probably present.

We are unaware of any publication concerning the association between *D. flexa* and/or *D. sigmoides* with maize tassels in the great American corn belt, which

partially overlaps the known distribution of the latter *Drosophila* species. It would be of interest to verify if the flies are really absent from those maize fields or if just nobody ever paid attention to them. There is a possibility that *D. sigmoides* is not attracted to maize tassels. Apparently, *D. flexa* has not been able so far to reach and colonize the area. Another possibility is that insecticides sprayed in the corn belt region aiming to control some hundreds of insect species that can damage maize could be responsible for the absence of *D. flexa* and/or *D. sigmoides* in the area.

Although additional and as yet undiscovered breeding sites may exist, the recently discovered association, in South America, between *D. flexa* and male inflorescences of the modern maize immediately raised the following question: what could be the original, primary natural host plant for this Neotropical species of *Drosophila*? The search for one putatively original host plant should take into consideration the most likely ancestors of the Indian corn.

The descent of man-made maize

The two closest known relatives of maize have been mostly regarded as candidates, either as the unique ancestor or, according to the hybrid origin hypothesis, as one of the ancestors: the annual teosinte *Zea mexicana* (SCHRADER) KUNTZE, now *Z. mays* L. spp. *mexicana* (SCHRADER), and the diploid perennial teosinte (*Zea diploperennis* ILTIS, DOEBLEY & GUZMAN), respectively, discussed by BEADLE (1980) and MANGELSDORF (1986). One quite convincing variant of, and somewhat complementary to, the old hypothesis revived by BEADLE (1980) of a unique ancestor for the domesticated maize was proposed by ILTIS (1983). According to his "catastrophic sexual transmutation" hypothesis the ear (female inflorescence) of the modern corn evolved from the lateral tassel (male inflorescence) rather than from the ear of the teosinte. It should be pointed out that as new information was accumulated regarding the phylogenetic relationships between the cultivated maize and the teosintes, the latter have been successively ascribed to different taxonomic units: initially described as belonging to the genus *Euchlaena*, they were later considered to be species of *Zea* and currently some of them are just considered as subspecies and/or varieties of *Zea mays* (DOEBLEY & ILTIS, 1980; ILTIS & DOEBLEY, 1980).

Other not so close relatives of maize, but formerly considered to be its likely ancestors, are the wild grasses belonging to the genus *Tripsacum*. According to SAVIDAN & BERTHAUD (1994), the genus *Tripsacum* occurs from the northern United States to southern Brazil and comprises 16 species, of which 12 occur in Mexico, considered to be the center of diversity of the genus. *Tripsacum dactyloides*, occurring from the northern USA (42°N) down to southeastern Brazil (24°S), is the most widespread of the 16 species and together with three of them has been used in crossings with maize. However, the tetraploid perennial teosinte (*Zea perennis* HITCHC., $2n = 40$), considered to be one of the most primitive taxa of the genus *Zea* and one of the closest relatives of maize, has been the major wild species to be used as a donor of wild germplasm for improvement of maize cultivars by means of introgression (MAGOJA & PISHEDDA, 1994). According to HEISER (1973) and BEADLE (1980), the annual teosinte ($2n = 20$, diploid), a coarse and wild grass widespread in Mexico, Guatemala and Honduras might be the ancestor of maize ($2n = 20$, diploid). This is an old hypothesis that has been reevaluated, as new archeological evidence was accumulated over the past decades, in spite of another mostly concurring hypothesis.

