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Revision of the *Drosophila bromeliae* Species Group (Diptera: Drosophilidae): Central American, Caribbean, and Andean Species

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ABSTRACT

Species in the *Drosophila bromeliae* group visit flowers, where most or all of the species probably breed. They are not collected in significant numbers. The group has thus far included five Neotropical species: *aguape* Val and Marques, 1996 (from southern Brazil), *bromeliae* Sturtevant, 1921 (Cuba), *bromelioides* Pavan and Cunha, 1947 (Brazil), *florae* Sturtevant, 1921 (type locality Cuba, also reported from the Caribbean and Central Ameria), and *speciosa* Silva and Martins, 2004 (northern Brazil). Based on specimens from various museums, collections by the author, and detailed study of some types, the following revisions are made to the group: *Drosophila florae* is known only on the basis of the holotype female from Cuba, and *bromeliae* is widespread throughout Central America, the Caribbean, and northern South America; both species are redescribed in detail. Nine new species are described: *Drosophila billheedi,* n. sp. (from Trinidad); *D. manni,* n. sp. (Bolivia); *D. mexiflora,* n. sp. (Mexico, possibly Jamaica); *D. paramanni,* n. sp. (Costa Rica); *D. penispina,* n. sp. (Dominican Republic and Costa Rica); *D. sevensteri,* n. sp. (Panama); *D. starki,* n. sp. (Dominican Republic); *D. stylipennis,* n. sp. (Dominican Republic and Puerto Rico); and *D. thurstoni,* n. sp. (Jamaica). Four additional species are reported but not described since they are based just on females. Brazilian/Amazonian species will be treated separately. Intra- and interspecific geographic variation is documented in widespread species, the immature stages of *Drosophila bromeliae* are described in detail, and a key to species based on adult males is provided to facilitate identification of these very similar species.

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INTRODUCTION

Alfred Sturtevant formally proposed the taxonomic system of species groups for the genus *Drosophila* in 1939–1942 (Sturtevant, 1939, 1942), but his earliest effort toward this was taken in his seminal work, *The North American Species of Drosophila* (Sturtevant, 1921). In that monograph were descriptions of two yellowish species collected from flowers in Cuba, *Drosophila bromeliae* and *D. florae*, placed in his *Drosophila* "group B," defined partly by the presence of prescutellar setae. Group B then became known as the *Drosophila bromeliae* species group (Pavan and Cunha, 1947; Patterson and Stone, 1952), the subject of the present treatment.

Studies on the biology and genetics of *Drosophila* have traditionally been carved up by species groups, with investigators often devoting years to the study of one species group, such as the *Drosophila melanogaster*, *obscura*, *repleta*, and *willistoni* groups (Lemeunier et al., 1986; Lakovaara and Saura, 1982; Wasserman, 1982; Ehrman and Powell, 1982, respectively). Flies in groups like these can be easily cultured on standard laboratory medium, necessary for experiments, but with the result that *Drosophila* biology today is highly biased by frugivorous groups. Anthophilic species, on the other hand, which breed in flowers, are notoriously difficult to culture, and so with a few exceptions (e.g., the *D. flavopilosa* species group [reviewed by Brncic, 1983]), the systematics and biology of anthophilic Drosophilidae is by comparison poorly known. In most flower breeders there is striking morphological and reproductive modification, particularly of the oviscapt (e.g., *Zapriothrica* Wheeler, *Zygothrica* Wiedemann, *Drosophila flavopilosa* group), which is often elongate or bears stout, heavily sclerotized pegs. Also, only one or a few mature eggs are laid at one time, and the eggs typically have the chorionic filaments reduced or lost (Brncic, 1983). Species and even entire groups range from monophagous, breeding in a single species or genus of flowers (e.g., *Drosophila flavopilosa* group in *Cestrum* [Solanaceae] and a few other plant genera, and some species in the *bromeliae* group breeding only in *Solanum*), to species that are highly polyphagous, breeding in the flowers of dozens of families.

Obligate anthophily has repeatedly evolved in Drosophilidae, mostly in the subfamily Drosophilinae (reviewed by Brncic, 1983). Major groups of anthophilic drosophilines include many (perhaps most) species in *Scaptodrosophila* (principally Old World), all species in the closely related Neotropical genera *Laccodrosophila* Duda and *Zapriothrica* Wheeler, and many species in the Neotropical genus *Diathoneura* Duda and perhaps in its sister genus *Cladochaeta* Coquillett. Some species of *Zygothrica* Wiedemann breed in or at least visit flowers, even though they rendezvous on fungi for mating (Endara et al., 2010; Grimaldi, 1987; dos Santos and Vilela, 2005). Within *Drosophila*, anthophily occurs in the subgenera *Phloridosa* Sturtevant, *Siphlodora* Patterson and Mainland, and *Drosophila*. Within the subgenus *Drosophila* anthophily occurs in all species of the *bromeliae*, *dreyfuysi*, *flavopilosa*, and *onychophora* groups, and many or some species of the *annulimana*, *guarani*, *mesophragmatica*, *peruviana*, and *tripunctata* groups. All these species groups are Neotropical, and so it seems that *Scaptodrosphila* and the other anthophilous drosophilines are ecological equivalents in the Old and New Worlds, respectively.

The present study was based on samples of Neotropical drosophilids originating largely from Central America and the Caribbean, collected by various drosophilists and entomologists primarily between the 1950s and 2000s. These specimens were collected using general methods

such as sweep netting and Malaise traps, but some were taken directly from flowers. Although there were some significant series, most samples consisted of only a few specimens or just one. Indeed, there are large areas of the neotropics that are still poorly sampled or completely unsampled for *bromeliae* group flies, including southern Mexico, western Brazil, and much of Andean South America. For example, no male specimens occur in collections from Colombia, Peru, and Venezuela, and there are less than 10 each from Ecuador and Bolivia. The largest series of museum specimens are from El Salvador, Honduras, and Nicaragua, collected by William B. Heed in the 1950s. Without question, the approach that is required to exhaustively treat the *Drosophila bromeliae* group is intensive, systematic sampling of flowers in these regions, like that done by Schmitz (2010) in eastern and southern Brazil. Schmitz (2010) sampled in 14 localities in Brazil (10 southern, 4 northeastern), collecting the flowers of 125 species in 47 families. Of those, the flowers of 56 species in 18 families were hosts for 28 species of Drosophilidae. Among those Drosophilidae were eight species in the *Drosophila bromeliae* group, six of them new (the two described ones were *bromeliae* Sturtevant and *bromelioides* Pavan and Cunha). The new Brazilian species will be described separately by H.J. Schmitz. At present, the *Drosophila bromeliae* species group is known to occur from southern Mexico and Cuba, south through Central America and the Caribbean, and throughout South America to Bolivia and Paraguay. Until intensive surveys are conducted throughout the neotropics it is hoped that the present revision serves as a useful update on the *bromeliae* group.

METHODS AND MATERIALS

All specimens in the present study were point mounted. Exemplar specimens of gross morphospecies from different localities were selected for dissection. Each dissected specimen was first relaxed by storing it in a jar with moist toweling soaked with vinegar for about two hours. When pliant, the tip of the abdomen was cut off using fine surgical scissors, macerated in warm 10% KOH for an hour, rinsed in water, dehydrated in 70% ethanol, then stored and disarticulated in glycerine using fine tungsten needles. Male and female terminalia were studied and illustrated by mounting the parts in a drop of molten glycerine jelly (1:1 agarose:glycerine), positioning them to the desired views, and allowing the drop to harden, then a coverslip applied. Terminalia were studied using a Wild compound scope with attached drawing tube at 100–400×. Measurements of pointed specimens were made at generally 60–100× using a Nikon SMZ 1500 stereoscope with a Nikon DSRi1 digital camera and NIS Elements software; error range is approximately ± 0.01 mm (including the variation due to positioning the specimen). Specimens of *Drosophila bromeliae* used for larval study and scanning electron microscopy derived from culture no. 15085-1682.00 in the *Drosophila* Species Culture Center, University of California, San Diego. This culture was initiated from flies from Grand Cayman Island, Bahamas.

Morphological terminology generally follows Grimaldi (1990), although paraphysis also refers to the *gonopod* or postgonite. Measurements followed the standard array used for drosophilids, described in detail by Bächli et al. (2004). A new measurement, which is very useful for the *bromeliae* group, is the *aedeagal angle*, which is measured by the angular separation of

two tangents: one drawn through the longest straight length of the distal portion of the aedeagus, and another through the longest straight length of the shaft of the aedeagus, both viewed in full lateral view of the male genitalia (fig. 17A). An aedeagal angle of 180°, for example, indicates a perfectly straight aedeagus; the smaller the angle, the more acute the bend between the apex and shaft. Also, it was found that lengths of each prescutellar seta in the pair on an individual fly often differed significantly, so an average length of the two was used. Numbering of oviscapt pegs, as seen in lateral view, was done to facilitate comparisons among species of the *bromeliae* group, a system not necessarily useful for other groups of drosophilids. It should be noted that the body coloration of a light drosophilid species can apparently differ depending on how specimens were preserved. Air-dried specimens and ones dried directly from ethanol can become slightly greasy, which will make the cuticle appear darker; specimens that were critical-point dried or treated with solvents (e.g., HMDS) will appear lighter, as well as being fully distended and cleaner.

Material used for study was from the following institutions; abbreviations are used in the descriptions:

AMNH American Museum of Natural History, New York, New York
CMNH Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (Chen Young)
INBiO Instituto Nacional da Biodiversidad, San José, Costa Rica (Manuel Zumbado) (this collection is now part of the Museo Nacional, Costa Rica)
LACM Natural History Museum of Los Angeles County, Los Angeles, California (Brian Brown) (this repository includes material formerly in the Utah State University Col lection, courtesy of Wilford Hanson)
NMNH National Museum of Natural History, Smithsonian Institution, Washington, D.C. (Wayne N. Mathis)
UGIC University of Guelph Insect Collection, Guelph, Ontario, Canada (Steve Marshall)

SYSTEMATICS

THE *DROSOPHILA BROMELIAE* SPECIES GROUP

Drosophila Group B: Sturtevant, 1921: 72.
Drosophila bromeliae species group: Patterson and Stone, 1952: 20; Silva and Martins, 2004; Val and Marques, 1996.

Diagnosis: A well-defined monophyletic group of small to medium-sized drosophilids (ca. 0.5–1.10 mm thorax length), body dull/bright yellowish to light brown; setae golden to dark brown-bronze in color, never black; arista with 3–4 dorsal and 1–2 ventral branches (usually 4-2); facial carina well developed, flat, but thinner than antennal pedicel and basal flagellomere, median sulcus faint or lacking; mesoscutum with one or two pairs of fine prescutellar setae; male genitalia simple (see below), ejaculatory apodeme either so vestigial as to be unobservable or completely lost; oviscapt slender, length 2.5–3.0× greatest width, with pegs; few very mature eggs, or even first-instar larvae are laid; eggs with two short subapical filaments.

FIG. 1. Habitus of exemplar species in the *bromeliae* group. **A.** *Drosophila manni*, n. sp. **B.** *D. penispina,* n. sp. **C.** *D. bromeliae* Sturtevant. **D.** *D. mexiflora,* n. sp.

General Description (Adults): Coloration of body generally yellowish to light brown, dull to slightly pollinose; never shiny; setae golden to dark brownish bronze in color, never black (fig. 1). *Head*: With very little variation in proportions and setation; eyes large, light to dull, dark red, with sparse interfacetal setulae frontally; dense, short setulae laterad (3 setulae surrounding each facet: fig. 3B); eye oval to slightly egg shaped in lateral view. Facial carina well developed, with anterior surface flattened and either lacking median sulcus or with faint sulcus; width of carina always less than that of antennal pedicel (fig. 3A). Gena shallow, depth usually less than 0.1× that of eye. One pair vibrissae present, subtended by row of 7–10 finer, shorter setae near ventral margin of gena. Length of frons moderate, frontal index varies from 0.93–1.55. Frontal vittae golden, microscopically striate and microtrichose, shiny, converge in anterior third (figs. 2, 4A). Fronto-orbital plates and ocellar triangle smooth, darker. Ocellar setae always divergent; base of ocellar seta either lying on tangent between median and lateral ocelli, or slightly outside tangent; postocellar setae generally short, orientations parallel, convergent, or even slightly cruciate at tips (fig. 2). Three fronto-orbital setae always present: proclinate (or1), anterior reclinate (or2) (ca. half the length and thick-

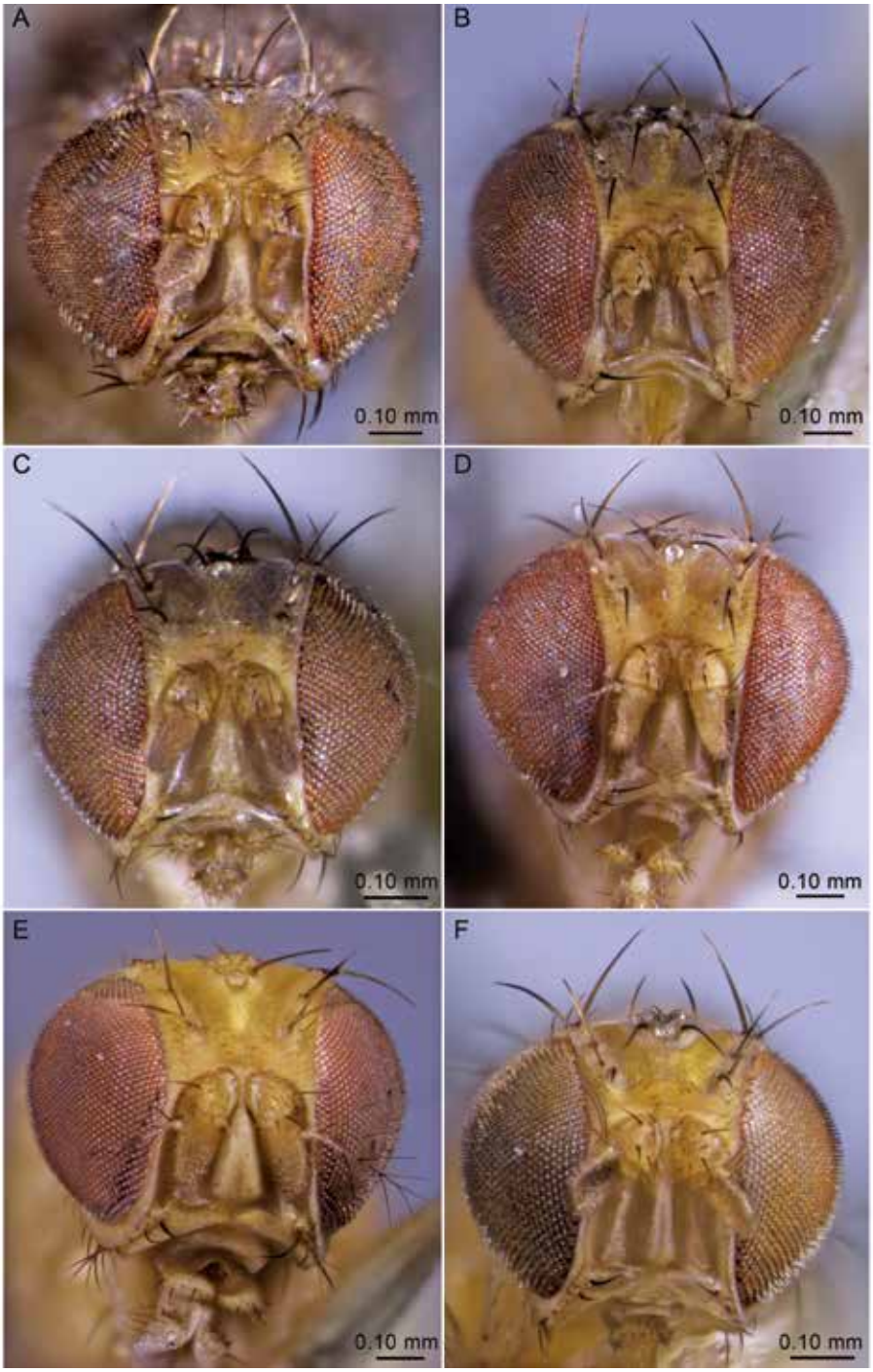


FIG. 2. Heads of exemplar species in the *bromeliae* group. **A.** *Drosophila penispina,* n. sp. (specimen DBG21) **B.** *D. billheedi,* n. sp. (DBG 2, holotype). **C.** *D. stylipennis,* n. sp. (DBG 12). **D.** *D. mexiflora,* n. sp. (DBG 41). Note supernumery left proclinate seta. **E.** *D. manni,* n. sp. (DBG 70). **F.** *D. bromeliae* Sturtevant (DBG 10). Numbers prefaced by DBG refer to specimens that were dissected.

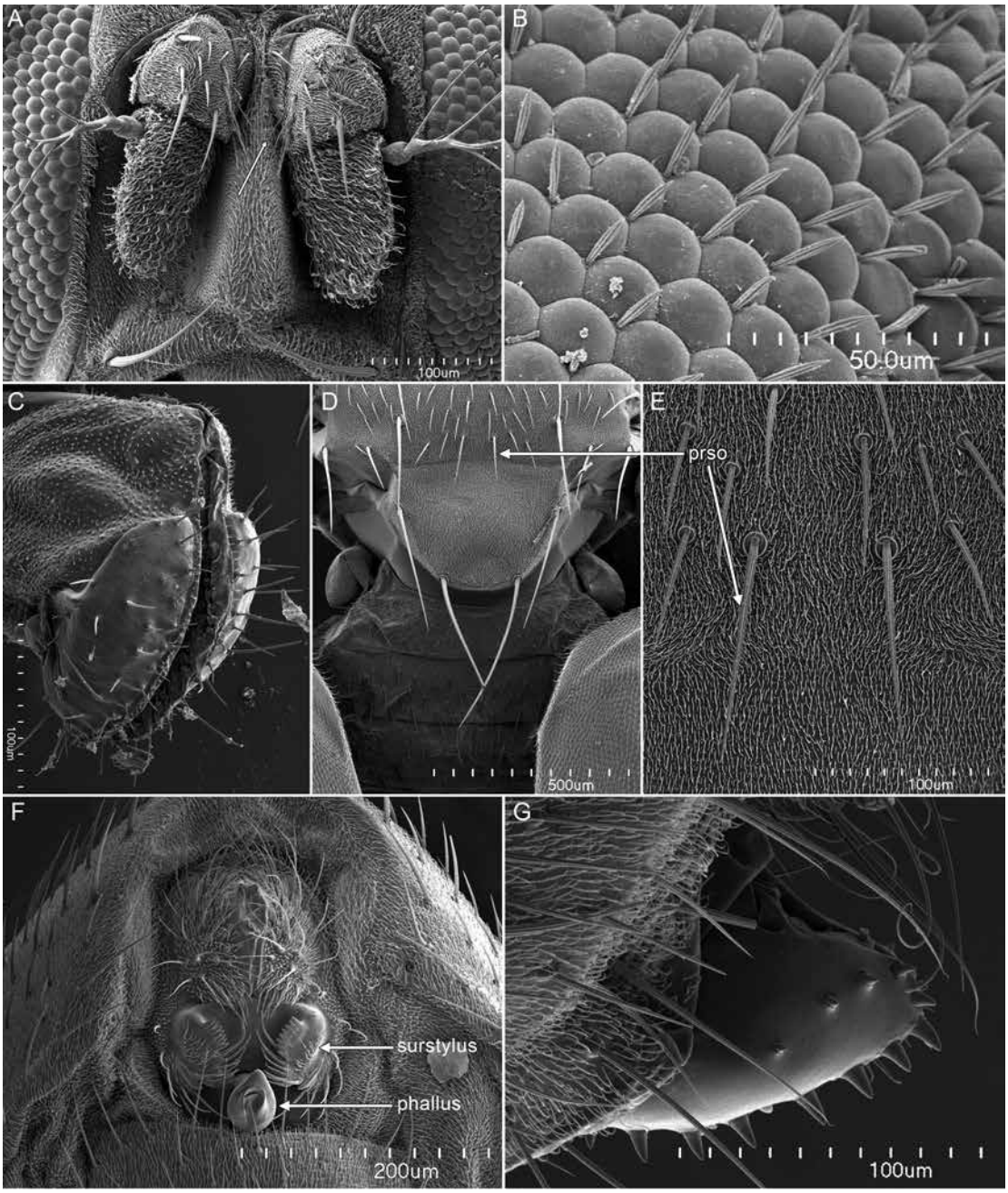


FIG. 3. Scanning electron micrographs of adult structures of *Drosophila bromeliae*. **A.** Face (arrow indicates fine setae on inner surface of pedicel). **B.** Detail of eye facets and interfacetal setulae. **C.** Labellum, folded closed. **D.** Posterior portion of thorax. **E.** Detail of D. **F.** Male terminalia. **G.** Female terminalia. Abbreviations: **prso,** prescutellar setae.

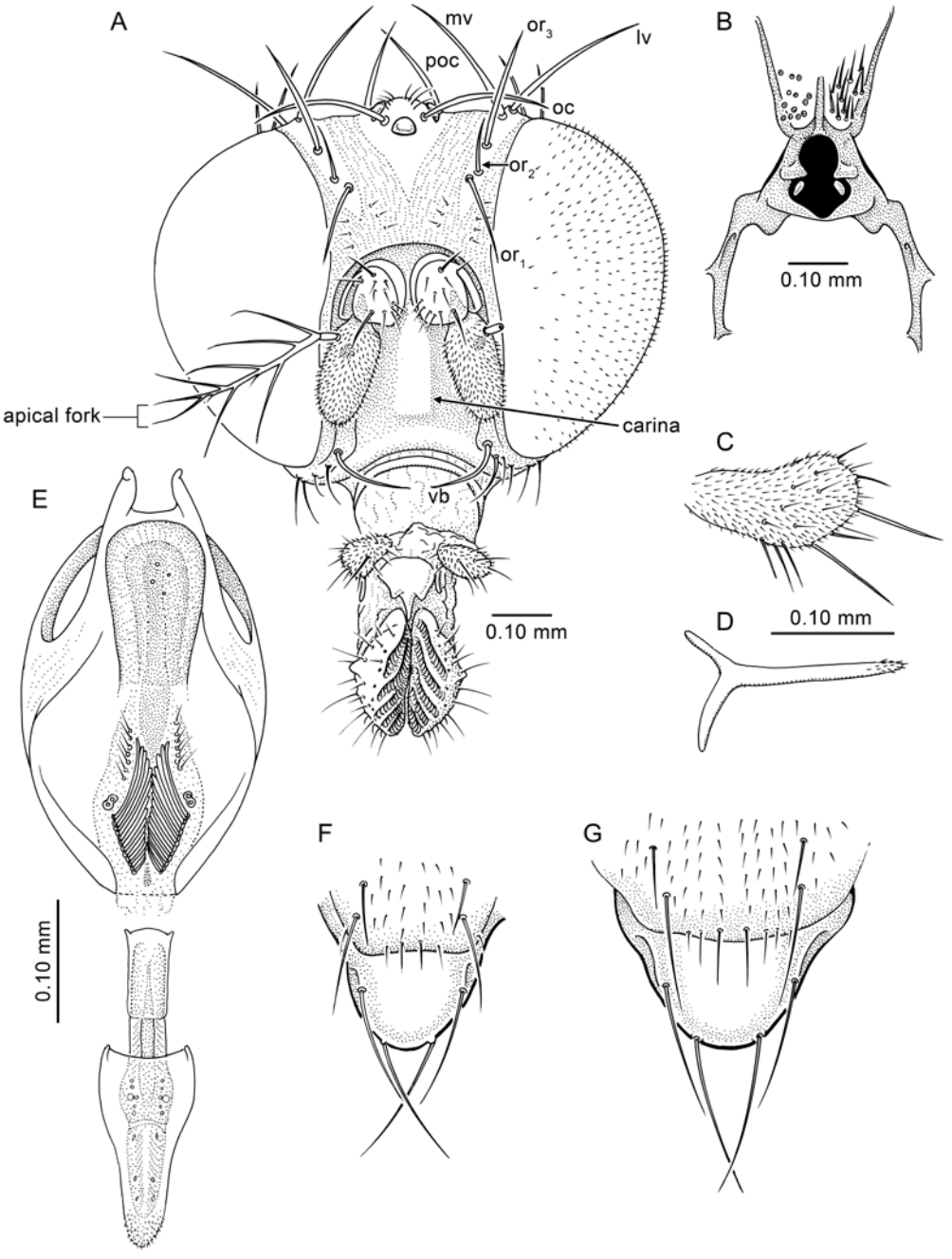


FIG. 4. Morphological details of *Drosophila bromeliae*. **A.** Head, with major setae and other structures labelled. **B.** Occipital foramen and posterior arms of tentorium. **C.** Palp. **D.** Lacinia. **E.** Cibarium (above, ventral view) and labrum + hypopharynx (below, dorsal view). **F, G.** Setation of posterior portion of thorax of *D. stylipennis,* n. sp., DBG 12 (F), and *D. penispina,* n. sp. DBG 9 (G). Abbreviations: **lv,** lateral vertical seta; **mv,** medial vertical seta; **oc,** ocellar seta; **or$_{1-3}$,** orbital setae 1–3 (proclinate, anterior reclinate, posterior reclinate, respectively); **poc,** postocellar seta; **vb,** vibrissa.

ness of other fronto-orbitals), and posterior reclinate (or3). Seta or3 is slightly thicker and shorter than or1; or2 is midway between other two fronto-orbital setae, or closer to or1. Ipsilateral seta or1, or3, and inner vertical always in line, with or2 usually slightly lateral to this tangent (fig. 2A–C, E, F), occasionally medial to tangent (fig. 2D). Inner verticals convergent, base of each very close to base of outer vertical; outer verticals strongly divergent. Inner and outer verticals approximately equal in length. Antenna with scape and pedicel yellowish to brown, pedicel with several setulae and microtrichia, including very fine longer ones on mesal surface; basal flagellomere slightly darker than pedicel, with uniformly short microtrichia (without long setulae). Arista with short, ringlike basal segment; terminal segment with 3–4 dorsal and 1–2 ventral branches (exclusive of short terminal fork) (usually 4-2 dorsal-ventral branches), lengths of longest branches about 0.5× length of entire arista (fig. 4A). Clypeus narrow, barely wider than widest portion of facial carina. Proboscis and palp generally yellowish, palp bilaterally asymmetrical (fig. 4-C), with longest setae on ventral margin; labellum small, lateral surfaces slightly sclerotized, without microtrichia, with short, stiff setae (fig. 3C); labellar lobe with 5–6 pseudotracheae; distal portion of proboscis (theca: labium + labellum) usually held forward in pointed specimens, at right angle to basal portion of proboscis. Cibarium (studied for only *D. bromeliae*) with floor having broad, sclerotized hypopharyngeal bulb (Grimaldi, 1990), with four sensilla/sieve pores over broad apex; medial sensilla short, trichodea type, in 2 rows of 7 each; posterior sensilla arranged in 2 even, long rows of approximately 15 long, blunt sensilla trichodea (fig. 4E). Labrum with acute, microtrichose apex (fig. 4E).

Thorax: Mesonotum yellowish to light brown, slightly pollinose; not shiny (fig. 1); with 6 or 8 irregular rows of acrostichal setulae. Two pairs of dorsocentral setae; prescutellar setae present in 1–3 pairs (usually just one), central pair always longest, lateral pairs often scarcely larger than acrostichal setae (figs. 3D, E; 4F–G). Lengths of prescutellar setae variable, as described for individual species. Scutellum with two pairs of setae; anterior scutellars (sc) slightly shorter and thinner than posterior sc; anterior sc strongly convergent, but not crossing; posterior scutellars often cruciate for 0.3–0.5× their length. Pleura same color as or slightly darker than notum (fig. 1). Notopleural area with three setae; two supraalar setae; two postpronotal setae. Katepisternum with two large setae, anterior seta slightly shorter than posterior one.

Legs: Yellowish, same color as or slightly lighter than notum and pleura, with typical array of setae; male protarsus without combs or fine, erect setae; mesotibia with stout, dark, ventroapical spurlike seta and shorter, dorsopreapical seta.

Wings: Clear, hyaline, never with patterns or infuscation; veins light, yellowish to infuscate (fig. 5). Venation very uniform. Costal vein ends at apex of $M_{1+2,}$ though segment between apex of R_{4+5} and M_{1+2} thinner than proximal portion of C; heavy spinules end midway between apices of R_{4+5} and M_{1+2} to 3/4 distance from apex of R_{4+5}; subcosta reduced, length half that of cell Sc. Tip of wing at apex of vein R_{4+5}; tip rounded to slightly pointed. Small cells at base of wing present, but cell bm incompletely closed; cell cup very small, closed. Vein A_1 present, but short; anal lobe of wing present. Ranges of wing indices: C 1.19–2.40; 4-C 0.90–1.3; M 0.50–0.70.

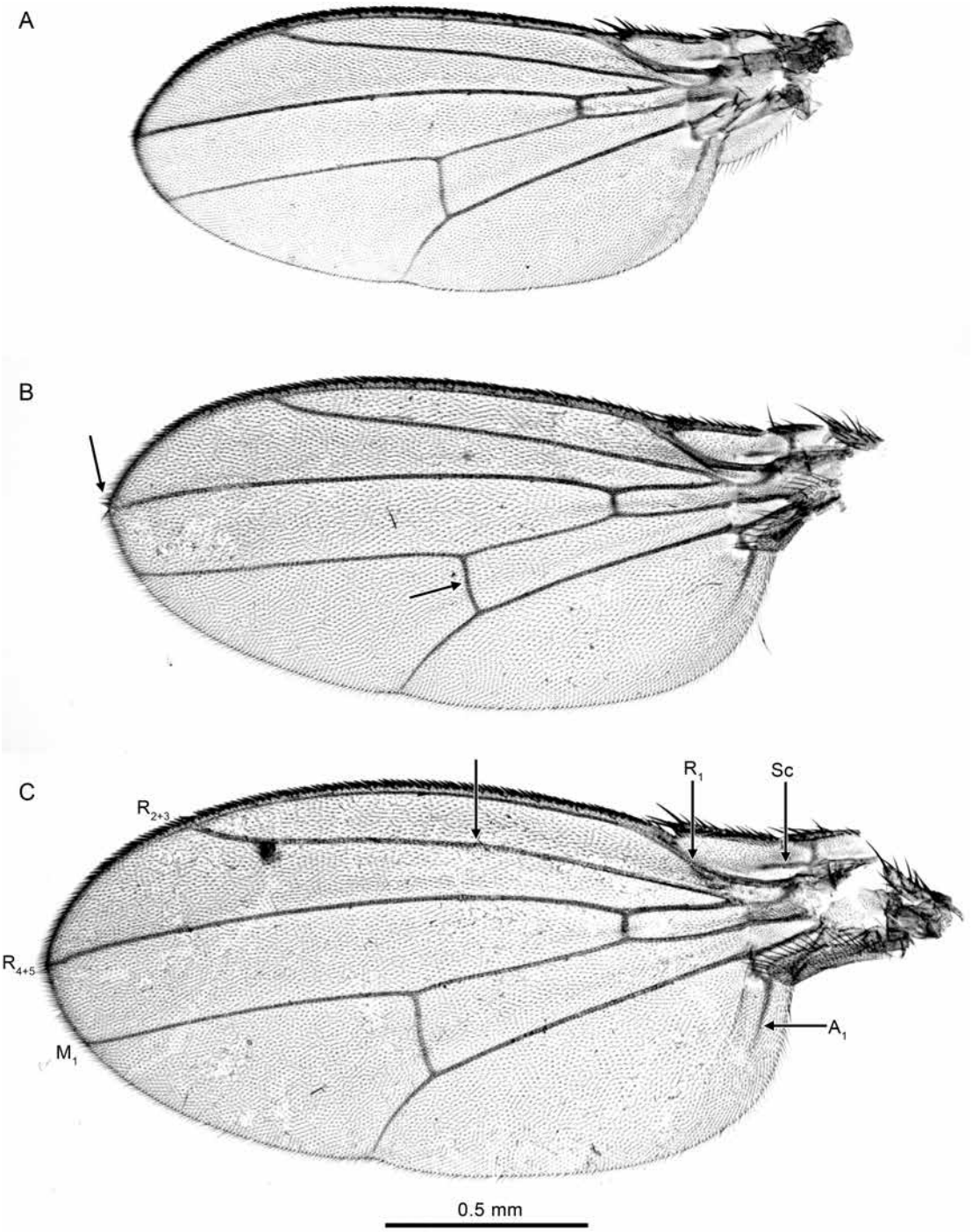


FIG. 5. Wings of exemplar species in the *bromeliae* group. **A.** *Drosophila bromeliae* Sturtevant (DBG 43: Ecuador). **B.** *D. thurstoni,* n. sp. (DBG 35). **C.** *D. penispina*, n. sp. (DBG 21). Arrows point to distinctive features: **B,** to slightly pointed wing tip, short crossvein dm-cu; **C,** to slightly sinuous vein R_{2+3}. To the same scale.

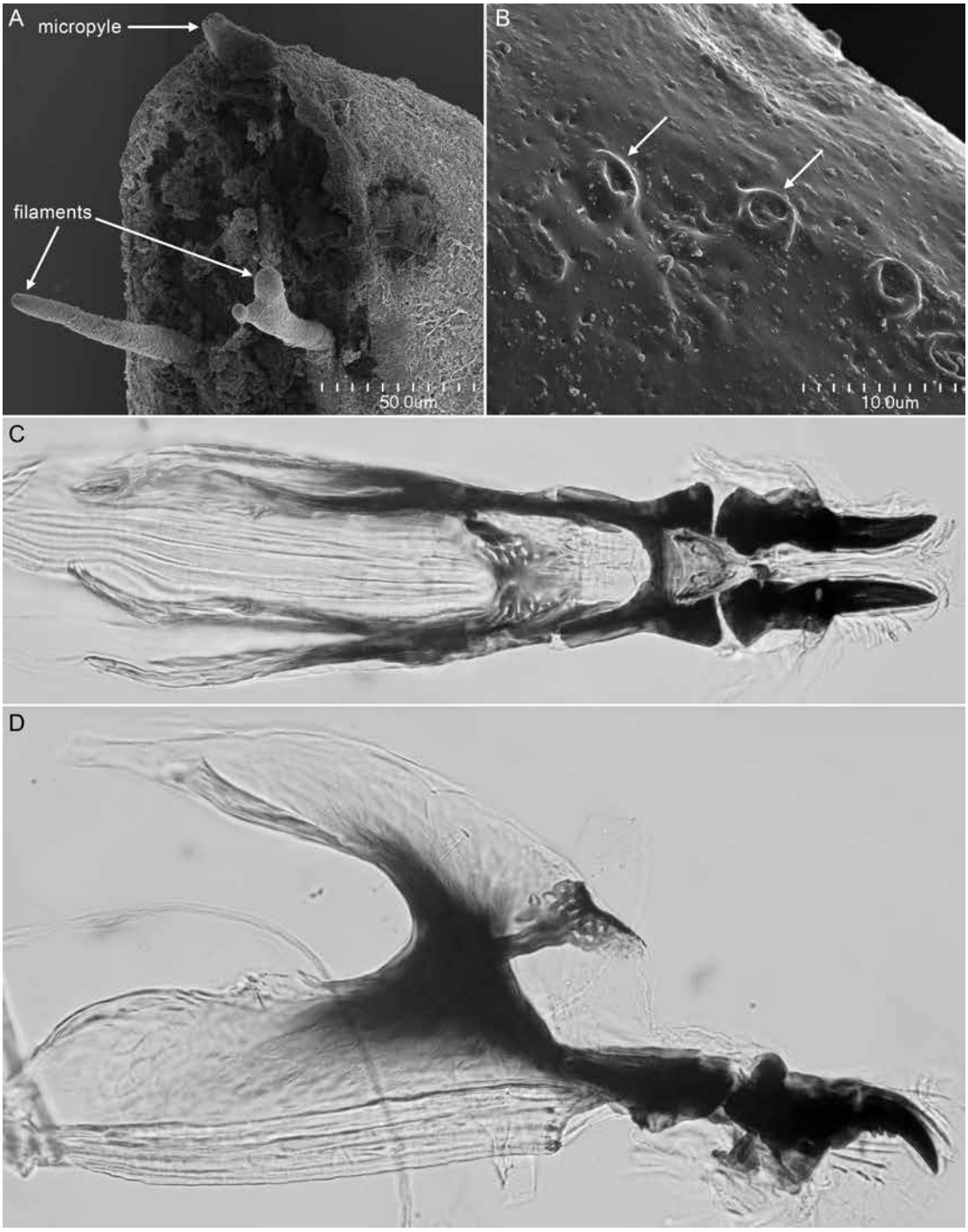


FIG. 6. Immature stages of *Drosophila bromeliae* (from culture). **A, B.** Scanning electron micrographs of egg. **A.** Anterior end, showing micropyle and filaments. One filament has a bifid apex. **B.** Array of porelike tubercles on surface. **C, D.** Cephalopharyngeal skeleton, third instar. **C.** Dorsal view. **D.** Right lateral view.

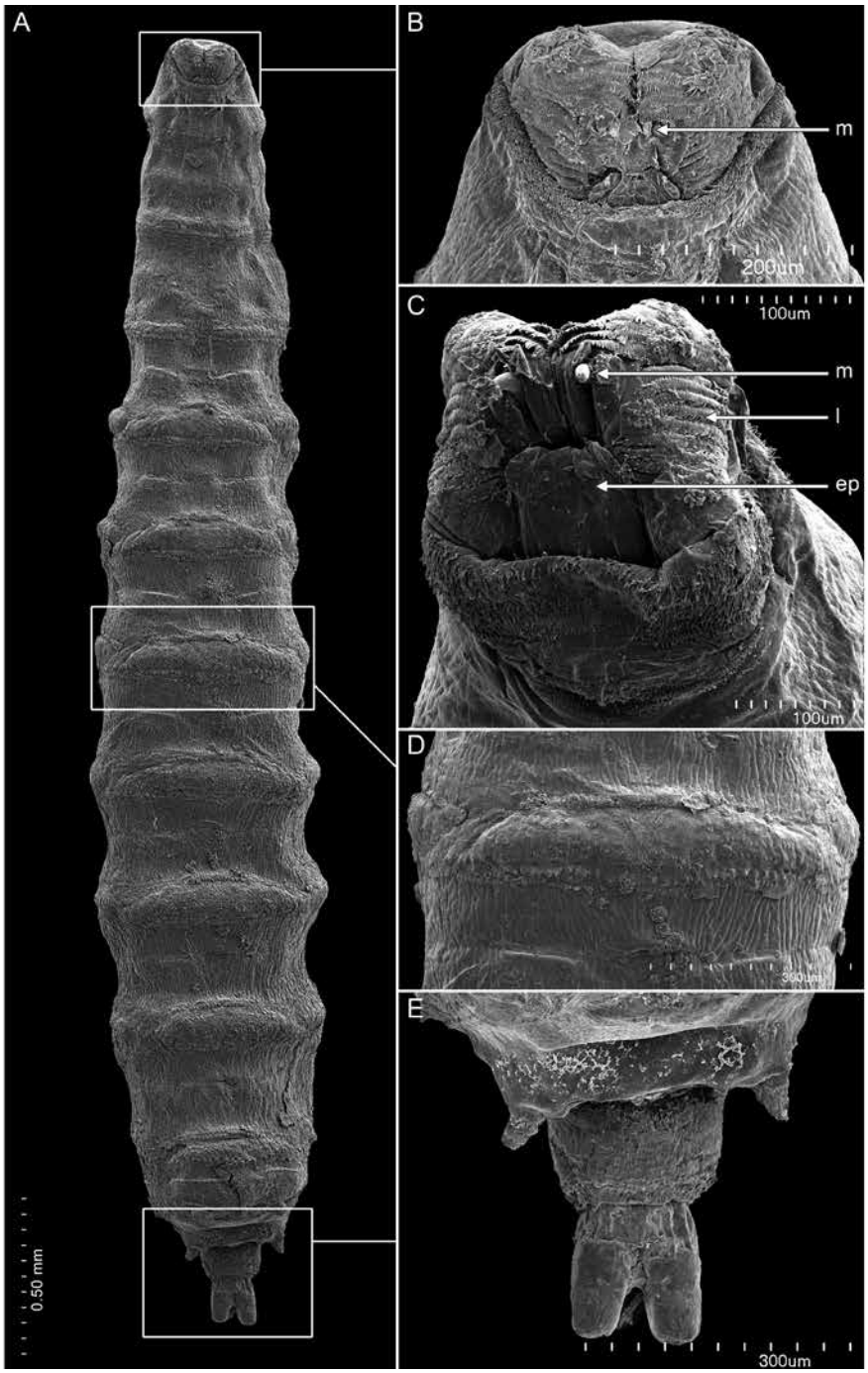


FIG. 7. Third-instar larva of *Drosophila bromeliae*, scanning electron micrographs. **A.** Entire larva, ventral view. **B.** Detail of head, ventral view (same specimen as in A). **C.** Detail of head, with oral cavity expanded and exposing the labial lobe. **D.** Creeping welt V (same specimen as in A). Note minute size of transverse hooks. **E.** Posterior end, ventral view (same specimen as in A), showing posterior spiracles and tubercles. Abbreviations: **ep,** labial lobe; **l,** lamellae; **m,** mandible.

Abdomen and terminalia: Abdominal tergites varying in color from dark yellowish to brown, sometimes uniform in color but often with diffuse dark bands on posterior margins of tergites. Tergal setae generally quite short, those on posterior margins longer. Male genitalia simple: Epandrium well developed, with setulae and microtrichia (except on ventral lobes), broadly connected laterally to cerci; hypandrium well developed, U-shaped to trapezoidal; no accessory lobes, pair of paramedian postgonites each with small apical setula; aedeagus a simple tube with enlarged distiphallus, the latter sometimes with a pair of ventrolateral spines; aedeagus in lateral view slightly to extensively arched. Aedeagal apodeme short; ejaculatory apodeme either so minute or vestigial as to be unobservable or completely lost. Subepandrial sclerite (decasternum) well developed, connecting surstyli. Surstylus with or without microtrichia, always with a row of 5–14 sclerotized prensisetae along dorsal portion of mesal margin (some thick setae ventral to prensisetae may be sclerotized); thinner, longer setae unsclerotized. Oviscapt with sclerotized pegs; oviscapt relatively long, length 2.5 to 3.0× greatest width in ventral view; apex of oviscapt narrow in lateral view, not broadly rounded. Spermathecal capsule sclerotized, simple; campanulate, sometimes with annuli on external surface.

Immatures: *Eggs* (known for *D. bromeliae* [herein], *D. bromelioides* [Pavan and Cunha, 1947]): subovoid, ca. 0.5 mm, slightly flattened on surface from micropyle to apex; micropyle raised into short tubercle; one pair of short preapical filaments present (ca. 200 μm length), tips of filaments blunt but not expanded or flattened, occasionally slightly bifid (fig. 6A); chorionic pattern of hexagonal cells externally not well developed, but with minute (ca. 0.5 μm) pores throughout and areas having small groups of raised, craterlike structures (fig. 6B).

Mature larva (based on *D. bromeliae*, herein): Amphineustic, with pair of anterior and pair of posterior spiracles; length ca. 4 mm, with 9 segments have creeping welts, only 7 abdominal welts appreciably raised (fig. 7); welts with transverse, irregular rows of minute, poorly sclerotized hooks (poorly visible under light microscopy, vs. dark to black, well-formed hooks in many saprophagous *Drosophila*). Antenna and maxillary palp typical, small and buttonlike; cephalic region with 4 transverse rows anterior to mandibles, separated by a median fissure; lateral to buccal atrium are another 8 rows of fine lamellae on each side; labial lobe well developed, apically comprised of 4 smaller lobes (figs. 7B, C).

Cephalopharyngeal skeleton (figs. 6C, D): typically cyclorrhaphan, mandibles ("mouth hooks") and sclerites between these and cornuas heavily sclerotized, cornuas less sclerotized; mandible hooklike, with two pairs of teeth on ventral margin (each pair on ventrolateral margin, separated by longitudinal ventral groove on mandible); mandibular teeth bifid (each comprised of two smaller teeth, fig. 6D); dentary and hypopharyngeal sclerites well developed, hypopharyngeal sclerite roughly H-shaped (figs. 6C, D); pharynx hardly sclerotized, with ca. 6 deep ventral grooves and several finer ones (fig. 6C); tentorial phragma heavily sclerotized, grading to very lightly sclerotized dorsal and ventral cornuas; labial sclerite lightly sclerotized, with paramedian pair of perforations; dorsal bridge of tentorium fully connected, less sclerotized than phragma, highly perforated on lateral surfaces. Anterior spiracles with 6 branches, tips of each branch with fine, rounded, liplike structure over opening. Posterior spiracles fused at base, short, ca. 175 μm, glabrous, with array of ecdysial scars typical of cyclorrhaphans.

Pupa (known for *D. speciosa* [Silva and Martins, 2004], *D. bromeliae* [herein], and *D. bromelioides* [Pavan and Cunha, 1947]): Light reddish brown; total length of anterior "horn" (everted anterior spiracle) 0.40–0.60 mm, base slightly longer than half total length (longer than everted spiracular tracheae, longest tracheae in center); anterior spiracle with 6 tracheae (*bromeliae*), 9–12 (*speciosa*), 11 (*bromelioides*).

Comments: Patterson and Stone (1952) erroneously mentioned that no prescutellar setae were present in the *bromeliae* group. Species are externally very homogeneous. Male and/or female terminalia are distinctive for some species, but ones in the *bromeliae* subgroup (see below) are very similar. Female genitalic features showing significant variation are the following: length in proportion to the width of the oviscapt in ventral view; number of ovisensilla pegs; size and proportions of spermathecal capsule. Male genitalic features include: shape of the hypandrium in full ventral view; shape of the aedeagus in lateral view (i.e., length; amount of curvature, as measured by the aedeagal angle); shape of the distiphallus in full ventral view; number of prensisetae on the surstylus, presence/absence of darkened setae on ventral portion of the surstylus, and sometimes the shape of prensisetae and vestiture of surstylus. Nongenitalic structures that are important for separating species include the following: body size, coloration, size and number of prescutellar setae (sizes can be rather variable intraspecifically), shape and width of facial carina, extent to which the posterior scutellar setae cross (i.e., are cruciate), number of dorsal branches of arista, and slight differences in the orientation and length of crossvein dm-cu.

Relationships: Monophyly of the *bromeliae* group is virtually certain based on morphological evidence, summarized above in the diagnosis. Relationships of the group, however, to other Drosophilinae have not been explored, although the *bromeliae* group is probably closely related to several other Neotropical flower-breeding groups. Pavan and da Cunha (1947) mentioned that *D. bromelioides* belongs in *Sophophora* (probably because the egg has two subapical filaments), but all other morphological evidence indicates that this similarity is only convergent. The large study on Neotropical drosophilids by Vilela and Bächli (1990) did not discuss the *bromeliae* group.

Flies in the *bromeliae* group are quite similar to those in the large genus *Scaptodrosophila,* of which there are hundreds of described and undescribed species in the Old World tropics. Similarities include the prescutellar setae, narrow carina, and flower-breeding habits. *Scaptodrosophila* markedly differs, however, from the *bromeliae* group by its distinctive male genitalia, in which there is a pair of projecting postgonite lobes, each with a longitudinal row of sensilla trichodea; one or more pairs of thick, long, stiff, projecting setae on the posterior margin of the hypandrium flanking the aedeagus; and the hypandrium being a short, broad, usually hemispherical plate. Moreover, an ejaculatory apodeme is present in *Scaptodrosophila* (distinctly absent in the *D. bromeliae* group), there are typically three large katepisternal setae (instead of two), and the eggs have 3–4 pairs of filaments (not the one pair seen in the *D. bromeliae* group). Morphological (e.g., Grimaldi, 1990) and molecular evidence (e.g., Robe et al., 2005; Morales-Hojas and Vieira, 2012) consistently places *Scaptodrosophila* at or near the base of the Drosophilinae, and so similarity to the *D. bromeliae* group appears to be just highly convergent.

With little question, the *Drosophila bromeliae* group lies within the "*virilis-repleta* radiation" of *Drosophila*, sensu Throckmorton (1975), morphologically distinguished in

part by a lateral fusion of the male cercus to the epandrium, and the lack of a hypandrial "hood" (a posterodorsal lobe lying above the aedeagus and articulating laterally to the posterior ends of the hypandrial arms). Males in the "*immigrans-tripunctata* radiation," in contrast, have a completely separated cercus and possess the hypandrial "hood." There is consistent molecular evidence for these two major clades of *Drosophila* (e.g., Robe et al., 2005; Morales-Hojas and Vieira, 2012).