DOEBLEY & ILLIS (1980), based mostly on the comparative morphology of the male inflorescence, considered all the species of teosinte as belonging to the genus *Zea*, which includes currently four species, namely *Z. diploperennis* ILLIS, DOEBLEY & GUZMAN, *Z. luxurians* (DURIEU & ASCHERSON) BIRD, *Zea mays* L. (with three subspecies *mays*, *mexicana* (SCHRADER) ILLIS and *parviglumis* ILLIS & DOEBLEY, and *Z. perennis* HITCHC. According to them the modern cultivated maize (*Zea mays* ssp. *mays*) is but a subspecies of its ancestor, one of the annual teosintes (*Zea mays* ssp. *mexicana*), which has three allopatric varieties endemic to central upland Mexico. However, according to DOEBLEY (1990) the apparent wild progenitor of maize is another teosinte (*Zea mays* ssp. *parviglumis*) instead. Moreover, WHITE & DOEBLEY (1998) believe that the genome of maize has likely been shaped both by transposable elements and polyploidy. They stated that maize has been thought to be an ancient tetraploid whose genome has reverted over time to functional diploidy, partially because maize has 10 gametic chromosomes whereas several species of the *Andropogonae* tribe to which it belongs have only five.

Further analysis aiming to study a putative species-specific association between *D. flexa* / *Z. mays* and *D. sigmoides* / *Tripsacum dactyloides* should take into consideration the likely existence in nature of hybrid specimens between maize and its wild relatives, mainly the teosintes. However, no hybrids between maize and *Tripsacum* spp. have ever been found in nature, although with special techniques it is possible for man to make the cross (HEISER, 1973). On the other hand, the hybrids of maize and *Tripsacum* spp. are fully male-sterile (BEADLE, 1980).

As far as is known, *D. flexa* and *D. sigmoides* are allopatric species but the distribution of their known host plants widely overlaps. We believe there is a strong possibility that modern maize, a relatively recent man-made plant (ca. 8,000 years old, according to DOEBLEY & ILLIS, 1980), could be a secondary host for *D. flexa* larvae. So, it would be interesting to find a probable main host plant for *D. flexa*, and the candidate would possibly be among the teosintes and perhaps the several as yet unanalyzed species of *Tripsacum*. Moreover, there is a possibility that both species of *Drosophila* also utilize some as yet undiscovered additional breeding sites.

Another interesting fact is that the teosintes, being tropical short day plants that also need warm temperatures, do not grow naturally in temperate areas such as the corn-belt of the USA (BEADLE, 1980). The teosintes still grow wild only in parts of Mexico, Guatemala and Honduras and do not occur in South America.

Taking all these facts into consideration, we think that perhaps a better look at the tassels of teosintes could reveal the primary and original host plant for *D. flexa* in Central America. If this is true it would be possible that *D. flexa*, except for the regions where teosintes are present, would currently occur only in tropical areas of the Americas where maize has been cultivated. *D. flexa*, probably restricted originally to Mexico, Guatemala and Honduras, would have expanded its distribution in the pre-Columbian times by way of being able to breed in the tassels of maize and have followed the spreading of this man-made plant by the Indians of tropical America. However, if this hypothesis is true we cannot find a good explanation for the apparent absence of *D. flexa* in the corn-belt of the USA.

Based on the known geographical distribution of *D. flexa* it is somewhat difficult to classify it in one of the traditional terms "wild" and "domestic" species, or even in their variants such as semicosmopolitan, exotic, foreign, alien or widespread synanthropic species. It may currently be in the process of becoming widespread as it could theoretically be dispersed with maize, its (or one of its) host plant (see WHEELER, 1981b for discussion of the terms).

Although we have not analyzed the intestine contents of the larvae collected in maize tassels we suppose they feed mainly on pollen. Maize pollen is scented and its odor could attract *D. flexa* as it may attract honey bees (FLOTTUM *et al.*, 1983). However, as maize tassels with unextruded anthers apparently are less or not at all attractive to the imagoes of *D. flexa* it was somewhat difficult to explain how the larvae can feed on pollen before it has been shed from the opening tips of the anthers.