It is quite likely that the *bromeliae* group, in fact, is closely related to several other species groups of Neotropical flower breeders such as the *dreyfusi* and *flavopilosa* groups. These flies tend to be light to very light in body color (even a whitish yellow), pollinose, never with black setae, and generally possess a narrow facial carina. The male genitalia in these groups are quite similar, often with a pair of subapical spines on the distiphallus. While the eggs of species in the *dreyfusi* group have four filaments (e.g., Pavan and Breuer, 1954), for those species in the *flavopilosa* group that have filaments (most do not) they possess a single pair of short, stublike filaments (Wheeler et al., 1962; Brncic, 1983). Each of these groups appears to be monophyletic, having distinctive, syapomorphic features: a retractorlike oviscapt with large teeth and a spermatheca lacking an introvert in the *flavopilosa group*; and for the *dreyfusi* group, minute spermathecae. Unfortunately, molecular studies (e.g., Robe et al., 2005; Morales-Hojas and Vieira, 2012) have not yet included any *bromeliae* group exemplars.

SPECIES SUBGROUPS

A preliminary arrangement of species, below, is based on the structure of the aedeagus. Species treatments in the text are presented in this order.

bromeliae Subgroup: distiphallus simple, with thick, liplike rim and no preapical spines
- *bromeliae* Sturtevant, 1921: widespread throughout Caribbean, Central America, and northern South America
- *florae* Sturtevant, 1916: Cuba (tentative placement, male unknown)
- *bromelioides* Pavan and Cunha, 1947: central to southern Brazil
- *aguape* Val and Marques, 1996: Mato Grosso, Brazil
- *speciosa* Silva and Martins, 2004: northern Brazil
- *billheedi* Grimaldi, n. sp.: Trinidad
- *mexiflora* Grimaldi, n. sp.: Mexico, Costa Rica
- *sevensteri* Grimaldi, n. sp.: Panama
- *thurstoni* Grimaldi, n. sp.: Jamaica

penispina Subgroup: distiphallus large, anteroventral margin having 3 small to large, scalelike spines
- *manni* Grimaldi, n. sp.: Bolivia
- *paramanni* Grimaldi, n. sp.: Costa Rica
- *penispina* Grimaldi, n. sp.: Central America, Caribbean

stylipennis Subgroup: Aedeagus very long, slender; distiphallus small and slender, with pair of minute subapical spines

stylipennis Grimaldi, n. sp.: Hispaniola, Puerto Rico

starki Subgroup: aedeagus short, linear; distiphallus bulbous, with preapical spines

starki Grimaldi, n. sp.: Dominican Republic

THE *BROMELIAE* SUBGROUP

Drosophila bromeliae Sturtevant, 1921
Figures 1C; 2F; 3, 4; 5A, 8–11A–H

Drosophila bromeliae Sturtevant, 1921: 72.

Diagnosis: Body yellowish to light brown, of small to average body size for group, thorax ca. 0.90 mm long (0.77–1.07); prescutellar setae large, no small lateral pairs; oviscapt shorter and with apex less acute than in *florae*, length 4.0× the depth in lateral view. Spermathecal capsule small, short (length approximately equal to width). Aedeagus fairly slender compared to distiphallus length, strongly arched in lateral view, aedeagal angle 99°–118° (mean 108°); distiphallus ovoid to slightly drop shaped in ventral view, with apex narrowed; hypandrium trapezoidal; surstylus with 7–10 blunt prensisetae (mode 9, mean 8.5), ventral setae of surstylus not sclerotized or darkened.

Description: *Male:* Head: Frons ochraceous yellow to light brown, especially ocellar triangle and fronto-orbital plates, which are also pollinose; margin at ptilinal suture lighter; frontal vittae shiny, finely striate, golden; frontal index 1.06 (0.96–1.12), top to bottom width ratio 1.43 (1.30–1.50). Ocellar triangle between ocelli slightly raised above rest of front, dark brown between ocelli, anterior tip of triangle ca. 0.7× length of frontal length. Bases of ocellar setae lying on tangent between median and lateral ocelli; postocellar setae parallel to slightly convergent, directed slightly posteriad (vs. vertically). Orbital setae dark brown-bronze in color (not black), or1:or3 ratio 0.97 (0.93–1.07), or2:or1 ratio 0.55 (0.53–0.71), postocellar setae 0.44× (0.37–0.51) and ocellar setae 0.69× (0.61–0.78) of frontal length; vt index 1.04 (0.85–1.12). Vibrissal index 0.44 (0.39–0.58). Face slightly lighter than fronto-orbital plates, especially frontal edge of carina. Carina well developed, thin (greatest width ca. 0.5× that of pedicel), frontal edge flattened, with slight sulcus. Cheek index about 0.08 (0.06–0.15). Eye index 1.43 (1.28–1.64). Occiput light brown, darker between tentorial sutures. Basal antennomeres slightly darker than front or face; arista with 3–4 dorsal and 1–2 ventral branches (4-2 most common), plus small to large terminal fork. Proboscis same color as antenna; palpus lighter, with one apical and one subapical seta.

Thorax length 0.83 mm (0.77–1.07): Scutum evenly ochraceous to very light brown; 6–8 uneven rows of acrostichal setulae. One large pair of prescutellar setae, lengths about 0.46 (0.30–0.60) of posterior dorsocentral setae; setae lateral to prescutellars ranging from ca. 2× length of acrostichals to barely differentiated h index 0.84 (0.70–0.06). Transverse distance of dorsocentral setae 2.66× that of longitudinal distance. Scutellum slightly lighter than scutum;

basal scutellars strongly convergent, apical scutellars crossed for nearly 0.5× their length; scutellar seta index 0.85 (0.78–0.92). Pleura approximately same color as scutum, little/no infuscation; sterno index 0.85 (0.65–0.87). Halter with stem lighter, bulb slightly darker than, pleuron. Legs lighter than pleura.

Wing hyaline, veins tan, length 1.72 mm (1.47–2.08), length to width ratio 2.33 (2.19–2.56). Indices: C, 2.15 (1.9–2.26); ac, 2.40 (2.22–3.00); hb, 0.55 (0.44–0.66), 4-C, 1.09 (0.96–1.24); 4V, 1.86 (1.54–2.11); 5x, 1.68 (1.39–2.0); M, 0.61 (0.50–0.70). Wing tips slightly pointed, vein R_{2+3} straight (not slightly sinuous).

Abdomen dark yellowish, posterior margin of tergites with thin, diffuse, pale brown band interrupted in middle of tergite; bands are thinner anteriorly.

Male terminalia (figs. 8–10): Epandrium with microtrichia, devoid of large setae on dorsal surface; ventral lobe blunt to rounded apically (not pointed), without microtrichia, with 5–7 setae. Cerci with microtrichia, laterally fused to epandrium. Surstylus with microtrichia on outer/lateral surface, with short mesal row of 7–9 prensisetae pegs and 6–7 fine setae. Subepandrial sclerite (not examined). Hypandrium trapezoidal, lateral margins straight (not convex), length 1.07× the width, anterior margin broad to narrow; gonopods fused to hypandrium, apical seta fine. Aedeagus fused to aedeagal apodeme; aedeagus fairly slender compared to distiphallus length, strongly arched in lateral view, aedeagal angle 99°–118° (mean 108°); distiphallus ovoid to slightly drop shaped in ventral view, with one end narrow. Aedeagal apodeme short, keellike.

Female: General morphology similar to males. Female measurements: Frontal index 1.03 (1.00–1.12); top to bottom width ratio 1.42 (1.40–1.55); or1:or3 ratio 0.95 (0.93–0.96), or2:or1 ratio 0.58 (0.53–0.64), lengths of postocellar setae 0.45× (0.41–0.48) and ocellar setae 0.72× (0.67–0.76) of frontal length, vt index 1.01 (0.87–1.16). Vibrissal index 0.48 (0.30–0.73). Cheek index about 0.08 (0.07–0.09). Eye index 1.42 (1.36–1.53). Thorax length 0.97 (0.90–1.04). Lengths of prescutellar setae 0.45× (0.37–0.64) that of posterior dorsocentral setae; h index 0.88 (0.82–0.95). Transverse distance of dorsocentral setae 2.53× (2.35–2.91) of longitudinal distance. Scutellar seta index 0.85 (0.77–0.90), sterno index 0.81 (0.65–1.03). Wing length 2.01 mm (1.60–2.23), length to width ratio 2.40 (2.10–2.65). Wing indices: C, 2.26 (2.00–2.52); ac, 2.49 (2.19–2.66); hb, 0.0.56 (0.53–0.66); 4-C, 0.1.04 (0.98–1.12); 4v 1.82 (1.79–1.92); 5x 1.49 (1.41–1.71); M, 0.0.56 (0.51–0.60).

Female terminalia: Valves of oviscapt rounded at tip (particularly so in holotype), ca. 280 μm long, with 17–20 marginal oviscapt pegs; length ca. 2.5× great width. Spermatheca cup-shaped, height approximately equal to width; basal introvert reaching about 0.7× length of capsule.

Type: Holotype, female: labeled: "Havana, Cuba, Jan. Feb. 1915" [printed]/ "TYPE" [printed]/ "ae5497" [handwritten]/ "*Drosophila bromeliae* Sturtevant" [written in Sturtevant's hand]. The specimen is double mounted with a minuten impaled through the pleura; head is lost; thorax, wings, and legs are intact; abdomen was removed and cleared (dissector unknown) and stored in a corked, glass microvial on same pin as thorax. Oviscapt valves had been separated by a prior dissector, making an intact ventral view impossible; spermathecae lost. In AMNH.

Other Specimens: **Cuba:** "Havana, Cuba, Jan.Feb. 1915 [printed]/ 1♂ 'florae' [written, in A.H. Sturtevant's hand], dissected by D.A.G.[DBG 14], 1♀ dissected by D.A.G.

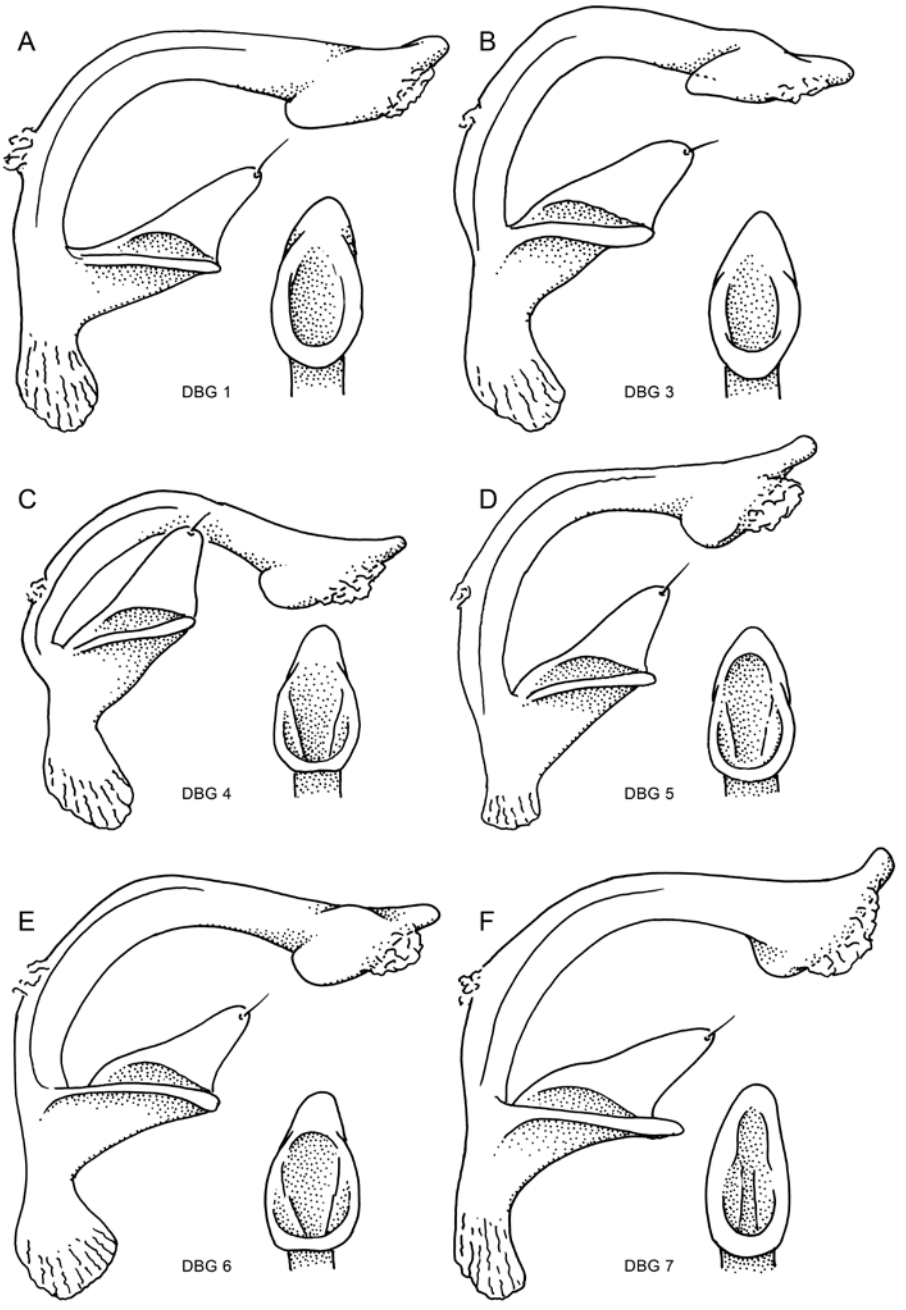


FIG. 8. Variation in the male genitalia of the most widespread species in the group, *Drosophila bromeliae* Sturtevant. All lateral views of aedeagus, aedeagal apodeme, gonopod, and full ventral view of distiphallus. All to the same scale. See text for specimen numbers. DBG numbers refer to individual specimen/dissection numbers (full data cited in text).

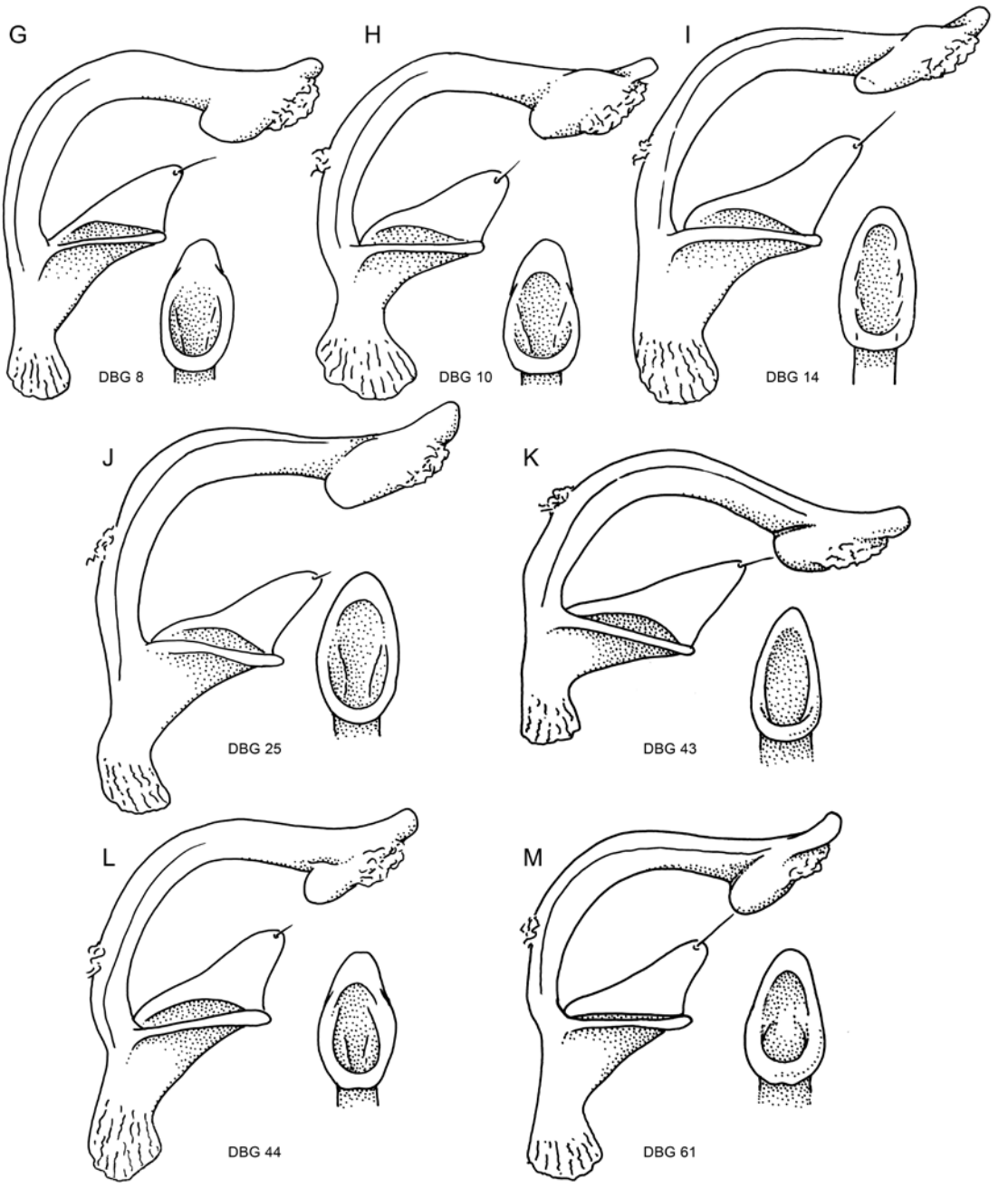


FIG. 9. Male genitalia of *Drosophila bromeliae*, continued.

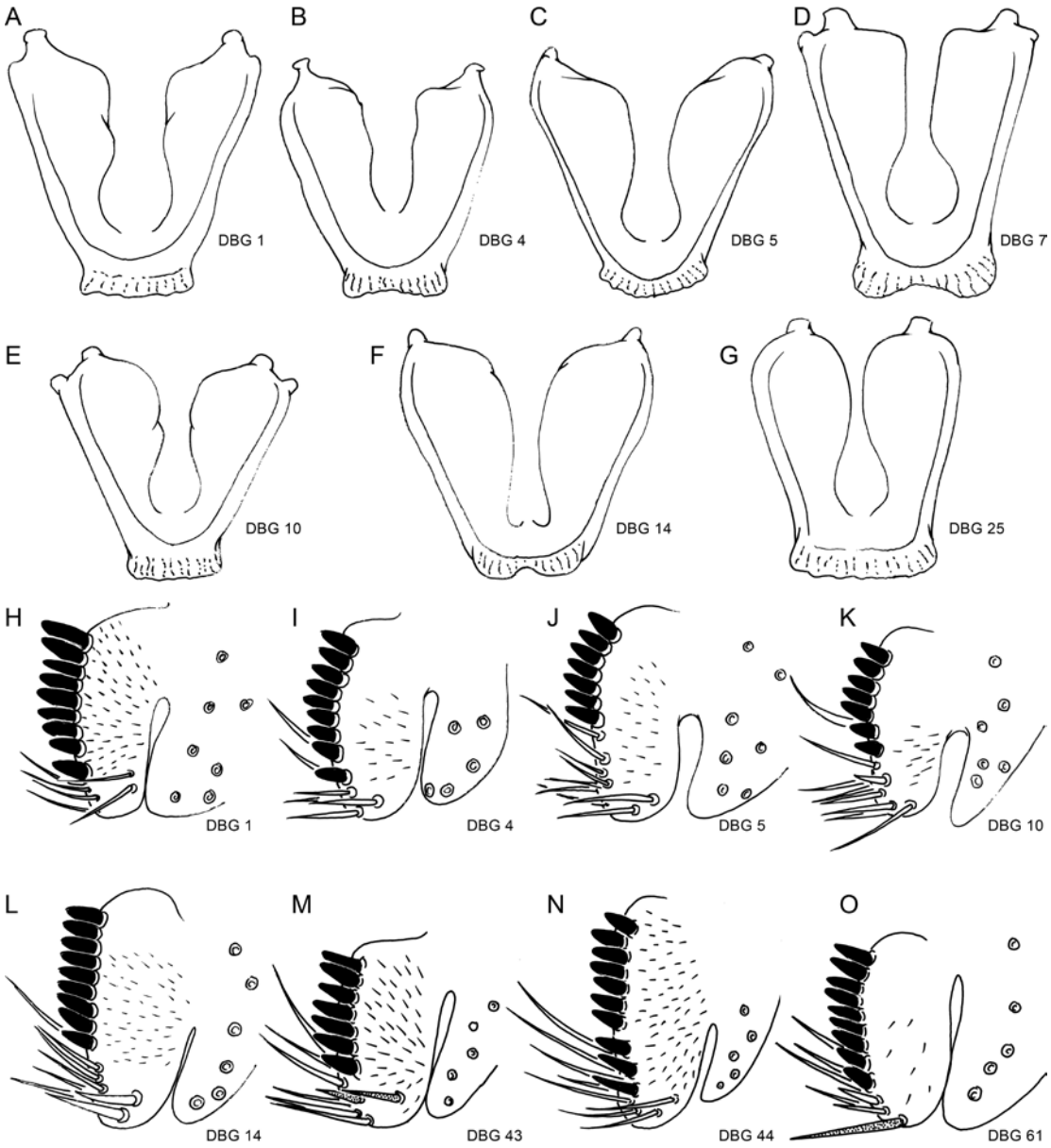


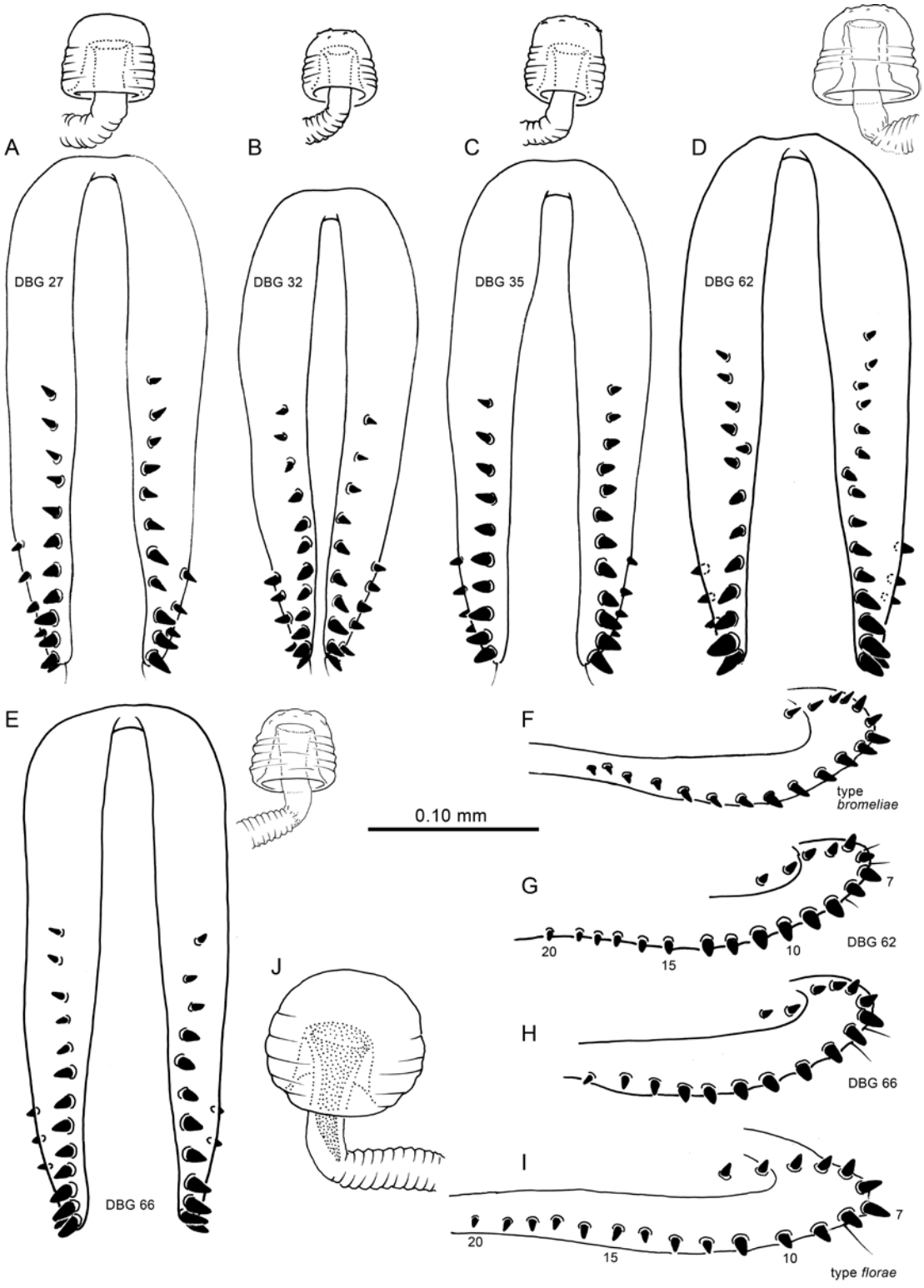
FIG. 10. Variation in the male genitalia of *D. bromeliae* Sturtevant. **A–F.** Hypandrium, all to same scale. **G–M.** Surstylus and ventral lobe of epandrium, all to same scale.

[DBG 15]." Manzo Abajo, 30 km SE Baracoa, 26-II-29, M. v. Tschirnhaus," 2♀♀ (dissected, DBG 65, 66). All in AMNH. "**Dominican Republic:** Peravia, 19 mi N San José de Ocoa, 3000 ft., 30/VII/91, in morning glory flowers, Grimaldi," 2♂♂ (1 dissected, DBG 61), 2♀♀ (1 dissected, DBG 62). In AMNH. "**Ecuador:** Orellana, Reserva Etnica Waorani, 00°39′25/7″S, 76°27′10.8″W, 216m, II-X/1995, Erwin et al., canopy fogging," 3♂♂ (2 dissected, sample 2072b1, DBG 43; sample 2072b2 DBG 44), 3♀♀ (samples 2074, 2078,

2072b1 [dissected: DBG 42]). In NMNH and AMNH. **El Salvador:** 1♂, "Laguna de Zapotitan [printed] 31a.b [handwritten]/Rep de El Salvador/Dec 3 1953, W.B. Heed" dissected by D.A.G. (DBG 7) (AMNH) (from the field notes of W.B. Heed: 31a,b "sweeping at Zapotitán (1500′), swampy forest"); 2♂♂, 2♀♀ "San Salvador/Rep de El Salvador," with following handwritten numbers and printed labels: "Oct 13 1953, W.B. Heed, 9.9" dissected by D.A.G. (DBG, 5♂), "Oct 14 1953, W.B. Heed, no. 11.5" dissected by D.A.G. (DBG 6, ♂), "Oct 11 1953, W.B. Heed, no. 5.2" dissected by D.A.G. (DBG 37, ♀), "Dec 10 1953, W.B. Heed, no. 37.6" dissected by D.A.G. (DBG 36, ♀) (from the field notes of W.B. Heed for 37.6: "sweeping in barranca just east of [illegible]" and "eggs have only 2 filaments but they are not blunt"); "Rep de El Salvador/Oct 1953, W.B. Heed/Santa Tecla, 12 km NW" dissected by D.A.G. (DBG 38♂). All in AMNH. **Honduras:** "Lancetilla, Honduras/Apr 1954, W.B. Heed" 4♂♂, dissected by D.A.G. (nos. DBG 10, 11, 25, 26), 2♀♀ dissected by D.A.G. (DBG 27, 28). "Honduras: Teguelgalpa, No. 27229 2723, VI/I/3/[19]17, F.J. Dyer" 1♂, dissected by D.A.G. (DBG 24); "Honduras: Teguelgalpa/ No. 27489 1.27507, VII/8/17, F.J. Dyer, 1♀, not dissected. In AMNH. **Jamaica:** 1♂ "Jamaica, B.W.I./Falmouth, July 1958/M Wasserman, W.B. Heed" dissected by D.A.G. (DBG 4) (AMNH). In AMNH. **Mexico:** 1♂ "Merida, Yucatan, Mexico/W.B. Heed, Sept. 1955 [printed]," dissected by D.A.G. (DBG 3). In AMNH. 2♂♂, "Mexico Quintana Roo, Cozumel S. Miguel, 29 Jan 1981, G.E. Bohart," both dissected by D.A.G. [DAG 43, 44]. In LACM. Nicaragua: 1♂ "Bluefields, Nicaragua [printed]/June 1954, W.B. Heed[printed]/55.13 [handwritten]" dissected by D.A.G. (DBG 1) (from the field notes of W.B. Heed for 55.13 "sweeping in second growth woods in back of town"). In AMNH. **Panama:** "Balboa, Canal Zone, Panama/W.B. Heed, Oct-Nov 1955" 2♂, dissected by D.A.G. (DBG 8, 22), same 1♀, dissected by D.A.G. (DBG 32). In AMNH.

Comments: This is the most common and widespread species of the group, occurring throughout Central America, the Caribbean, and northern parts of South America (Ecuador [herein] to northern Brazil [Schmitz, 2010: Pernambuco, Pará]). However, there is significant variation even in male and female terminalia (see figs. 8–11A–H), and so there may be some morphocryptic species under the present concept of *D. bromeliae*, ideal for examination using molecular data. Based on the present study the identification of *D. bromeliae* mentioned in earlier reports can be confirmed, from Cayman Islands, El Salvador, Honduras, Jamaica, Mexico (Yucatán) (Clayton and Wasserman, 1957; Heed and Wheeler, 1957; Wheeler, 1970). The identification of *bromeliae* cannot be confirmed from Martinique (David, 1973), Colombia (Wheeler, 1970), Puerto Rico, or São Paulo, Brazil (Hsu, 1949). Although I have not seen any material from the Lesser Antilles, it would not be surprising if *D. bromeliae* occurred in Martinique, and given its presence in Hispaniola its occurrence in Puerto Rico is expected. Only female specimens were available from Colombia, so species from this country cannot be assessed at present. The presence of *D. bromeliae* in southern Brazil is doubtful (Schmitz, 2010).

Like *D. bromelioides*, this species appears to be very polyphagous. In northern Brazil this species has been reared from flowers in five families (Schmitz, 2010).


A
DBG 27
B
DBG 32
C
DBG 35
D
DBG 62
E
DBG 66
0.10 mm
F
type
bromeliae
G
7
20
15
10
DBG 62
H
DBG 66
J
I
7
20
15
10
type florae

Drosophila florae Sturtevant, 1916

Figures 11I–J

Drosophila florae Sturtevant, 1916: 339.

Diagnosis: Body yellowish, large, thorax length 1.11 mm; prescutellars large, with smaller pair laterally, prescutellar index 0.56; oviscapt long, length 5.0× the depth (in lateral view); spermathecal capsule unique in group: spherical, with short introvert and sclerotized funnel within introvert.

Description: (based on holotype, ♀): Head: Frons dark yellow-ochraceous, pollinose on fronto-orbital plates and ocellar triangle; frontal vittae relatively broad, golden, shiny, finely striate. Frontal length 0.32 mm; frontal index 1.03, top to bottom width ratio 1.22. Ocellar triangle only slightly raised above rest of front, dark brown between ocelli; anterior apex of triangle ca. 0.7× length of front. Orbital setae dark brown-bronze in color, or1:or3 ratio 1.06, or2:or1 ratio 0.50, lengths of postocellar setae 0.47× and ocellar setae 0.65× that of frontal length; bases of ocellar setae outside of tangent between median and lateral ocelli; postocellar setae slightly convergent; vt index 1.10. Vibrissal index 0.53. Face slightly darker than front. Carina well developed, frontal edge somewhat flattened, with faint sulcus; edge width ca. 0.7× width of pedicel. Cheek index 0.11. Eye index 1.57. Occiput (not observable). Basal antennomeres slightly darker than face and front; arista with 4 dorsal and 2 ventral branches, plus small terminal fork. Proboscis very light brown; palpus lighter, with one apical and one subapical seta.

Thorax length 1.11 mm. Scutum deep ochraceous yellow, pollinose; 8 rows of acrostichal setulae. One large pair of prescutellar setae, lateral pair and pair just anterior to prescutellars barely differentiated from acrostichals; lengths of large prescutellars 0.56× that of posterior dorsocentral setae; h index 0.86. Transverse distance of dorsocentral setae 4.0× the longitudinal distance. Scutellum same color as scutum, pollinose; basal scutellars convergent, apical scutellars cruciate for ca. 0.5× their lengths; scutellar index 0.83. Pleura same color as scutum, sterno index 0.71. Halter stem same color as scutellum; bulb slightly infuscate brown. Legs lighter than scutum and pleura.

Wing hyaline, veins light brown, length 2.20 mm, length to width ratio 2.36. Indices: C, 2.38; ac, 2.47; hb, 0.54, 4-C, 1.00; 4V, 1.75; 5x, 1.58; M, 0.57. Wing tip not pointed; vein R_{2+3} virtually straight; section of C near Sc break with 2 thicker spinules.

Abdomen overall color similar to that of scutum, posterior margins of tergites with faint, diffuse, light brown infuscation.

Male terminalia: Unknown. Female terminalia: Valves of oviscapt acute but not pointed at tip in lateral view, ca. 400 μm long, with 20 ovisensilla pegs (4 discal and 16 marginal). Sper-

FIG. 11. Female terminalia (oviscapts and spermathecal capsules) of two species in the *bromeliae* group. **A–H.** *Drosophila bromeliae* Sturtevant. **F.** Holotype specimen of *D. bromeliae*. **I, J.** *Drosophila florae* Sturtevant, holotype specimen. **A–E.** Oviscapts in ventral view. **F–I.** Same, lateral view of apex. Numbers (G, I) refer to homologous oviscapt pegs in these and subsequent diagrams. All structures to the same scale; see text for specimen numbers.

matheca spherical, height approximately equal to width; basal introvert reaching about 0.60× length of capsule.

Type: Holotype, ♀: "Havana, Cuba, Jan. Feb. 1915" [printed]/ "Melon flow.[er]" [written]/ "TYPE" [printed]/ "Am. Mus. Nat. Hist. Dept. Invert. Zool. No. [printed] 24141 [written]"/ "Drosophila florae Sturtevant" [written in Sturtevant's hand]. The specimen is double mounted, impaled with a minuten through the pleura; head was dislodged by a prior investigator, but is complete and was stored in a corked, glass microvial pinned to the specimen; it was carefully glued back on to the thorax by D.A.G. The thorax, wings, and legs are intact; the abdomen was removed and cleared (dissector unknown) and stored in a corked, glass microvial on same pin as thorax. Oviscapt valves had been separated in the original dissection, making a fully intact ventral view impossible. In AMNH.

Other Specimens: Known with certainty only from the type specimen.

Drosophila bromelioides Pavan and Cunha, 1947

Drosophila bromelioides Pavan and Cunha, 1947: 24. Val (1982): redescription (male genitalia).

Diagnosis: Yellow to pale brown, average thorax length 1.02 (♂) to 1.14 (♀) mm; arista with 4-2 dorsal-ventral branches; most similar to *bromeliae* Sturtevant but differs most notably by the aedeagal shaft in *bromelioides* nearly straight in lateral view (vs. acutely bent, sometimes at 90°); distiphallus slightly shorter, wider, anteroventral margin more lobate in *bromelioides*; oviscapt 300–320 μm, spermatheca higher than wide, introvert ca. 0.6× capsule length.

Description: See Pavan and Cunha (1947) (external, internal soft organs, immatures, chromosomes), redescription by Schmitz (2010) (especially genitalia).

Type: Not reported by Pavan and Cunha (1947).

Distribution: Southern Brazil, states of Rio Grande do Sul, Santa Catarina, Parańa, São Paul, Goías, Minas Gerais, Bahia (summarized in Schmitz, 2010).

Comments: A highly polyphagous species, taken/reared from 42 species of flowers in 16 families (Schmitz, 2010). Like *D. bromeliae*, this species can, with care, be cultured on standard lab medium (Schmitz, 2010).

Drosophila aguape Val and Marques, 1996

Diagnosis: Externally distinctive, body dark brown, frons reddish brown, thorax with "ochre pollinosity," tergites with dark posterior bands; arista with 3-2 dorsal-ventral branches, one pair of prescutellars. Terminalia: surstylus with 8–9 prensiseta pegs; hypandrium trapezoidal; distiphallus thick, length > 0.5× that of aedeagal shaft; oviscapt with 18–20 pegs; spermatheca similar to that of *bromeliae* and *bromelioides*, height approximately equal to width, introvert about 0.5× capsule height.

Description: see Val and Marques (1996).

Type: Holotype, ♂: **Brazil:** Mato Grasso, Estaçaõ Ecológica da Ilha de Taiamã (16°50′S, 57°38′W). In Museu da Zoologia de São Paulo, SP Brazil.

Distribution: Known only from the type locality.

Comments: Collected and reared from the flowers of water hyacinth, *Eichhornia azurea* (Pontederiaceae), in the Brazilian Pantanal (Val and Marques, 1996). I did not examine specimens of this species.

Drosophila speciosa Silva and Martins, 2004

Diagnosis: Body yellowish, palpus pale brown; arista typically with 4-2 dorsal-ventral branches; surstylus with 11–13 long prensisetae pegs; hypandrium trapezoidal; oviscapt with ca. 15 pegs. Most similar to *D. bromeliae* and *bromelioides*.

Description: See Silva and Martins (2004).

Type: Holotype, ♂: **Brazil:** "obtained 05 July 2001 from isofemale strain N06012.01 from inflorescence of *Theobroma speciosum* collected: Brazil, Pará, Belém, germplasm collection, 01°20′S, 48°03′W; A.A.R. da Silva, 14 June 2001." Paratype males and females from this and other strains, same locality, plus Curuçá (Caxiuaña Scientific Station), Pará, Brazil. All deposited in Museu Paraense Emílio Goeldi, Belém, Pará, Brazil.

Comments: I did not examine specimens of this species.

Drosophila billheedi, new species

Figs. 2B, 12A–C

Diagnosis: A larger-bodied species (thorax length 1.02 mm); dull, dark yellowish/light brown; facial carina very thin, head narrow relative to depth (head width index 1.01); prescutellar setae 0.40× length of post dorsocentrals, no smaller lateral pairs; most distinctive on basis of short, thick aedeagus, length 6.0× the greatest width, slightly curved in lateral view, aedeagal angle 106°; distiphallus short and broad in full ventral view, length 1.3× the greatest width; surstylus with 7 large, pointed prensisetae; hypandrium trapezoidal with slightly concave lateral margins.

Description: Male: Head. Frontal length 0.29 mm; frontal index 1.11, top to bottom width ratio 1.81. Front mostly dark ochre in color, ocellar triangle and fronto-orbital plates dull, frontal vitae finely striated and golden; ocellar triangle barely raised above front of head, slightly darker than rest of front. Orbital setae dark brown (not black), or1:or3 ratio 1.00, or2:or1 ratio 0.58, postocellar setae 0.51 and ocellar setae 0.68× the frontal length, postocellars crossing at tips; vt index 1.29. Vibrissal index 0.54. Face same color and texture as fronto-orbital plates. Carina narrow, thinner than basal antennomeres; edge flattened, without sulcus. Cheek index about 0.09. Eye index 1.58. Occiput slightly darker than front of head. Basal antennomeres same color as face; arista with 4 dorsal and 2 ventral branches, plus small terminal fork. Proboscis lighter than face, lateral surfaces of labellum slightly darker; palpus light, with one apical and one subapical seta.

Thorax length 1.02 mm. Scutum dull dark yellowish; 6 rows of acrostichal setulae. One large pair of prescutellar setae, 0.40× length of posterior dorsocentral setae; setae lateral to this

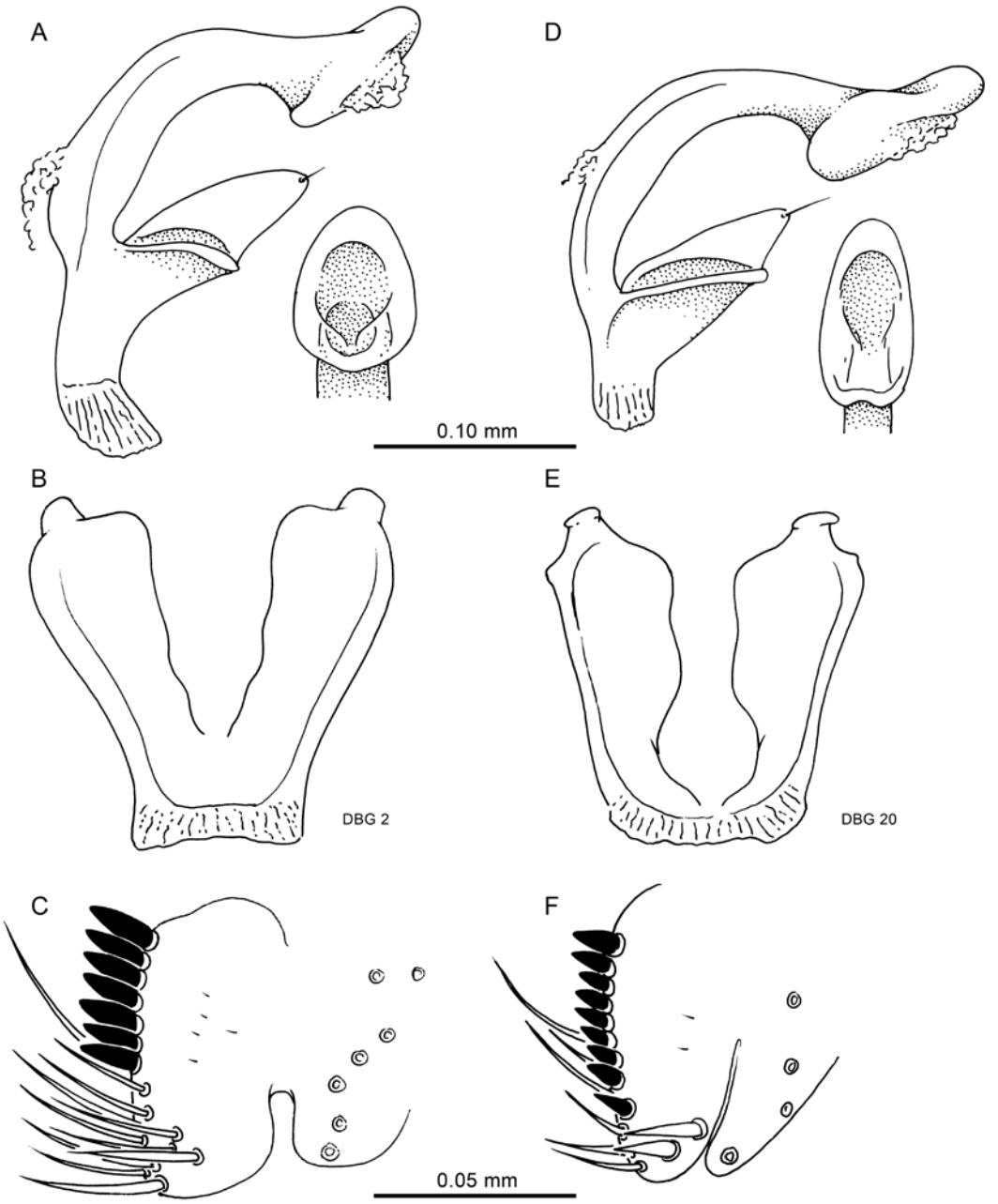


FIG. 12. Male genitalia of two *bromeliae* group species. **A–C.** *Drosophila billheedi,* n. sp. (DBG 2, holotype). **D–F.** *Drosophila sevensteri,* n. sp. (DBG 20). **A, D.** Lateral views of aedeagus, aedeagal apodeme, gonopod, and full ventral view of distiphallus. **B, E.** Hypandria. **C, F.** Surstyli and ventral lobes of epandrium.

barely larger than acrostichals; h index 0.83. Scutellum slightly lighter than scutum; basal scutellars slightly convergent; apical scutellars crossing; scut index 0.62. Pleura generally lighter than scutum, with small, slight infuscate areas near mesopleural suture, sterno index 0.74. Halter darker than pleura. Legs light, tan, without distinctive setation.

Wing hyaline, veins light brown, length 1.78 mm, length to width ratio 2.22. Indices: C, 2.38; ac, 2.31; hb, 0.47, 4-C, 1.00; 4V, 1.72; 5x, 1.73; M, 0.59, prox. Wing tip slightly pointed; vein R_{2+3} straight (vs. slightly sinuous).

Abdomen color mostly dark yellowish, posterior margins of tergites with faint, diffuse light brown coloration.

Male terminalia (fig. 12A). Epandrium with dense microtrichia, ventral lobe only with setae; ventral lobe small, apically blunt, with 7–8 setae. Cerci fused laterally to epandrium. Surstylus virtually bare of microtrichia (with only 4–5 microtrichia); inner marginal row of 7 prensisetae pegs, pegs large and pointed; surstylus with about 11 ventral setae. Hypandrium trapezoidal, lateral margins slightly concave; greatest width equal to length, width of anterior margin 0.5× the length. Gonopods fused to hypandrium and aedeagal apodeme, with small, fine apical seta. Aedeagus fused to aedeagal apodeme; aedeagus short and thick, length 6.0× the greatest width, slightly curved in lateral view, aedeagal angle 106°; distiphallus broadly ovoid in full ventral view, with thick rim, length 1.3× the greatest width. Aedeagal apodeme keel shaped.

Female: Unknown.

Type: Holotype, ♂: "Trinidad: Arima Valley/ 107.12 [field notebook number]/ W.B. Heed, Dec. 1955." Specimen is in good condition, point mounted, abdomen removed and cleared; genitalia dissected by D.A.G. (no. DBG 2), stored in glass microvial on same pin as specimen. In AMNH.

Other Specimens: Known only from the holotype.

Etymology: Patronym for the late William B. Heed, who collected this and many other *Drosophila* specimens throughout Central and South America in the 1950s and early 1960s.

Comments: The aedeagus of this species is similar to that of *D. aguape* Val from southern Brazil, but differs by having a broader distiphallus and a surstylus with seven large prensisetae (vs. 8–9 smaller ones). It is also similar to *D. mexiflora* and *D. sevensteri*, n. spp., from Central America, by the short, thick, slightly arched aedeagus. It differs from those species by the thicker shaft (as seen in lateral view), the broader distiphallus, the very large prensisetae, and by the lateral margins of the hypandrium being slightly concave (vs. convex). From the field notes of W.B. Heed, for specimen 107.12 (holotype): "400 ft. elev—sweeping over grapefruits in nice wooded ravine—also some nutmeg trees and fruit."

Drosophila mexiflora, new species

Figures 1D, 2D, 13–15

Diagnosis: Moderate size (thorax length 0.94 mm), body brownish; arista with 3–4 dorsal and 1–2 ventral branches; prescutellar index ca. 0.50, no smaller lateral pairs; aedeagus short and thick, length 6.8× greatest width, barely curved in lateral view (aedeagal angle 129°–142°, mean 133°); distiphallus large, length 0.4× that of aedeagus; surstylus with 8–11 slender prensisetae, ventral setae sclerotized; hypandrium U-shaped to trapezoidal. Oviscapt unique in the group: short (180 μm), with only 8–9 oviscapt pegs (pegs 1–3 and 12–20 lost); spermatheca similar to that of *D. bromeliae*.