Morphology and anthesis of male maize flowers

After reading a chapter of CHENG & PAREDDY (1994) it occurred to us that a better understanding of the peculiar morphology and maturation of the male maize flowers could provide an explanation. So, before discussing this aspect it is worthwhile to quote their comment on the morphology of the male maize inflorescence (tassel) and on its maturation [the **bold** sectors and comments between brackets are ours]: “The tassel is a branched inflorescence located at the tip of the main stem. It consists of a central spike (rachis) and about 10-50 lateral branches. The paired spikelets (pedicellate and sessile) occur in many ranks around the central spike, but are arranged in only two rows on the lower (adaxial) surface of the lateral branches. Each spikelet contains two florets, the upper and the lower floret. **The development of the upper floret is about 2-3 days ahead of the lower floret measured at anthesis** [according to HSU *et al.*, 1988, it varies from 1.8 to 4.6 days depending on the genotype and on the tassel maturity]. Each spikelet has a pair of leaflike glumes, which encase two florets. Within the glumes, each floret is further enclosed with a pair of thin scales, a lemma (located adjacent to the glume), and a palea (located opposite to the lemma, between two florets). Two of the anthers present in each floret are located adjacent to the palea; the third is located adjacent to the lemma and is flanked by two lodicules. **These lodicules swell at anthesis allowing extrusion of anthers by elongation of the filaments** [according to FLOTTUM *et al.* (1983) the lodicules swell to three or four times their normal size due to water uptake forcing the opening of lemma and palea and in turn of the glumes]. Following extrusion, anthers dangle downward and shed pollen from openings at tip“ (for detailed figures see DOEBLEY & ILLIS, 1980; FLOTTUM *et al.* 1983; CHENG & PAREDDY, 1994, and GALINAT, 1994).

So, if the hypothesis that the larvae of *D. flexa* feed on maize pollen is further confirmed, an explanation for the fact that the extrusion of the anthers and the attraction of the imagoes in one given tassel could occur without affecting the availability of pollen for the larvae would be as follows: The extrusion of the anthers of the upper floret followed by their pollen shedding would attract the imagoes that could oviposit on the surface of the lower floret of each paired spikelet. So, during the next 2-4 days, preceding the anthesis of the lower floret, the larvae that have entered between the lemma and the palea could in some way prevent the swelling of the lodicules, and in turn the extrusion of the anthers, allowing the larvae to feed on the pollen of the unopened floret.

Another possibility that the larvae could reach the florets previously to the opening of the spikelet is given by the fact that we have found some parasitoids which died during their emergence from undoubtedly unopened spikelets. On the other hand, there is a possibility that not all the spikelets on the same tassel extrude the anthers of upper florets synchronously.

Moreover, based on the observation that some eggs of *D. flexa* were laid directly on the surface of unopened maize spikelets we suppose that upon hatching

the first instar larvae migrate to the margin of the outer glume where it partially overlaps the inner glume, and/or to the spikelet tip, enter the spikelet reaching the internal softer scales (lemma and palea) before the anthesis of the spikelets. Once inside the spikelet the larvae would enter through the overlapping margins of the scales and look for the anthers and pollen, upon which they most probably feed. It should be pointed out that, after the emergence of the flies from the maize tassels collected in Santa Isabel on 25.I.1993 (F82), the remains of the spikelets were dissected and their contents analyzed. It was observed that many anthers, mostly those from spikelets containing puparia, have been partially or entirely eaten by the larvae. This observation supports the hypothesis that they are pollen-feeders.

According to FLOTTUM *et al.* (1983) the maize pollen is easily microscopically identified when dry but it bursts when wetted. This fact should be taken into consideration in further analysis of the contents of the larval intestine.

The flat and wide oviscapt is probably well adapted to insert the eggs between the outer and inner glumes of the unopened spikelets and/or between the lemma and the palea of unopened florets.

Final comments

Considering that in some non-irrigated areas of tropical America many cultivars (varieties and hybrids) of the putative primary host plant (maize) for *D. flexa* bloom only once a year for a short period during summer the following question remains open: how these tropical/temperate flies reproduce during the absence of maize pollen. Overwintering would be one possibility, polyphagy with several feeding and breeding substrates another. The same consideration can be made on the association between *D. sigmoides* and *Tripsacum dactyloides*.

Although the specificity of the breeding sites of these two *Drosophila* species belonging to the subgenus *Siphlodora* must still remain in doubt, a better understanding of their association with *Zea mays* and its relatives may shed some light on the still enigmatical origin of man-made maize.

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