Description: Male: Head: Front of head light brown on ocellar triangle and fronto-orbital plates, with faint bluish pollinosity; frontal vitta narrow, golden and shiny, finely striate; frontal

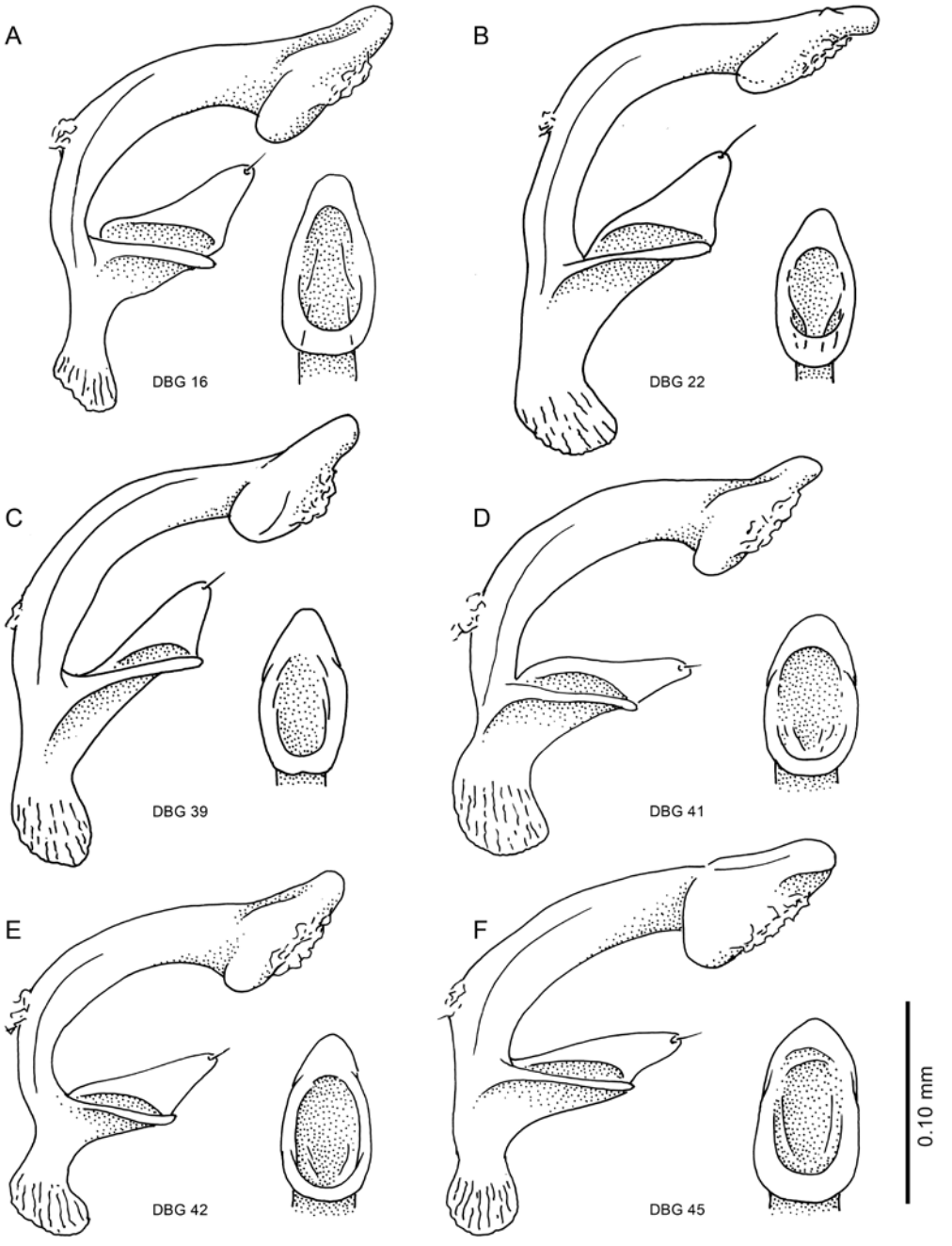


FIG. 13. Male genitalia of *Drosophila mexiflora* Grimaldi, n. sp., showing variation in lateral view of aedeagus, aedeagal apodeme, gonopod, and full ventral view of distiphallus. See text for specimen numbers.

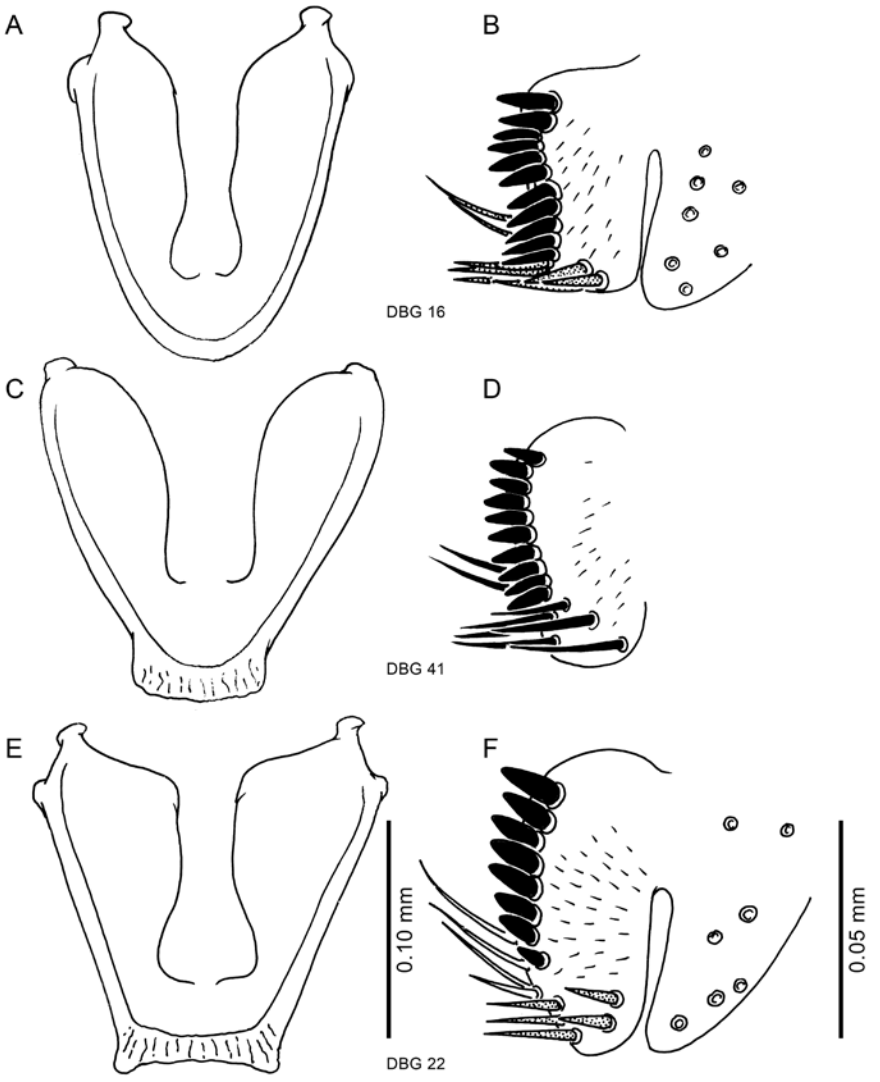


FIG. 14. Male genitalia of *Drosophila mexiflora* Grimaldi, n. sp., showing variation in hypandrium (A, C, E) and surstylus + ventral lobe of epandrium (B, D. F).

margin near ptilinal suture a dull tan; frontal index 1.01 (0.96–1.14), top to bottom width ratio 1.47 (1.42–1.53). Ocellar triangle raised slightly above rest of front, area between ocelli dark brown, anterior corner extended to ca. 0.7× length of front. Orbital setae brownish bronze (not black), or1:or3 ratio 0.93 (0.78 [Jamaica specimen no 16]–1.00), or2:or1 ratio 0.62 (0.47–0.81 [Jamaica specimen 16]), postocellar setae 0.42 (0.36–0.48) and ocellar setae 0.69 (0.62–0.78) of frontal length; vt index 1.01 (1.00–1.05). Base of ocellar seta lying just outside tangent between median and lateral ocelli; postocellar setae parallel and directed slightly posteriad in Oaxaca specimens; convergent in Nayarit specimens. Vibrissal index ca. 0.40 (0.20–0.53). Face slightly lighter than front; carina well developed, frontal surface flattened and very narrow (width ca. 0.7× that of pedicel), sulcus faint to absent. Cheek index 0.09 (0.07 [Jamaica specimen 16]–

0.11). Eye index 1.41 (1.28–1.63). Occiput light brown. Basal antennomeres slightly darker than front, especially pedicel; arista with 3–4 dorsal and 1–2 ventral branches, plus terminal fork. Proboscis light brown; palpus lighter, with one apical and one subapical seta.

Thorax length 0.94 mm (0.68 [Jamaica specimen 16]–1.08). Scutum dark yellowish to light brown, pollinose; approximately 8 very uneven rows of acrostichal setulae; one large pair of well-developed prescutellar setae, 0.51× (0.36–0.57) length of posterior dorsocentral setae, with one to two pairs of smaller, lateral prescutellars slightly differentiated from acrostichals; h index 0.79 (0.64–0.87). Transverse distance of dorsocentral setae 2.82× (2.46–3.27) that of longitudinal distance. Scutellum slightly lighter than scutum, also pollinose; basal scutellars convergent, apical scutellars convergent to crossing; scutellar seta index 0.85 (0.76–1.02). Pleura slightly darker than scutum, with very slight, brownish infuscation, sterno index 0.77 (0.73–0.83). Halter similar color to pleura, legs lighter than pleura or scutum.

Wing hyaline, veins light brown, length 1.92 mm (1.42 [Jamaica specimen 16] –2.19), length to width ratio 2.38 (2.23–2.61). Indices: C, 2.12 (1.90–2.41); ac, 2.33 (2.10–2.52); hb, 0.55 (0.51–0.60), 4-C, 1.09 (0.98–1.29); 4V, 1.88 (1.75–1.86); 5x, 1.50 (1.22–1.63); M 0.58 (0.53–0.63). Wing tip slightly pointed; Vein R_{2+3} very slightly sinuous, not straight, section of C basal to Sc break with 3–4 thicker spinules.

Abdomen overall light brown, posterior margin of tergites with thin, faint, diffuse brown band.

Male terminalia (figs. 13, 14). Epandrium with microtrichia on dorsal portion but without setae; ventral lobe not extended beyond ventral margin of surstylus, apex blunt (but not rounded), with 8–10 setae, without microtrichia. Cerci fused laterally to epandrium. Surstylus with microtrichia, medial margin with row of 8–11 long, pointed prensisetae pegs, ca. 8 ventral setae that are moderately to distinctly sclerotized. Hypandrium shape varying from trapezoidal to U-shaped. Gonopods fused to hypandrium and aedeagal apodeme, with fine, short, apical seta. Aedeagus short and thick, length 6.8× greatest width, barely curved in lateral view (aedeagal angle 129°–142°, mean 133°); distiphallus large, length 0.4× that of aedeagus. Aedeagal apodeme short and keel shaped.

Female: General morphology similar to males. Measurements: Thorax length 0.58 mm. Frontal width index 1.41; frontal index 0.96. or1:or3 ratio 0.94, or2:or1 ratio 0.56, postocellar setae 0.77× and ocellar setae 0.71× the frontal length, vt index 1.10 Vibrissal index 0.66. Eye index 1.41. Prescutellar setae 0.50× the posterior dorsocentral setae; h index 0.86. Transverse distance of dorsocentral setae 3.66× the longitudinal distance. Scutellar seta index 0.91, sterno index 1.00. Wing length 2.10 mm, length to width ratio 2.36. Wing indices: C, 1.96; ac, 2.75; hb, 0.54; 4-C, 1.19; 4v 1.93; 5x 1.55; M, 0.61.

Female terminalia: Valves of oviscapt rounded at tip, ca. 180 μm long, with only 8–9 oviscapt pegs (pegs 1–3 and 12–20 lost); spermatheca structure and shape similar to that of *D. bromeliae*, height 0.79–1.03× the width; basal introvert reaching about 0.8× length of capsule.

Type: Holotype, ♂: "**Mexico:** Nayarit, San Blas area, 16–21 III/83, W.J. Hanson." Type is point mounted, in good condition, abdomen removed and cleared, genitalia dissected by D.A.G., and stored in glass microvial on same pin as specimen. In LACM.

Other Specimens: Paratypes, all from **Mexico:** 2 ♂♂ "Mexico: Oaxaca, 60 mi. S. Oaxaca, IX/6–IX/7/47 1807.1 [field notebook number], M.R. Wheeler/F.A. Cowan," both dissected by D.A.G. (nos. 22, 39). From M.R. Wheeler's field notes for 1807.1: "Flies captured in flowers of a wild sp. of *Hibiscus*...@ 60 mi south of the city of Oaxaca, Oax., Mexico...on am 9-7, flowers in bloom evening before + on which flies were taken are now collapsed and shriveled," dissected (DBG 42). 1♂: same data as holotype (dissected, DBG 39). In AMNH. 2♂♂, "Mexico: Nayarit, San Blas area, 16-21 III/83, W.J. Hanson" (printed label), dissected (DBG 41, 42); 11♀♀, "Mexico: Nyarit, San Blas LeBajada, 6-21/III/83, W.J. Hanson" (printed labels), 3 dissected (DBG 80–82); 1♂ "Mexico: Jalisco, 18 mi N Barro de Navidad, 23/VIII/1973, Hanson, Schwartz" (printed label), dissected (DBG 45). In LACM; 1♂, 1♀ in AMNH. Two other male specimens are not being designated as paratypes (see below): "**Jamaica**, Ocho Rios, BWI/ W.B. Heed, M Wasserman July 1958." (AMNH). "**Costa Rica:** Heredia, IX 1963, N.H.L. Krauss collector" (AMNH, dissected, DBG 83).

Etymology: From Mexico, country of type series, and *-flora* (L., flower), referring the flower-visiting habit of the species.

Comments: The short, thick aedeagus of *D. mexiflora* is similar to that of *D. billheedi* and *D. sevensteri*, n. spp., and the Brazilian species *D. aguape*, but it is less curved in lateral view and the distiphallus differs as shown in fig. 13. Also, the surstylus of *D. mexiflora* has 8–12 slender, pointed prensisetae and ventral setae that are sclerotized; versus 7–9 shorter, more blunt prensisetae in the other species and ventral setae that are not sclerotized. The following features differ with *bromeliae*: aedeagus distinctly shorter and shaft thicker in lateral view, aedeagal angle 129°–142° (vs. bent at nearly a right angle in *bromeliae*), ventral setae of the surstylus moderately to distinctly sclerotized.

Female genitalia confirm the species distinction of *D. mexiflora*, with a reduced number of oviscapt pegs unique for the group. Females in the *bromeliae* group typically have 15 or more oviscapt pegs; *mexiflora* has only 8–9. This reduction is due to loss of pegs 1–3 and pegs 12 and higher.

The Jamaica specimen (DBG 16) is distinctively smaller than the Mexican specimens (ca. 0.68× the thorax length, 0.70× the wing length), and it differs from the Mexican specimens in orbital seta ratios (see description above). As a unique specimen the consistency of these differences cannot be evaluated, and since the proportions and shape of the aedeagus are identical to those of the Mexican specimens the conservative approach is to include these into one species until additional data may prove otherwise. Male genitalia of the Costa Rica specimen (DBG 83) is nearly identical to that of the Mexican specimens except that DBG 83 has the distiphallus more drop-shaped in full ventral view, and prensisetae shorter.

Drosophila sevensteri, new species

Figures 12D–F

Diagnosis: A medium-sized (thorax length 0.81–1.04 mm), brownish yellow species; frontal vitta darker (orange) than surrounding portions of front (yellowish); prescutellars consis-

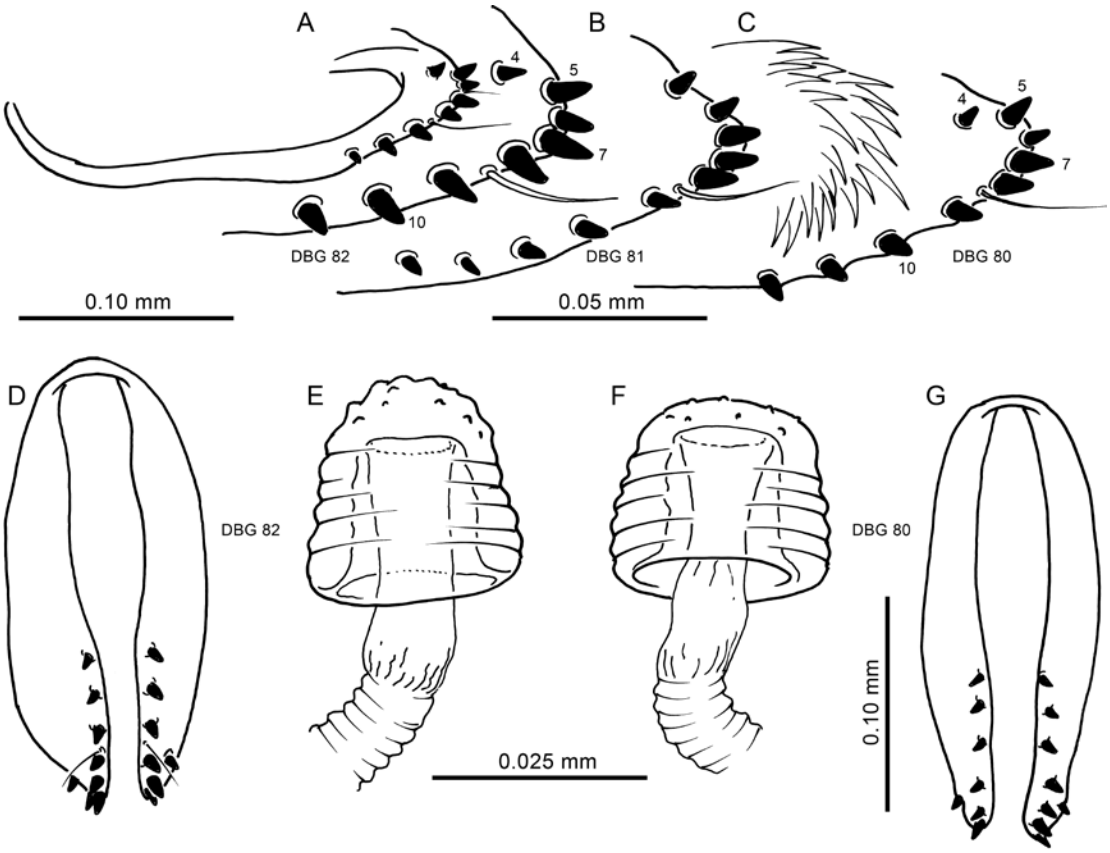


FIG. 15. Variation in the distinctive female terminalia of *Drosophila mexiflora* Grimaldi, n. sp. **A–C.** Oviscapts in lateral view, also showing details of posterior end. Note how oviscapt pegs 1–3 and ≥13 have been lost. **D, G.** Oviscapts in ventral view. **E, F.** Spermathecae. A, D, G to same scale. Refer to text for specimen numbers.

tently ≤ ca. 0.5× posterior dorsocentrals, no lateral pair; basal scutellar setae parallel; aedeagus of moderate thickness (length 5.5× the width), with significant curvature in lateral view; distiphallus large, bulbous, length 0.5× that of aedeagal shaft; surstylus with 8–9 short prensisetae, ventral setae of surstylus not sclerotized, two of these setae stout, spinelike; surstylus virtually bare of microtrichia; hypandrium trapezoidal, base broad.

Description: Male: Head: Frontal length 0.29 mm; frontal index (not measureable). Ocellar triangle barely raised above rest of front, dark brown between ocelli, anterior tip extended to about 0.6× the frontal length. Orbital setae dark brown, slightly brassy (not black), or1:or3 ratio 1.0, or2:or1 ratio 0.54, postocellar setae small 0.37×, ocellar setae 0.62× frontal length, bases of ocellar setae lying just outside tangent between median and lateral ocelli; postocellars slightly crossed at tips; vt index 1.0. Ocellar triangle and fronto-orbital plate dull, ochraceous yellow; frontal vitta darker, bronze, slightly shiny and finely striate. Vibrissal index 0.47. Face same color as most of dull parts of front, carina edge slightly lighter. Carina narrow, short, edge flattened, without sulcus. Cheek index 0.10. Eye index 1.36. Occiput light brown. Antenna with

pedicel same color as frontal vitta, flagellomere 1 lighter; arista with 4 dorsal and 2 ventral branches, plus short terminal fork. Proboscis and clypeus slightly darker than face/front; palps lighter, each with one apical and one subapical seta.

Thorax length 0.81 mm (holotype ♂). Scutum ochraceous, dull; 6–8 irregular rows of acrostichal setulae. One pair of prescutellar setae, about 0.52× the length of posterior dorsocentral setae; setae lateral to prescutellars not differentiated from acrostichals; h index 0.84. Transverse/longitudinal distances of dorsocentral setae (dc index) (not measureable). Scutellum slightly lighter than scutum; basal scutellars parallel, apical scutellars crossing for ca. 0.5× their length; scut index 0.88. Pleura about same color as scutum (slightly darker dorsally), sterno index 0.86. Halter light, yellowish. Legs light, without darker/infuscate areas.

Wing hyaline, veins yellowish, length 2.01 mm, length to width ratio 2.21. Indices: C, 2.32; ac, 2.20; hb, 0.66, 4-C, 1.02; 4V, 1.76; 5x, 1.41; M, 0.56. Subcostal section of C with strong spinules on apical half only, wing tip rounded, vein R_{2+3} nearly straight (not slightly sinuous).

Abdomen overall light ochraceous yellow, posterior margins of tergites faintly diffuse brown graded into lighter color.

Male terminalia (figs. 12D–F). Epandrium with just microtrichia, long setae only on ventral lobe; ventral lobe small, slender, with 4–5 setae, apex acute but not pointed. Cerci fused laterally to epandrium. Surstylus virtually bare of microtrichia, medial margin with row of 9 short prensisetae pegs (lengths only ca. 2–3× the width), about 8 ventral setae, 2 lateral ones stout and spinelike, none are sclerotized. Hypandrium trapezoidal, length 1.05× greatest width. Gonopods fused to hypandrium and aedeagal apodeme; apical seta fine, approximately 0.5× length of gonopod. Aedeagus of moderate thickness (length 5.5× the width), with significant curvature in lateral view, aedeagal angle 114°; distiphallus large, bulbous, length 0.5× length of aedeagal shaft, suboval in fully ventral view (apex slightly narrower). Aedeagal apodeme short, keel shaped.

Female: General morphology similar to males. Measurements based on dissected ♀ paratype (DBG 18): Frontal length 0.32 mm; top to bottom width ratio (not measureable). Ocellar triangle about 0.6× the frontal length; or1:or3 ratio 1.0, or2:or1 ratio 0.58, postocellar seta 0.42× and ocellar seta 0.68× frontal length, vt index 1.0. Vibrissal index 0.53. Cheek index 0.09. Eye index 1.38. Thorax length 1.04 mm. Prescutellar setae 0.46× the length of posterior dorsocentral setae; h index 0.85; dc index not measureable; scut index 0.96, sterno index 0.83. Wing length 2.01 mm, length to width ratio 2.23. Wing indices: C, 2.08; ac, 2.72; hb, 0.57; 4-C, 1.22; 4v 2.12; 5x 1.76; M, 0.75.

Female terminalia: Valves of oviscapt rounded at tip in lateral view, ca. 320 μm long, with 17–19 ovisensilla pegs; length of oviscapt 2.90× the greatest width in ventral view. Spermatheca cup shaped, height 1.00× the greatest width; basal introvert 0.73× the length of capsule.

Type: Holotype, ♂: "**Panama:** Gatun L[ake], Barro Colorado Is. 8F/Jan Sevenster no. 39:HY/bred from *Hibiscus* flower." Abdomen removed, cleared, genitalia dissected by D.A.G. (DBG 20) and stored in a glass microvial on same pin as specimen. In AMNH.

Other Specimens: Three paratypes (2♀♀, 1♂) same data as holotype, two dissected by D.A.G. (DBG 17♂, 18♀). Portions of all specimens collapsed during drying, thus preventing some measurements. In AMNH.

Etymology: Patronym for Jan Sevenster, in recognition of his collection of the type series and for his excellent monograph on the ecology of fruit-breeding drosophilids (Sevenster, 1992).

Comments: This species is one of five Central American members in the *bromeliae* complex, all with very similar male and female genitalia. It is most reliably distinguished, as described in the diagnosis, on the basis of greater curvature of the aedeagus, bulbous distiphallus, and surstylus virtually bare of microtrichia and having short prensisetae. Female terminalia are essentially indistinguishable from most other species in the complex; it was only on the basis of the type series of specimens having been reared from the same flower that the sexes could be associated.

Drosophila thurstoni, new species

Figures 5B; 16A–C

Diagnosis: A smaller (thorax length ca. 0.90 mm), light brown to deep ochraceous-yellow species, prescutellars approximately 0.3× length of posterior dorsocentrals, lateral pairs barely differentiated; postocellar setae slightly convergent to parallel (vs. strongly convergent or even with tips crossing); aedeagus long (length 11.0× the width), strongly arched in lateral view (aedeagal angle 114°); distiphallus similar to that of *bromeliae*, except with much narrower apex in full ventral view; surstylus with 12 slender prensisetae, no sclerotized ventral setae; hypandrium trapezoidal.

Description: Male: Head: Frons light brown, pollinose on fronto-orbital plates and ocellar triangle, frontal vitta golden, shiny, finely striate; frontal index 0.96, top to bottom width ratio 1.38. Ocellar triangle slightly raised above rest of frontal surface, dark brown between ocelli, anterior corner of triangle reaching ca. 0.6× length of front. Orbital setae dark brown with bronze highlights (not black), or1:or3 ratio 0.93, or2:or1 ratio 0.40, postocellar setae 0.48× and ocellar setae 0.76× frontal length, postocellar setae slightly convergent to parallel; vt index 1.05. Vibrissal index 0.60. Face same color as ocellar triangle. Carina well developed, frontal edge flattened, with slight sulcus, greatest width of frontal edge ca. 0.6× the width of pedicel. Cheek index about 0.10. Eye index 1.43. Occiput light brown. Basal antennomeres same color as face; arista with 3 dorsal and 2 ventral branches, plus large terminal fork. Proboscis light brown; palpus slightly lighter, with one apical and one subapical setae.

Thorax length 0.89 mm. Scutum light brown, pollinose; 6 rows of acrostichal setae. One large pair of prescutellar setae, lengths about 0.33× that of posterior dorsocentral setae; setae lateral to prescutellars slightly larger than acrostichals; h index 0.85. Transverse distance of dorsocentral setae 3.33× that of longitudinal distance. Scutellum same color as scutum, pollinose; basal scutellars convergent, apical scutellars crossing at tips; scutellar seta index 0.92. Pleura slightly lighter than scutum, less pollinose, sterno index 0.74. Halter stem light, bulb slightly darker than pleura. Legs lighter than pleura.

Wing hyaline, veins yellow-tan, length 1.78 mm, length to width ratio 2.22. Indices: C, 2.20; ac, 2.25; hb, 0.60, 4-C, 1.04; 4V, 1.74; 5x, 1.41; M, 0.56. Wing tip rounded, vein R_{2+3} virtually straight; section of C between h and Sc breaks with ca. 10 thicker spinules.

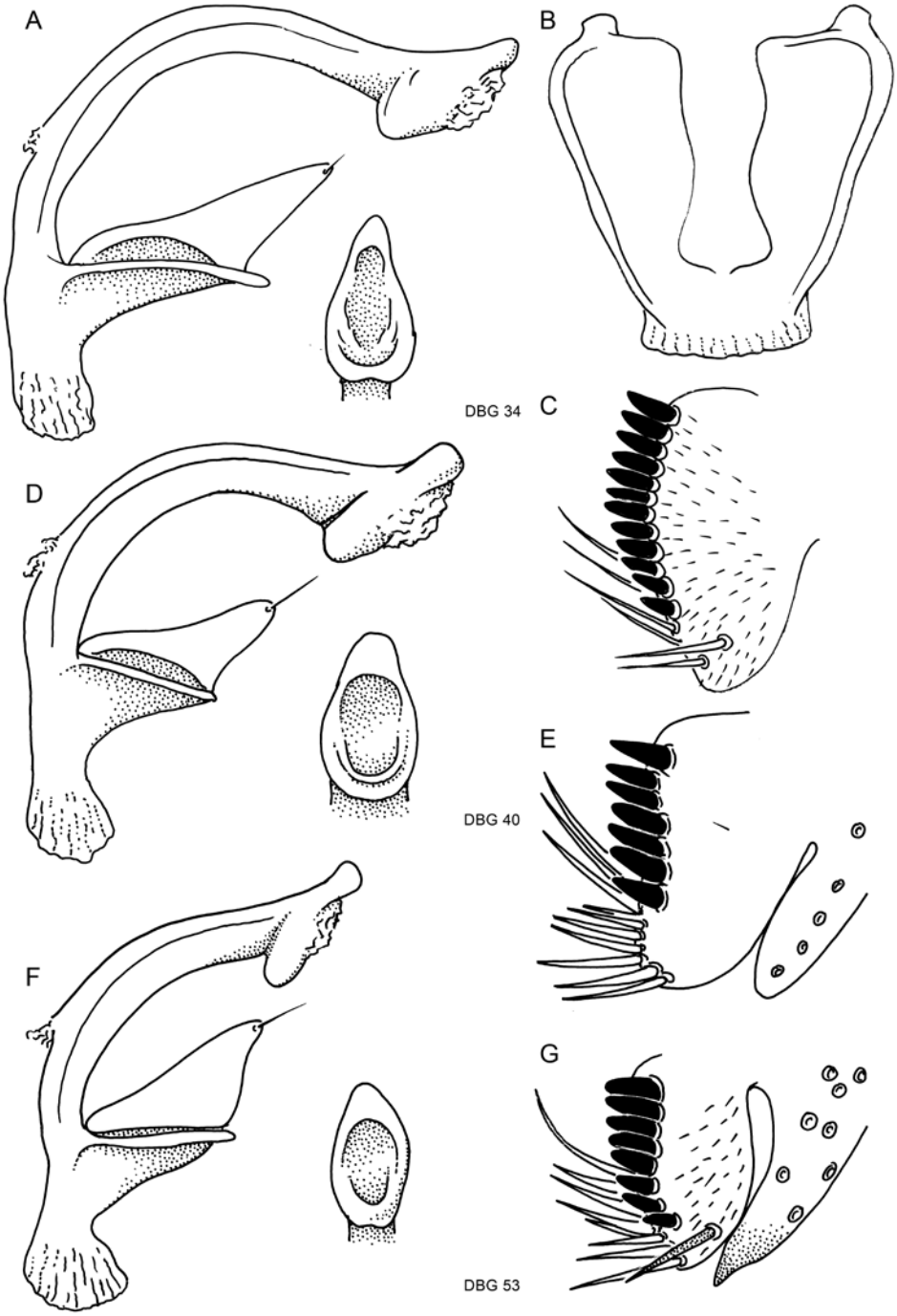


FIG. 16. Male genitalia of three species in the *bromeliae* group. **A–C.** *Drosophila thurstoni,* n. sp. (DBG 34). **D, E.** Species indet. (DBG 40: "Panama: Darién Province: El Real XI-29-963 Sarah B. Pipkin"). **F, G.** Species indet. (DBG 53: "Ecuador: Loja, 45 km SSE Portovelo, Rio Yaguachi, 080 m, 4 November, 1987/R. Davidson, J. Rawlins, C. Young, riparian scrub").

Abdomen light brown, pollinose; posterior margin of tergites without noticeable dark, diffuse markings.

Male terminalia (fig. 16A, B). Epandrium with microtrichia, lacking setae on dorsal surface; ventral lobe apically rounded, without microtrichia, having ca. 5 setae. Cerci with microtrichia, laterally connected to epandrium. Surstylus with extensive microtrichia on outer (lateral) surface, with inner marginal row of 12 long peglike prensisetae (vs. 7–9, as in *bromeliae*), about 6 other, finer setae (none sclerotized). Subepandrial sclerite (not examined). Hypandrium trapezoidal, length 0.89× the greatest width, lateral margins straight (not convex). Gonopods fused to hypandrium; apical seta fine, minute. Aedeagus fused to aedeagal apodeme, strongly and evenly arched in lateral view, length 11.0× the width, aedeagal angle 114°; distiphallus with very narrowed tip in full ventral view; aedeagal apodeme short, keellike.

Female: General morphology similar to males. Measurements: Thorax length 0.94; Frontal top to bottom width ratio 1.41. or1:or3 ratio 0.93, or2:or1 ratio 0.66, lengths of postocellar setae 0.50× and ocellar setae 0.71× that of frontal length, vt index 1.00. Vibrissal index 0.56. Cheek index about 0.08. Eye index 1.41. Lengths of prescutellar setae 0.48× that posterior dorsocentral setae; h index 0.94. Transverse distance of dorsocentral setae 2.61× the longitudinal distance. Scutellar seta index (not measurable), sterno index 0.75. Wing length 1.81 mm, length to width ratio 2.26. Wing indices: C, 2.02; ac, 2.66; hb, 0.60; 4-C, 1.23; 4v 2.05; 5x 1.86; M, 0.71.

Female terminalia: Valves of oviscapt of moderate length, length 2.5× greatest width, ca. 280–300 μm long, tip slightly acute (not fully rounded) in lateral view; valves with 14–16 marginal oviscapt pegs. Spermatheca short, cup shaped, height approximately equal to width; basal introvert extending to ca. 0.7× the length of capsule.

Type: Holotype, ♂: "**Jamaica** B.W.I. [British West Indies, printed]/Hardware Gap [handwritten]/W.B. Heed, M Wasserman July 1958 [printed]," dissected by D.A.G. (DBG 34), stored in a glass microvial on same pin as specimen. In AMNH.

Other Specimens: Paratype female: "Jamaica B.W.I. [printed]/Falmouth July 1958 [printed]/M.W. Wasserman W.B. Heed [printed]," dissected by D.A.G. (DBG 35), genitalia in glass microvial on same pin as specimen. Paratype female: "Jamaica B.W.I. [printed]/Hermitage Reservoir [printed]/ W.B. Heed M.W. Wasserman July 1958 [printed]," genitalia dissected by D.A.G. (DBG 17), in glass microvial on same pin as specimen. In AMNH.

Etymology: Patronym for Steve Thurston, Senior Scientific Assistant and graphic artist in the Division of Invertebrate Zoology at the AMNH, in recognition of his many years of superb skill and artistry.

Comments: This species is distinguished from the widespread *Drosophila bromeliae* by the slightly smaller body size; light brown, pollinose body; and by the male genitalia: the surstylus dentition (12, vs. 7–9 prensisetae), distiphallus shape, and especially the aedeagal length (ca. 0.31 mm, vs. 0.22 in *bromeliae*). When corrected for body size (using thorax length as a proxy), the aedeagal length of *thurstoni* is 33% longer than in *bromeliae*. Female terminalia are nearly identical, although the oviscapt pegs in *thurstoni* are slightly thicker and stouter than in the type of *bromeliae*.

THE *PENISPINA* SUBGROUP

Drosophila penispina, new species

Figures 1B, 2A, 5C, 17–18

Drosophila florae Sturtevant, 1921: 72 (Costa Rican specimens: misidentification).

Diagnosis: Moderate body size, thorax length 0.48–1.02 mm, light brown in color; prescutellars large (0.38–0.75 prescut index), laterally with pair or two of small prescutellars (sometimes barely larger than acr); wing tip slightly pointed (vs. rounded), R_{2+3} slightly sinuous (vs. straight); aedeagus large, slightly curved in lateral view (aedeagal angle 117°–124°, mean 120°), thick, length 7.5–7.8× greatest width; ventroproximal margin of distiphallus with three small spines; oviscapt distinctively long, length 2.7× the width in ventral view, spermathecal capsule large, length ca. 1.2× the width.

Description: Male: Head: Frontal length 0.29 mm; frontal index 0.98 (0.93–1.03), top to bottom width ratio 1.42 (1.34–1.50). Ocellar triangle slightly raised and darker than surrounding front. Orbital setae dark and bronzed (not black), or1:or3 ratio 0.93, or2:or1 ratio 0.63 (0.60–0.66), postocellar setae 0.50× (0.48–0.52) and ocellar setae 0.70× of frontal length; oc setae slightly outside of ocellar triangle; vt index 1.025 (1.00–1.05). Vibrissal index 0.54 (0.43–0.66). Face tan, lighter than front of head. Carina edge rounded, with or without slight sulcus. Cheek index 0.95. Eye index 1.35 (1.29–1.41). Occiput diffuse, light brown. Antenna same color as face; arista with 4 dorsal and 2 ventral branches, plus terminal fork. Proboscis and palps very light yellow.

Thorax length 0.79 mm (0.48–1.02). Scutum ochre to light brown, with diffuse, slightly darker paramedian areas; 6–8 rows of acrostichal setulae, rows irregular. Pair of large prescutellar setae, 0.4–0.7× length of posterior dorsocentral setae; setae lateral to prescutellars ca. 0.3–0.5× as long as prescutellars; h index 0.81 (0.71–0.86). Transverse distance of dorsocentral setae 2.55× (2.05–3.09×) the longitudinal distance. Scutellum same color as scutum; basal scutellars convergent to nearly parallel; scut index 0.80 (0.74–0.90); apical scutellars convergent to slightly crossed at tips. Pleura slightly lighter than scutum, sterno index 0.71 (0.71–0.83). Halter and legs light, cream colored.

Wing hyaline, veins yellowish, length 2.02 mm (1.95–2.06), length to width ratio 2.22 (2.12–2.38). Indices: C, 2.31 (2.30–2.40); ac, 2.46 (2.10–2.78); hb, 0.53 (0.51–0.58), 4-C, 0.98 (0.90–1.02); 4V, 1.66 (1.54–1.80); 5x, 1.51 (1.30–1.83); M, 0.52 (0.49–0.58).

Abdomen overall color yellowish, posterior margins of tergites with pale, brownish bands fading into yellow; bands very faintly interrupted in middle of tergites.

Male terminalia (fig. 17): Epandrium with microtrichia, only ventral lobe with setae; ventral lobe narrowed, apex pointed to blunt, with 3–8 fine setae. Cerci fused laterally to epandrium, microtrichose. Surstylus with microtrichia over half of outer surface, with inner marginal row of 7–10 peglike prensisetae (ventralmost peg weakly sclerotized in some), 10–11 setae ventrally (several of ventralmost setae more sclerotized). Hypandrium roughly trapezoidal in shape, with short, flat anterior margin, lateral margins straight to slightly convex; greatest width nearly equal to length. Gonopods fused to hypandrium and aedeagal apodeme; each lobe

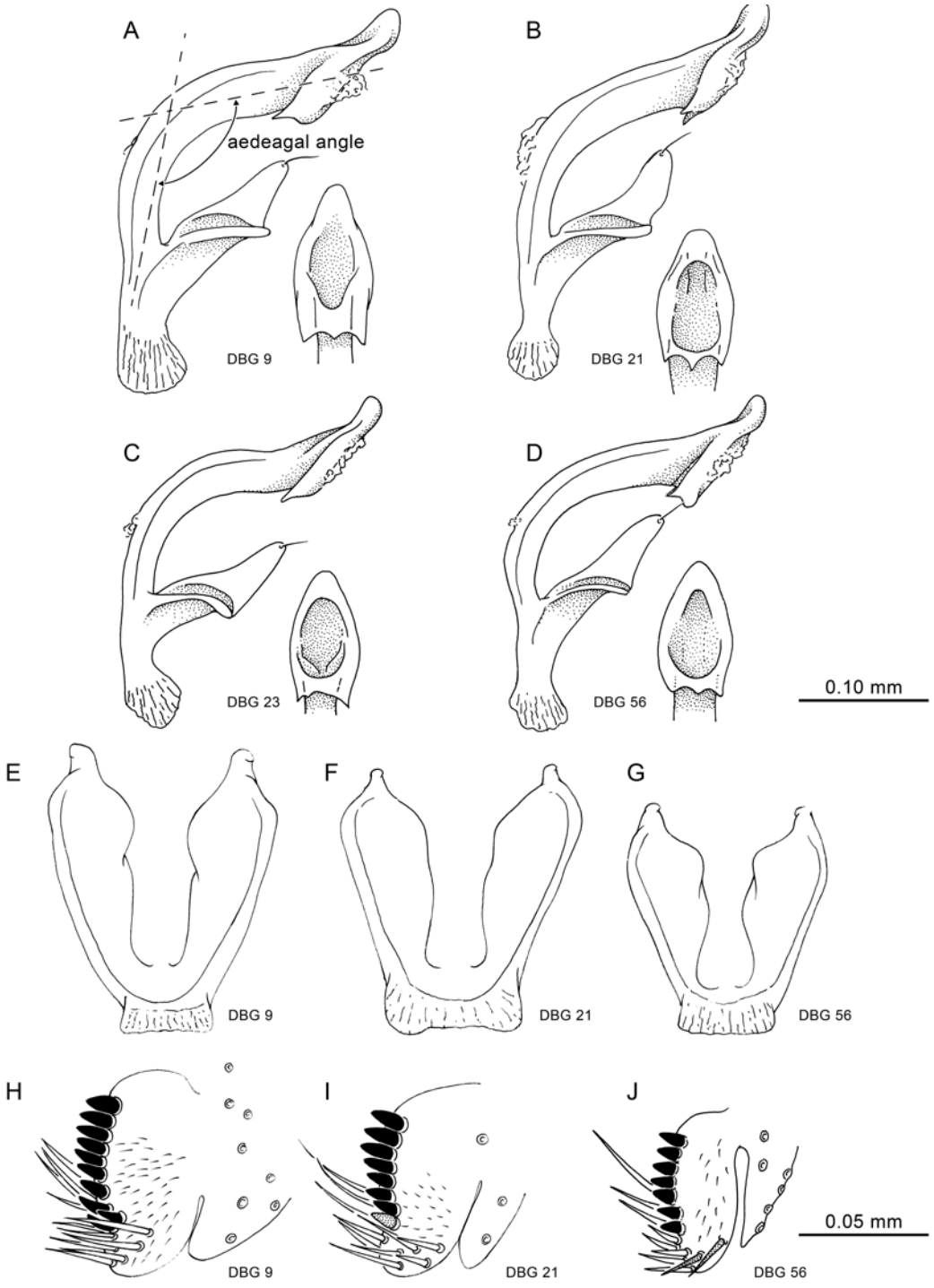


FIG. 17. Male genitalia of *Drosophila penispina*, n. sp. **A–D.** Variation in lateral view of aedeagus, aedeagal apodeme, and gonopod, as well as full ventral view of distiphallus; A, axes indicate aedeagal angle. **E–G.** Hypandrium. **H–J.** Surstylus and ventral lobe of epandrium.

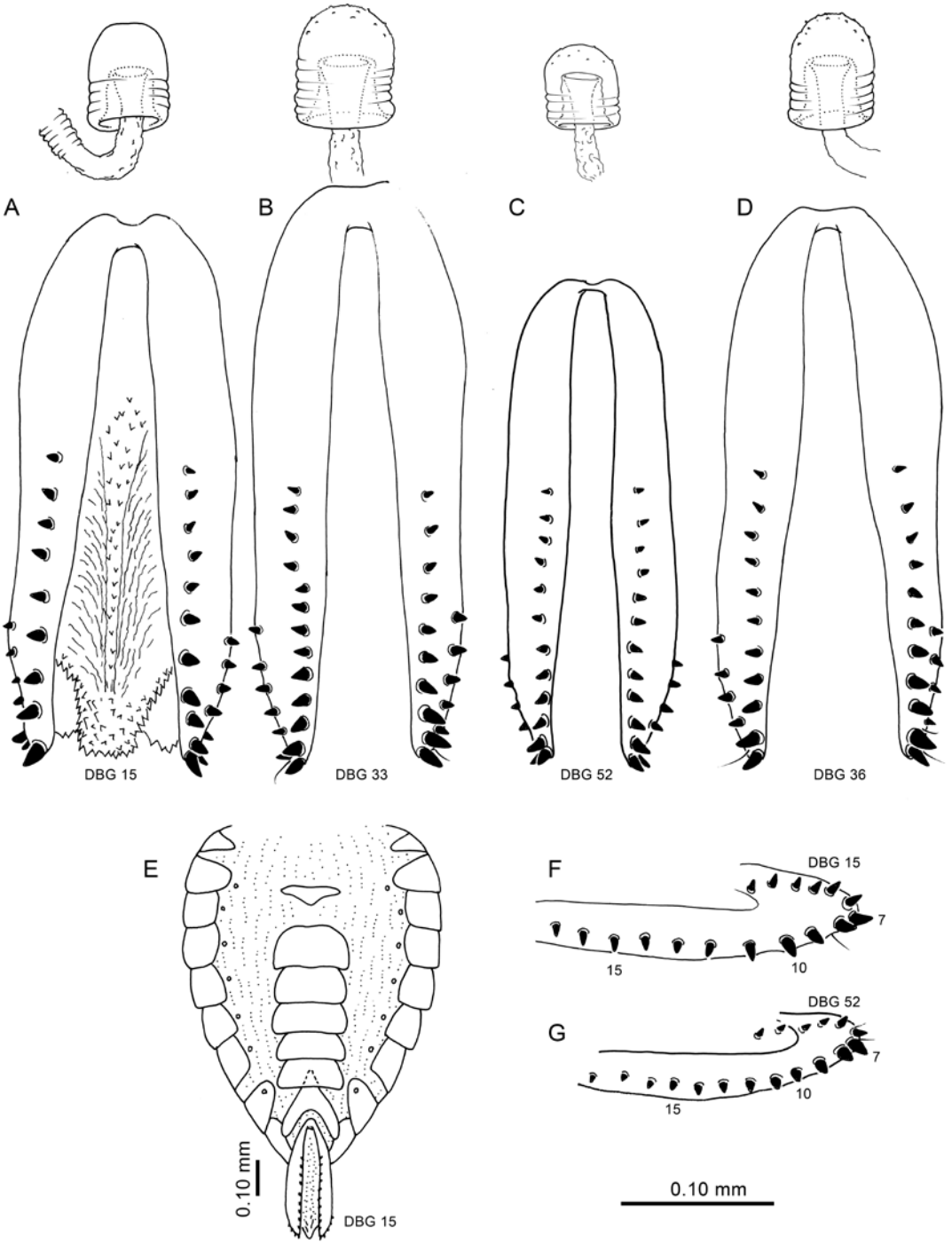


FIG. 18. *Drosophila penispina* Grimaldi, n. sp., female terminalia (oviscapts and spermathecal capsules: A–D, F, G) and whole abdomen (E). **A–D.** Oviscapts in ventral view, with respective spermathecae. **E.** Abdomen, ventral view, showing sclerite arrangement and spiracles. **F, G.** Oviscapts in lateral view. Homologous oviscapt pegs are numbered. All structures to the same scale; see text for specimen numbers.

with fine apical seta. Aedeagus fused to aedeagal apodeme; aedeagus large, slightly curved in lateral view (aedeagal angle 117°–124°, mean 120°), thick, length 7.5–7.8× greatest width; distiphallus with three shallow points on ventroproximal margin, as seen in fully ventral view, apex of distiphallus narrowed. Aedeagal apodeme short.

Female: General morphology similar to males. Proportions: Thorax length 0.88 mm; frontal index 1.08 (1.00–1.17); frontal width index 1.08 (1.32–1.50); or1:or3 ratio 1.04 (0.88–1.16); or2:or1 ratio 0.56 (0.50–0.61); postocellar index 0.61 (0.40–0.85); ocellar index 0.65 (0.63–0.65); vibrissal index 0.43 (0.31–0.53); cheek index 1.42 (1.36–1.46); h index 0.74 (0.66–0.82); dc distance 2.70 (2.38–3.22); scutellar index 0.76; sternopleural index 0.75 (0.67–0.83); vt index 1.03 (1.00–1.06); head width index 1.36 (1.22–1.70); prescutellar index 0.46 (0.43–0.50); wing index 2.46 (2.14–2.69); C index 2.13 (2.04–2.39; ac index 2.73 (2.42–3.28); hb index 0.54 (0.50–0.59); 4-C index 1.16 (1.06–1.27); 4V index 1.98 (1.90–2.13); 5x index 1.53 (1.44–1.64); M index 0.62 (0.55–0.70).

Female terminalia: Valves of oviscapt long, length 2.7× the greatest width, acute at tip, ca. 320 μm long, with 15–19 ovisensilla pegs. Spermatheca dome shaped, height 1.23× the width; basal introvert reaching about 0.65× length of capsule.

Type: Holotype, ♂: "Dominican Republic, La Vega Prov.: 6.5 mi NE Jarabacoa, 1700 ft., 28/VII/91 Grimaldi and Stark: banana trapped." Specimen is in good condition, pointed; abdomen removed and cleared; genitalia dissected by D.A.G. (DBG 56), stored in polypropylene microvial on same pin as specimen. In AMNH.

Other Specimens: Paratypes: 1♂ 2♀♀ (1 dissected, DBG 57), with same data as holotype (collected in series) (AMNH). 2 ♀♀ "**Dominican Republic:** Pedernales, Upper Las Abejas, 38 km NNW Cabo Rojo. 18-09N, 71-38W/1350m. 22 July 1990. L. Masner, Mesic deciduous forest; sweeping" (CMNH). 1♀ (dissected, DBG 52) "Dominican Republic: Pedernales 1 km S Los Arroyos, 1125 m., 18-14N, 71-45W/18 October 1991, R. Davidson, C. Young, S. Thompson, J. Rawlins, second growth forest" (CMNH). 1♂, "San José, Costa Rica, March 1915/ 'Metatype' [red printed label, des. A.H. Sturtevant for *D. florae*]," dissected by D.A.G. (DBG 21). 1♀, same label as holotype, dissected by D.A.G. (DBG 33). "Costa Rica: San José, VIII/11/56, 179.13 [field notebook number], W.B. Heed, H.L. Carson, M. Wasserman" (from the field notes of W.B. Heed for 179.13: "Bernal brought in 2 vials from his back yard collected over mango."). All in AMNH. "Mexico**:** Veracruz, Hansen and Poff, 1972, 1♂ [no. DBG 85]." Another specimen, not designated as paratype: ♂, "Rep de El Salvador/ Santa Tecla 12 klm NW/ Oct. 1958 W.B. Heed" [all printed labels], dissected by D.A.G. (DBG 23) (in AMNH) (specimen is in poor condition, missing head and most of wings).

Etymology: Derived directly from "penis" and *-spina* (Latin, "spine, thorn"), in reference to the ventral, subapical spines on the aedeagus.

Comments: Specimen DBG 23, from El Salvador, is significantly smaller and darker than the other specimens (brownish with slight greenish pollinosity, vs. deep yellowish); also, its acrostichals are not in regular rows and it has two distinct pairs of prescutellars. It is on the basis of these features it was not designated as a paratype, but the male genitalia have only slight differences with that of the other specimens. Interestingly, four specimens, including the

holotype, were collected in the Dominican Republic in a trap baited with yeasted bananas, and Heed (above) collected specimens over mangos in Costa Rica, indicating that the species can be attracted to fermenting fruits.

Drosophila manni, new species

Figures 1A, 2E; 19A–C; 21A, E

Diagnosis: A relatively large species for the group (thorax length 1.03 mm [0.94–1.12]), body light to deep yellow overall (even abdomen and ocellar triangle); prescutellar seta ca. 0.52× length of posterior dorsocentral; aedeagus arched in lateral view, distiphallus with distinctive pair of large, ventral spines; surstylus with relatively few (7) prensisetae, tip of epandrial lobe pointed; oviscapt long (length 3.0× width), spermathecal length 1.26× the width.

Description: Male: Head: Frons uniform deep yellow; frontal index 1.00, top to bottom width ratio 1.47 (1.39–1.55). Ocellar triangle slightly raised above rest of front, yellow (not brown) between ocelli; triangle with anterior corner ca. 0.7× length of front. Orbital setae bronzed (lighter in lateral views), or1:or3 ratio 1.09 (1.06–1.13), or2:or1 ratio 0.60 (0.56–0.64), postocellar setae 0.52× and ocellar setae 0.81× the frontal length, postocellar setae convergent; bases of ocellar setae lying slightly outside of tangent between medial and lateral setae; vt index 0.95. Vibrissal index 0.41 (0.33–0.50). Face slighty lighter than frons. Carina well developed, edge flattened, without sulcus, width of edge slightly less than that of pedicel. Cheek index about 0.12. Eye index 1.38 (1.34–1.42). Occiput largely deep yellow, except for infuscate brown area between occipital apodemes. Antenna slightly darker than front; pedicel with 2–3 extremely fine, light setae on inner surface; arista with 4 dorsal and 2 ventral branches, plus small terminal fork. Proboscis entirely light yellow; palpus slightly deeper yellow, with two subapical setae.

Thorax length 0.96 mm (0.94–0.99). Scutum uniformly deep yellow; 8 rows of acrostichals; 1 large pair of prescutellar setae, lengths 0.50 (0.41–0.59)× that of posterior dorsocentral setae; setae lateral to prescutellars only slightly differentiated from acrostichals; h index (not measureable). Transverse distance of dorsocentral setae 2.38× that of longitudinal distance. Scutellum same color as scutum; basal scutellars convergent; apical scutellars crossing 0.3–0.4× their lengths; scut index 1.22. Pleura same deep yellow as scutum, sterno index (not measureable). Halter very slightly infuscate. Legs slightly lighter than thoracic trunk.

Wing hyaline, veins dull yellowish, length 1.92 mm, length to width ratio 2.32 (2.20–2.44). Indices: C, 2.20 (2.15–2.25); ac, 2.52; hb, 0.56 (0.52–0.60); 4-C, 1.02 (0.98–1.06; 4V, 1.82; 5x, 1.34 (1.31–1.37); M, 0.48 (0.42–0.55). Vein C with 4–5 thicker spinules in Sc section; wing tip very slightly pointed, vein R_{2+3} very slightly sinuous, not straight.

Abdomen entirely light yellow, even posterior margins of tergites; completely lacking dark, infuscate markings.

Male terminalia (fig. 19A–C): Epandrium with microtrichia, lacking setae except on ventral lobe of epandrium; ventral lobe with narrow tip (not rounded), lacking microtrichia but with ca. 6 setae. Cerci fused laterally to epandrium. Surstylus with microtrichia on lateral/outer

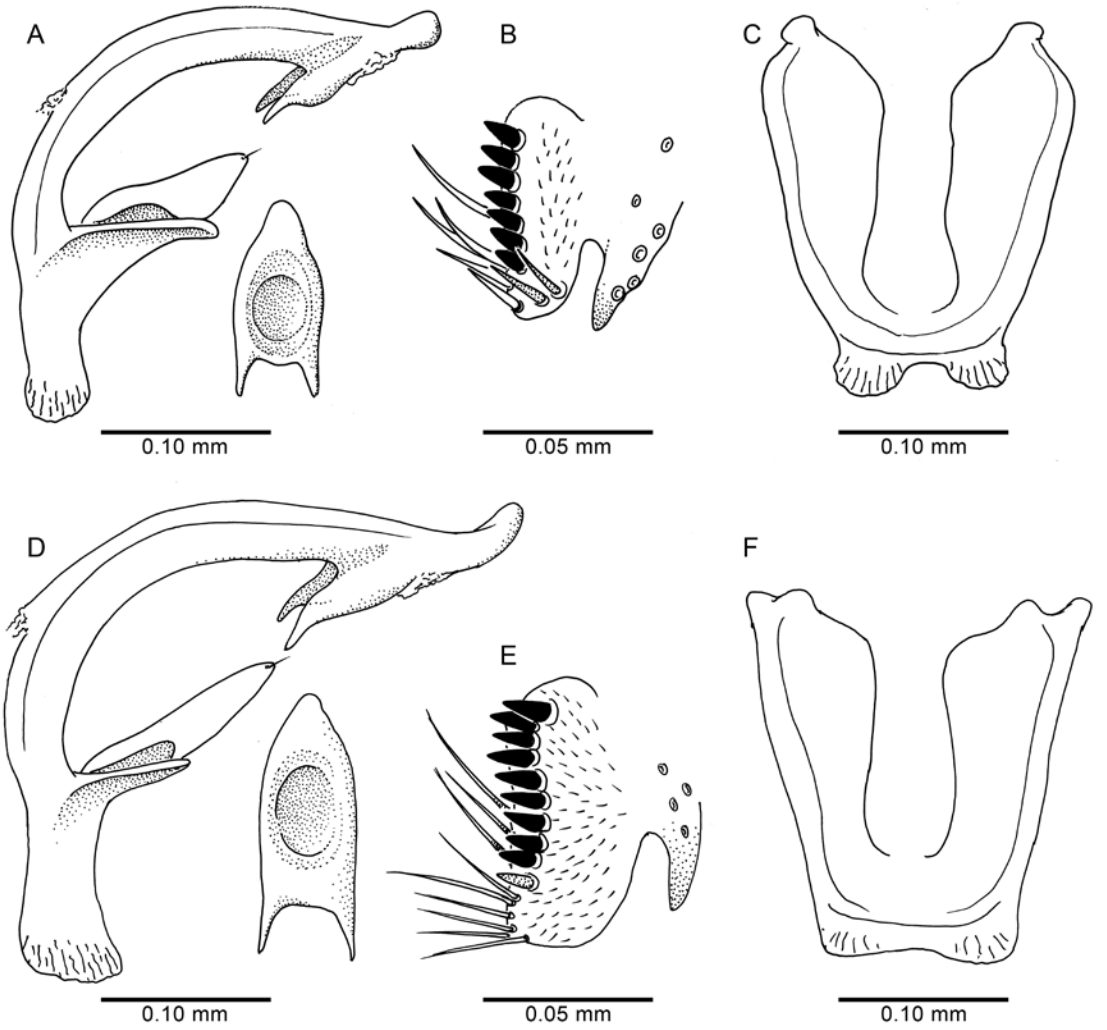


FIG. 19. Male genitalia of two closely related species: (A–C) *Drosophila manni*, n. sp. (DBG 55) and (D–F) *Drosophila paramanni,* n. sp. (DBG 86). **A.** Lateral view of aedeagus, aedeagal apodeme, postgonite, and full ventral view of distiphallus of *D. manni*. **B.** Surstylus and ventral lobe of epandrium. **C.** Hypandrium. **D.** Lateral view of male genitalia, with full ventral view of distiphallus. **E.** Surstylus and ventral lobe of epandrium. **F.** Hypandrium.

surface, having mesal row of 7 large peglike prensisetae, plus 7–8 fine setae (several ventral ones slightly sclerotized). Subepandrial sclerite (not examined). Hypandrium slightly trapezoidal in shape, slightly longer than broad (L/W 1.15), lateral margins slightly convex, anterior edge emarginate in middle. Postgonites fused to hypandrium, each with short, minute apical seta. Aedeagus fused to aedeagal apodeme, evenly arched in lateral view, aedeagal angle 45°, shaft of aedeagus of moderate and even thickness throughout (length of shaft 7.5× the width); distiphallus long, length ca. 0.5× the aedeagal shaft, in ventral view with narrow tip, base with pair of large spines; aedeagal apodeme relatively long, rudderlike.

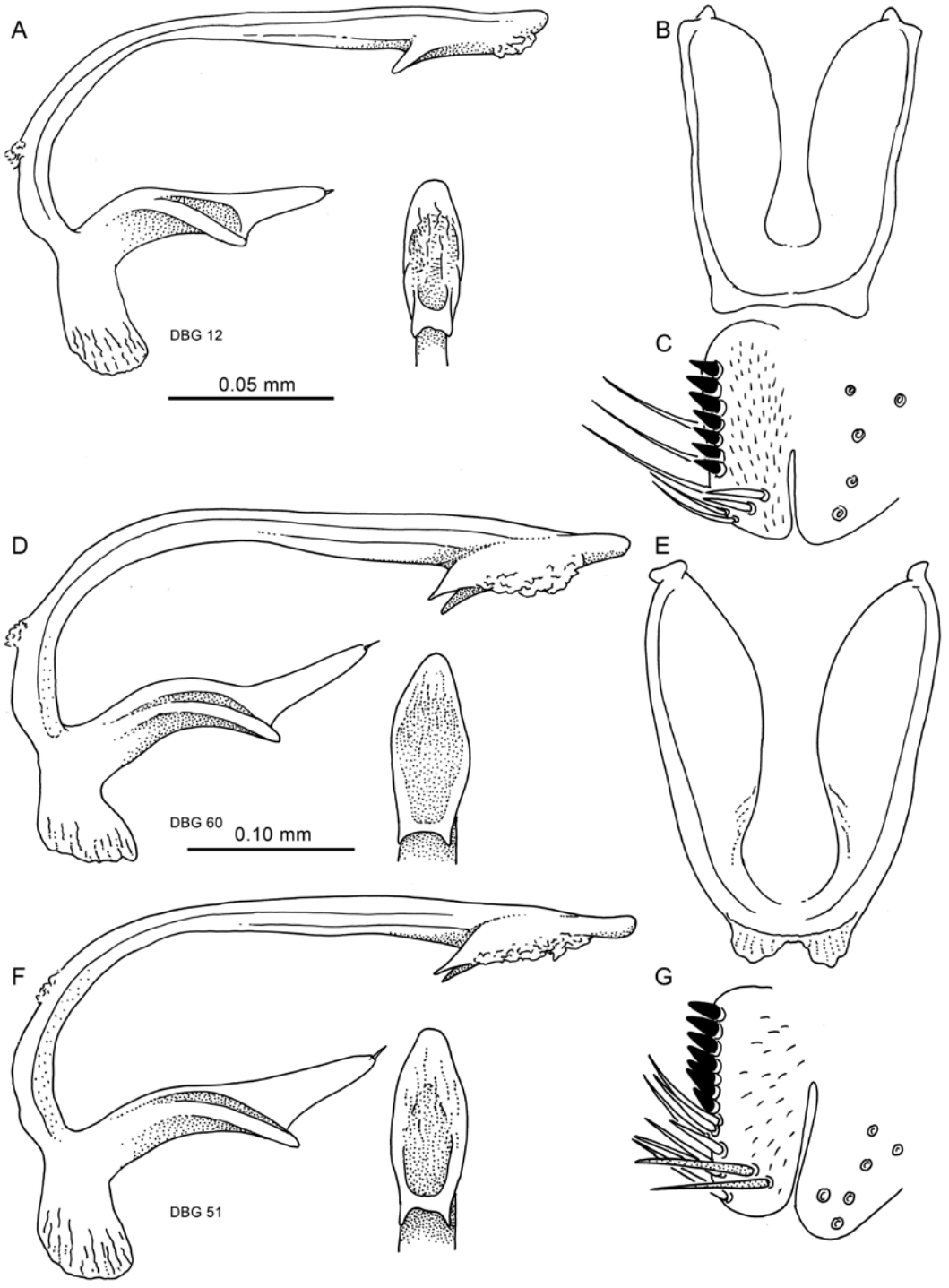


FIG. 20. Male genitalia of *Drosophila stylipennis* Grimaldi, n. sp., showing variation. **A, D, E.** Lateral view of aedeagus, aedeagal apodeme, gonopod, and full ventral view of distiphallus. **B, E.** Hypandrium. **C, G.** Surstylus and ventral lobe of epandrium. See text for specimen numbers.

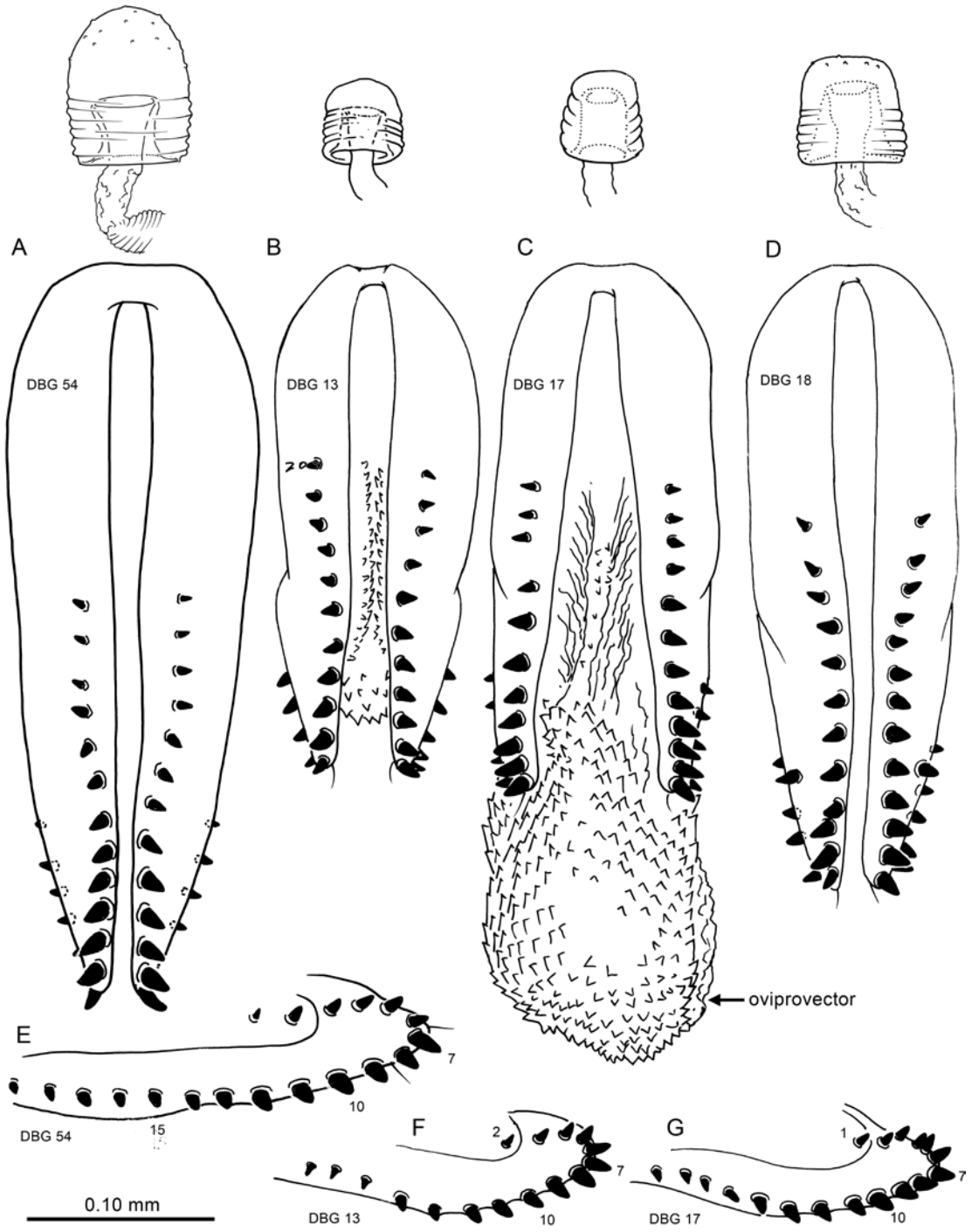


FIG. 21. Female terminalia of two species in the *bromeliae* group. **A, E.** *Drosophila manni* Grimaldi, n. sp. (DBG 54). **B–D, F, G.** *Drosophila stylipennis* Grimaldi, n. sp. All structures to the same scale; see text for specimen numbers.

Female: General morphology similar to males. Measurements: Thorax length 1.11 mm; frontal width index 1.36 (0.96–1.03). or1:or3 ratio 1.05 (1.06–1.13), or2:or1 ratio 0.55, postocellar setae 0.48× and ocellar setae 0.70× the frontal length, vt index (not measurable). Vibrissal index 0.55. Cheek index about 0.12. Eye index 1.44. Prescutellar seta length 0.54× that posterior dorsocentral setae; h index (not measurable). Transverse distance of dorsocentral setae 2.96× the longitudinal distance. Scutellar seta index 0.83, sterno index (not measurable). Wing length 2.21 mm, length to width ratio 2.38. Wing indices: C, 2.52; ac, 2.39 (2.28–2.50); hb, 0.58 (0.55–0.66); 4-C, 0.92 (0.86–0.98); 4v 1.66 (1.57–1.76); 5x 1.52 (1.44–1.61); M, 0.51 (0.46–0.57).

Female terminalia (figs. 21A, E): Oviscapt long, ca. 400 μm, length 2.8× the greatest width; valves narrow at tip in lateral view, with 19–20 marginal, peglike ovisensilla. Spermatheca relatively long, cup shaped, height 1.26× the width; basal introvert reaching about 0.40× length of capsule.

Type: Holotype, ♂: "Huachi Beni, **Bolivia**, Wm. M. Mann/Aug/Mulford BioExpl, 1921–22." Type in good condition, with distal 2/3 of abdomen removed, genitalia dissected by D.A.G. (DBG 56) and stored in glass microvial on same pin as specimen. In NMNH. The locality probably refers to Huachi in El Beni Province, northeastern Bolivia, near the border with Rondônia, Brazil.

Other Specimens: Paratypes: 3 ♀♀, 1♂ with same label data as holotype; 1 ♀ is dissected (DBG 54) (genitalia stored in microvial on specimen's pin). Specimens in this type series are preserved in remarkably good condition, particularly given their 90 year age; cuticle of the specimens shows virtually no collapse or fading, and is very clean (the specimens may have been collected directly from their host flowers). In NMNH.

Etymology: Patronym for William M. Mann (1886–1960), collector of the type series, myrmecologist, and eventually director of the National Zoo in Washington, D.C. Mann was the sole entomologist on the ill-fated Mulford Expedition, an engaging account of which was provided in the 1926 book *White Waters and Black* by the expedition's guide, Gordon MacCreagh. Mann, aka "the entomologist" in the account, was one of the few intrepid expedition members, and for whom the book was dedicated: "To the bug-hunter, stout companion of the trail."

Drosophila paramanni, new species

Figures 19D–F

Diagnosis: Thorax length 0.92 mm, body light yellow overall (even abdomen and ocellar triangle); prescutellar seta ca. 0.54× length of posterior dorsocentral; aedeagus arched in lateral view, distiphallus with distinctive pair of large, ventral spines; tip of epandrial lobe pointed. Very similar to *D. manni*, except that *paramanni* has: longer, larger distiphallus (0.43× total aedeagus length, vs. 0.38×; W/L of distphallus 0.36 [vs. 0.46]); paraphysis longer, narrower (W/L 0.21, vs. 0.32); surstylus with 9 prensisetae (vs. 7), lateral surface entirely covered with microtrichia (vs. partly).

Description: Male: Head: Frons uniform deep yellow; frontal index 1.14, top to bottom width ratio 1.76. Ocellar triangle almost at same level as rest of front, yellow (not brown) between ocelli; triangle with anterior corner ca. 0.5× length of front. Orbital setae bronzed (lighter in

lateral views), or1:or3 ratio 1.00, or2:or1 ratio 0.47, postocellar setae 0.52× and ocellar setae 0.75× the frontal length, postocellar setae parallel or slightly convergent; bases of ocellar setae lying slightly outside of tangent between medial and lateral setae. Vibrissal index 0.43. Face same color as frons. Carina well developed, edge flattened, without sulcus, width of edge slightly less than that of pedicel. Cheek index about 0.10. Occiput largely deep yellow, except for infuscate brown area between occipital apodemes. Antenna slightly darker than front; pedicel with 3 strong setae on inner surface; arista with 4 dorsal and 2 ventral branches, plus small terminal fork. Proboscis and palp entirely light yellow; palpus with two subapical setae.

Thorax length 0.92 mm. Scutum uniformly light yellow; 8 rows of acrostichals; 1 large pair of prescutellar setae, lengths 0.54× that of posterior dorsocentral setae; setae lateral to prescutellars only slightly thicker than acrostichals (but not longer); h index 0.86. Transverse distance of dorsocentral setae 2.54× that of longitudinal distance. Scutellum same color as scutum; basal scutellars parallel; apical scutellars crossing at very tip; scut index 0.86. Pleura same hue of yellow as scutum, sterno index 0.72. Halter slightly lighter than rest of thorax. Legs slightly lighter than thoracic trunk.

Wing hyaline, veins dull yellowish, wing length 1.98 mm, length to width ratio 2.27. Indices: C, 2.27; ac, 2.47; hb, 0.59; 4-C, 0.96; 4V, 1.61; 5x, 1.36; M, 0.49. Vein C with 3–4 thicker spinules in Sc section; wing tip very slightly pointed, vein R_{2+3} very slightly sinuous, not straight.

Abdomen entirely light yellow, even posterior margins of tergites; completely lacking dark, infuscate markings.

Male terminalia (fig. 19A): Epandrium with microtrichia, lacking setae except on ventral lobe of epandrium; ventral lobe with narrow tip (not rounded), lacking microtrichia but with ca. 6 setae. Cerci fused laterally to epandrium. Surstylus with microtrichia on entire lateral/outer surface, having mesal row of 9 large peglike prensisetae, plus 6–7 fine setae (several ventral ones slightly sclerotized). Subepandrial sclerite (not examined). Hypandrium trapezoidal in shape, slightly longer than broad (W/L 0.9), lateral margins straight, anterior edge almost straight. Postgonite slender, W/L 0.21, fused to hypandrium, with short, minute apical seta. Aedeagus fused to aedeagal apodeme, evenly arched in lateral view, aedeagal angle ca. 45°, shaft of aedeagus of moderate and even thickness throughout (length of shaft 7× the width). Distiphallus large in proportion to entire aedeagus, 0.43× total aedeagus length, in ventral view with narrow tip and parallel sides, base with pair of large spines; aedeagal apodeme relatively long, rudderlike.

Female: Unknown.

Type: Holotype, ♂: "**Costa Rica:** Prov. San José. Moravia. Zurquí de Moravia, Tower path. 1600 m. 30 Mar.–6 ABR 2013, Proyecto ZADBI. Malaise trap #1, 0 m, ZADBI-647, -84:00:57 10:02:58 #106495/ ([bar code label] INBio 0004432774)." Type in good condition, with distal 2/3 of abdomen removed, genitalia dissected by D.A.G. (DBG 86) and stored in polypropylene microvial on same pin as specimen. In INBio.

Other Specimens: Paratype: 1♂ with same label data as holotype, (bar code label) INBio 0004424373 (dissected (DBG 87), stored in polypropylene microvial on same pin as specimen. In AMNH.

Etymology: From Greek *para,* "next to," and *manni*, in reference to the close resemblance between these two widely separated species.

THE *STYLIPENNIS* SUBGROUP

Drosophila stylipennis, new species

Figures 2C; 20, 21B–D, F, G

Diagnosis: A small to medium-sized species (thorax length ca. 0.86 mm [0.75–0.99]), light brown to yellowish species with a uniquely long, slender aedeagus, length 16.0× the greatest width; basal third of aedeagus strongly arched, aedeagal angle ca. 84°; distiphallus narrow in full ventral view, length 2.5× the width, with pair of slightly pointed lobes on proximal margin; surstylus with 7 pointed, thornlike prensisetae.

Description: Male: Head: Frontal index 1.08 (0.92–1.20), top to bottom width ratio 1.46 (1.33–1.64). Ocellar triangle slightly raised above rest of front, dark brown in middle, about 0.6× length of front. Frons uniform light brown to ochraceous in color, ocellar triangle and fronto-orbital plates dull; frontal vitae golden, finely striate, shiny; margin around ptilinal suture ochre. Orbital setae dark brown with brassy highlights, or1:or3 ratio 0.91 (0.82–1.00), or2:or1 ratio 0.56 (0.50–0.66), postocellar setae 0.51 and ocellar setae 0.74× the frontal length; base of ocellar seta just within tangent between median and lateral ocelli; postocellar setae from nearly parallel to minutely crossed at tips; vt index 1.08 (1.04–1.13). Vibrissal index 0.38 (0.33–0.44). Face same color as front, edge of carina lighter. Carina low and narrow, greatest width slightly >0.5× width of pedicel; edge slightly flattened, without sulcus in Puerto Rican specimens, with sulcus in Dominican Republic specimens. Cheek index about 0.09. Eye index 1.48 (1.39–1.65). Occiput brown, pollinose. Antenna with flagellomere 1 same light brown to ochraceous as most of front; pedicel lighter; arista with 3–4 dorsal and 2 ventral branches, plus large terminal fork. Proboscis dark to light yellowish; palpus slightly lighter, with one apical and one subapical seta.

Thorax length 0.90 mm (0.77–0.99). Scutum light, dull brown (Puerto Rico specimens) to ochraceous yellow (Dominican Republic specimens); 6 rows of acrostichal setulae; pair of prescutellar setae from small to well differentiated: barely differentiated from acrostichals in holotype, 0.25× length of posterior dorsocentral setae, to 0.36–0.57× in other specimens; setae lateral to prescutellars undifferentiated from acrostichals; h index 0.91. Transverse distance of dorsocentral setae 2.49× (2.14–2.77) the longitudinal distance. Scutellum slightly lighter than scutum, dull; basal scutellars strongly convergent, apical scutellars crossing for about half their length; scut index 0.33 (0.25–0.40). Pleura slightly darker than scutum (dorsally more infuscate), slightly shiny, without pollinosity; sterno index 0.77 (0.64–0.89). Halter light brown. Legs dull yellowish.

Wing hyaline but slightly dusky; veins light brown, length 1.89 (1.43–2.24) mm. Indices: Wing index 2.40, C, 2.10; ac, 2.84 (2.60–3.00); hb, 0.52 (0.47–0.57); 4-C, 1.13 (1.06–1.18); 4V, 1.89 (1.81–2.00); 5x, 1.54 (1.33–1.70); M, 0.59 (0.54–0.65). Subcostal section of C with heavy spinules; wing tip slightly pointed, vein R_{2+3} nearly straight (not slightly sinuous).

Abdomen overall color dark yellowish brown, posterior margins of tergites with diffuse, slightly darker transverse bands that grade into lighter areas.

Male terminalia (fig. 20): Epandrium with dense microtrichia, only ventral lobe with setae; ventral lobe small, apex blunt, barely extended beyond ventral margin of surstylus, with 5 setae. Cerci fused laterally to epandrium. Surstylus with abundant microtrichia; mesal margin of surstylus with row of 7 prensisetae pegs, about 7 ventral setae. Subepandrial sclerite (not examined).

Hypandrial shape from virtually rectangular with straight sides to more rounded (sides slightly convex), length 1.3× greatest width. Gonopods fused to hypandrium and aedeagal apodeme; seta at tip of lobe a minute spinule. Aedeagus distinctive: long, slender, length 16.0× the greatest width; basal third of aedeagus strongly arched, aedeagal angle 84°; distiphallus narrow in full ventral view, length 2.5× the width, with pair of slightly pointed lobes on proximal margin; base of aedeagus fused to aedeagal apodeme. Aedeagal apodeme short, keel shaped.

Female: General morphology similar to males. Measurements (based on specimen 13): Thorax length 0.75 mm. Frontal length 0.22 mm; top to bottom width ratio 1.41. or1:or3 ratio 1.00, or2:or1 ratio 0.50, postocellar setae 0.50 and ocellar setae 0.82× the frontal length, vt index 0.94. Cheek index 0.10. Eye index 1.53. Thorax length 0.75 mm. Prescutellar setae 0.57× length of posterior dorsocentral setae. Transverse distance of dorsocentral setae 2.45× the longitudinal distance. Scut index 0.88, sterno index 0.84. Wing length 1.69 mm. Wing indices: 4v 1.89; 5x 1.76; M, 0.62.

Female terminalia (figs. 21B–D, F,G): Valves of oviscapt of moderate length, length 2.46× greatest width in ventral view, tip rounded in lateral view, with 16 ovisensilla pegs. Spermathecal capsule small, cup shaped, height slightly less than greatest width; basal introvert reaching about 0.60× length of capsule.

Type: Holotype, ♂: "**Puerto Rico**, Mayaguez/ Jul–Aug 1957, W.B. Heed." Type is point mounted, in good condition, abdomen removed and cleared, genitalia dissected by D.A.G. (DBG 12) and stored in glass microvial on same pin as specimen. In AMNH.

Other Specimens: Paratypes, 2 ♀♀ (one dissected, DBG 13), with same labels as holotype (AMNH). Nontypes: **Dominican Republic:** "La Vega Prov., 7.2 m S Constanza, rd to San José de Ocoa, 5000 ft., 29/VII/91, Grimaldi and Stark" (1♂, dissected by D.A.G., DBG 60) (AMNH); "Las Abejas [Pedernales Prov.] 1300 m, cloud for[est], sweep, 17.1.1989, J.E. Swann" (1♂, dissected, DBG 51)(UGIC).

Etymology: Derived from *stilus* (L., a pointed instrument for writing on wax tablets, a stylus) and *-pennis*, a derivation of *penis* (Latin), in reference to the long, thin aedeagus.

Comments: In the holotype (male) specimen of *D. stylipennis* the prescutellars are very small, barely differentiated from the acrostichals; in other specimens (including paratype female DBG 13, also from the type locality), the prescutellars are nearly twice the length of the holotype prescutellars. There are slight differences between males from Puerto Rico and the western Dominican Republic, the latter having a longer aedeagus with longer gonopods (possibly due to the 20% larger body size of the latter), and more rounded hypandrium. Dominican specimens are also lighter in body color, being yellow/ochraceous instead of light brown.

THE *STARKI* SUBGROUP

Drosophila starki, new species

Figure 22

Diagnosis: Small (0.73 mm thorax length), light brown species with very thin carina and highly distinctive male genitalia: hypandrium narrow, length 1.2× the width; aedeagus straight

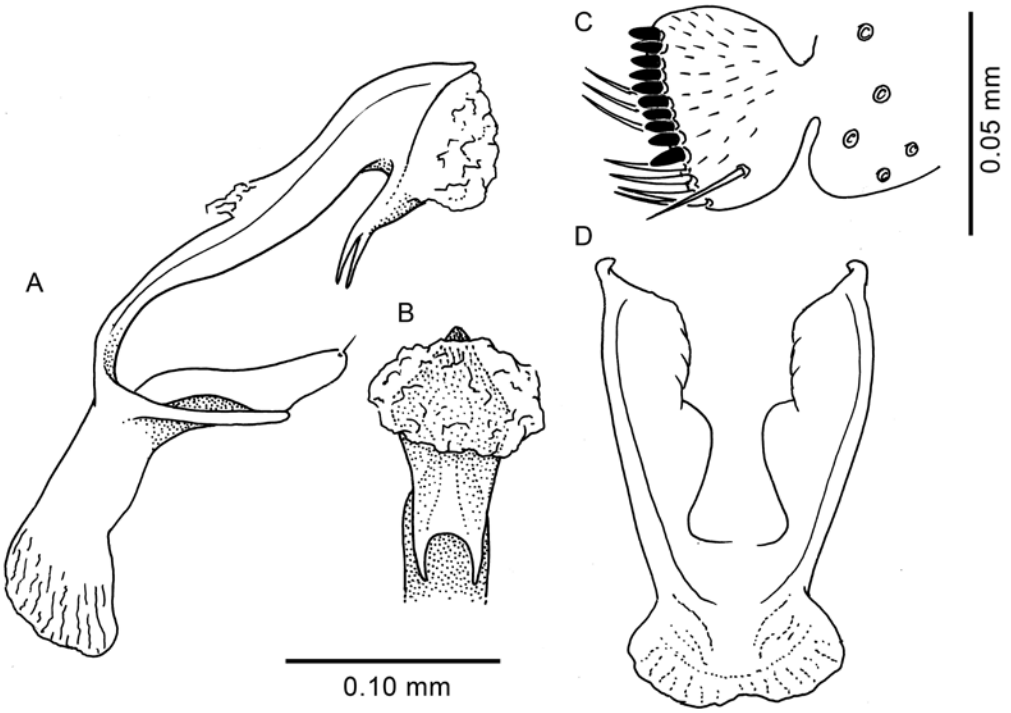


FIG. 22. Male genitalia of *Drosophila starki* Grimaldi, n. sp. (DBG 59). **A.** Lateral view of aedeagus, aedeagal apodeme, and gonopod. **B.** Full ventral view of distiphallus. **C.** Surstylus and ventral lobe of epandrium. **D.** Hypandrium.

(not arched), base very narrow; aedeagus apex bulbous, with extensive membrane and flat ventral lobe bearing pair of spines.

Description: Male: Head. Frons light brown (yellowish on anterior margin); frontal vitta thin, lighter than rest of front, golden, finely striate; frontal index 1.15, top to bottom width ratio 1.65. Ocellar triangle slightly raised above rest of front, dark brown, anterior apex meeting ptilinal suture. Orbital setae dark brownish bronze (not black), or1:or3 ratio 1.00, or2:or1 ratio 0.77, ocellar seta 0.74× the frontal length (postocellar and vertical setae lost on unique specimen); base of ocellar seta slightly outside of tangents between median and lateral ocelli. Vibrissal index 0.25. Face same color as front. Carina very thin, width ca. 0.5× that of antennal base; edge slightly flattened, no sulcus. Cheek index about 0.09. Eye index 1.32. Occiput slightly darker than rest of head. Basal antennomeres light brown (anterior surface of pedicel darkest); arista with 4 dorsal and 2 ventral branches, plus large terminal fork. Proboscis ochre to light brown; palpus slightly lighter, with one apical and one subapical seta.

Thorax length 0.73 mm. Scutum light brown, slightly shiny; 6 rows of long acrostichal setulae; 1 pair of long prescutellar setae, 0.62× the posterior dorsocentral setae; setae lateral to prescutellars not differentiated from acrostichals; h index 0.79. Transverse distance of dorsocentral setae 2.45× the longitudinal distance. Scutellum dull, same color as scutum, basal scutellars (lost in unique specimen); scut index (not determinable; scut setae lost). Pleura light,

infuscate brown, sterno index 0.66. Halter infuscate. Legs light, diffuse light brown near middle of femora and tibiae.

Wing hyaline, veins light brown, length 1.70 mm, length to width ratio (not determined). Indices: C, 2.00; ac, 2.75; hb, 0.59, 4-C, 1.15; 4V, 1.86; 5x, 1.57; M, 0.58. Wing tip rounded, vein R_{2+3} straight (not slightly sinuous).

Abdomen color overall light, infuscate brown, posterior margins of tergites darker and diffusely grading into light areas.

Male terminalia (fig. 22): Epandrium with microtrichia, without setae except for those on ventral epandrial lobes; ventral lobe blunt (not pointed), without microtrichia, with ca. 5 setae. Cerci microtrichose, fused laterally to epandrium. Surstylus with microtrichia over most of outer surface, with row of 10 small, peglike prensisetae, about 8 other, fine setae. Subepandrial sclerite (not examined). Hypandrium narrow, length 1.2× greatest width, with slightly flared anterior margin. Gonopods slender in lateral view, not fused to hypandrium, with short, fine apical seta. Aedeagus nearly straight, not arched, fused to aedeagal apodeme; in lateral view base very narrow, gradually expanded distad to bulbous apex; distiphallus bulbous, with extensive apical membrane and flat lobe bearing pair of apical spines directed anteriad. Aedeagal apodeme fairly large, keel shaped.

Female: Unknown.

Type: Holotype (unique specimen), ♂: "**Dominican Republic:** La Altagracia, mouth of Rio Chavón, 29/II/92, Grimaldi and Stark, sweeping along shores." Type is point mounted, in fair condition (some orbital, all scutellar setae are lost); abdomen was removed and cleared, genitalia dissected by D.A.G. (dissected, DBG 59), dissection and left wing stored in a glass microvial on the same pin as specimen. In AMNH.

Etymology: Patronym, for Julian Stark, dipterologist, colleague, and friend of the author, who collaborated in fieldwork in the Dominican Republic and Costa Rica.

Comments: The male genitalia of the type and only specimen of this species are unique for the *bromeliae* group: the aedeagus is short and straight, with a very slender base; the distiphallus is bulbous, with extensive membrane and a ventral shelf bearing a pair of spines; gonopod and surstylus are relatively small, and the aedeagal apodeme is large. Moreover, it was not collected at flowers, but by sweeping the muddy shores of a river in eastern Dominican Republic.

UNNAMED SPECIES

The following four species were recognizable as distinct from the above, described species, but are not being named/formally described since they are only known from females.

Species A

Figures 23A–D

Specimen: 1 ♀, **Ecuador:** Orellana, Reserva Etnica Waorani, 00°39′25/7″S, 76°27′10.8″W, 216m, II-X/1995, Erwin et al., canopy fogging, sample 1118 (dissected, DBG 46). In NMNH.

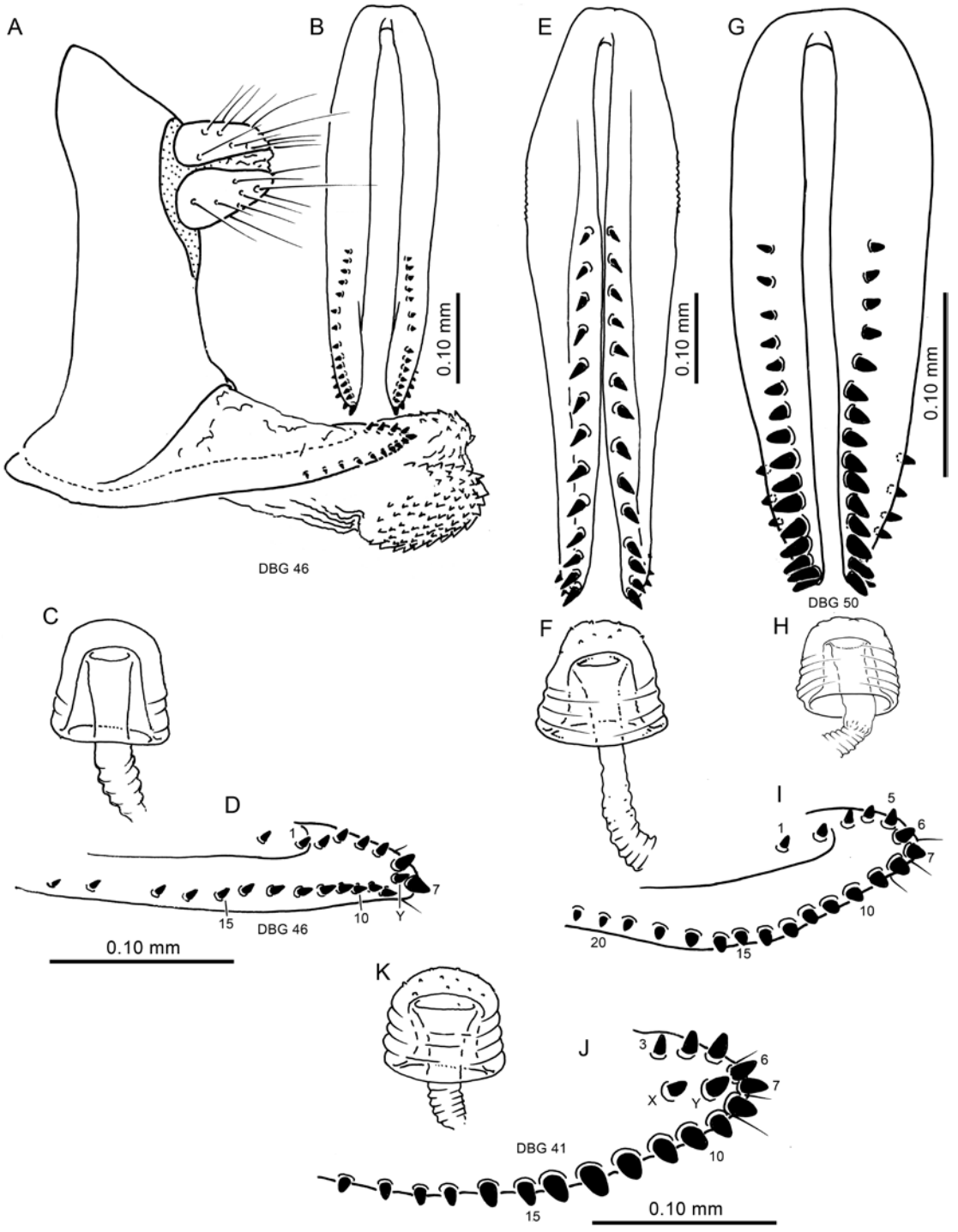


FIG. 23. Female terminalia of four undescribed species in the *bromeliae* group. **A–D.** sp. A (DGB 46, Ecuador, Orellana). **E, F.** sp. B (DBG 88, La Paz, Bolivia). **G–I.** sp. C (DBG 50: Dominican Republic, Puerto Plata). **J, K.** sp. D (DBG 41: Panama: Darién).

General Features: Body dull yellowish overall; arista with 3-2 dorsal-ventral branches; wing tip slightly pointed; thorax length 1.10 mm. Distinctive for the very long, slender oviscapt with minute pegs, length ca. 430 μm, length/ventral width 3.71, with 19 very small oviscapt pegs; oviscapt very slender in lateral view, apically pointed; spermathecal shape like that of *D. bromeliae*, height ca. 1.04× the width, introvert 0.80× capsule height (figs. 23A–D). Tergite IX tall, height slightly greater than length of oviscapt. Based on the oviscapt structure it can be predicted that this species might have a narrow host range.

Species B

Figure 23E, F

Specimen: 1♀: "**Bolivia:** Depto. La Paz, 8 km S Chulumani, nr. Apa Apa, 1700–1800 m, 1622′S 6730.4′W, 9.iii.2001, S.D. Gaimari." Matrix code label: USNMENT 01204326 (dissected, DBG 88). In NMNH.

General Features: Body dark yellow to ochre; arista with 4-2 dorsal-ventral branches; wing tip rounded; thorax length 1.12 mm. Oviscapt very long and slender, length 700 μm; ventral length/ventral width 3.87; with 20 pegs; pegs slender, pointed, widely spaced. Spermathecal structure typical of *bromeliae* group, height 1.0× the width, introvert 0.75× the capsule height (fig. 23F). The long, narrow oviscapt suggests that this species too, like sp. A, has a narrow host range.

Species C

Figures 23G–I

Specimen: 1 ♀: "D.R. **[Dominican Republic]:** Puerto Plata, 23.1.1999, seep over muddy trail, S.A. Marshall" (dissected, DBG 50). In UGIC.

General Features: Dark, dull yellow to very pale, infuscate brown; frontal vitta deep ochre; arista with 4-2 dorsal-ventral branches; thorax length 0.91 mm. Oviscapt of moderate length, 300 μm, length/ventral width 2.80, notable for the large, crowded oviscapt pegs; 21 pegs present, oviscapt narrowed apically (not rounded); spermathecal shape like that of *D. bromeliae*, height slightly shorter than (0.81×) the width, introvert 0.73× capsule height (figs. 23 G–I).

Species D

Figure 23J, K

Specimen(s): 1 ♀, "**Panama**, Darién Province: El Real, XI-29-1963, Sarah B. Pipkin/ex: short red *Heliconia* sp. flower" (dissected, DBG 41). In NMNH.

General Features: Body dark-dull yellow ochre, thorax length 0.92 mm, arista with 4-2 dorsal-ventral branches; carina sulcate; wing tip pointed; prescutellars noticeably thicker than acrostichals (about same as anterior dc); oviscapt distinctive for the presence of two preapical pegs on the lateral surface (fig. 23J); oviscapt with 20 marginal pegs; spermatheca (fig. 23K) like that of *bromeliae*, height = width, introvert 0.7× capsule height.

KEY TO MESOAMERICAN AND ANDEAN SPECIES

(based on male terminalia)

1a. Distiphallus with pair of ventral spines. 2
1b. Distiphallus without pair of ventral spines (complex of very similar species) 6
2a. Aedeagus very short, not arched in lateral view, with bulbous distiphallus (fig. 22A) . . . . . *starki,* n. sp. (Hispaniola).
2b. Aedeagus long, length 7.5–16× thickest part of shaft, arched in lateral view, distiphallus not bulbous 3
3a. Aedeagus very long, length 16× shaft width (figs. 20A, D) . . *stylipennis,* n. sp. (Caribbean).
3b. Aedeagus length ca. 7–8× shaft width. 4
4a. Epandrial lobe not pointed; distiphallus drop shaped, with three small spines on anteroventral margin (figs. 17A–D) . . . . . *.penispina,* n. sp. (Central America, Caribbean).
4b. Epandrial lobe pointed; distiphallus harpoon shaped, with two large spines. 5
5a. Distiphallus long (W/L 0.36), paraphysis long (W/L 0.21), microtrichia over all of surstylus (fig. 19D) . . . . . *paramanni,* n. sp. (Costa Rica).
5b. Distiphallus shorter (W/L 0.46), paraphysis shorter (W/L 0.32), surstylus with very sparse microtrichia (fig. 19A) . . . . . *manni,* n. sp. (Bolivia).
6. Length of aedeagal shaft ca. 11× the width, surstylus with 12 prensisetae pegs (fig. 16A–C) . . . . . *thurstoni* (Jamaica).
6b. Length of aedeagal shaft 6.2–7.2× the width, surstylus with 7–9 pegs 7
7a. Aedeagus short, shaft length ca. 5.5× the width; distiphallus large, bulbous (almost 1/2 length of shaft) (figs. 12D–F). . . . . *sevensteri* (Panama).
7b. Aedeagus longer, shaft length ca. 6.2–7.0× the width; distiphallus smaller 8
8a. Aedeagus only slightly arched, aedeagal angle ca. 135°; prescutellar fairly large, prescutellar index 0.40–0.60. (fig. 13) . . . . . *mexiflora,* n. sp. (Central America).
8b. Aedeagus significantly arched, almost a right angle (100°–115°); prescutellars generally smaller (pi 0.30–0.45) 9
9a. Surstylus virtually bare of microtrichia; aedeagus length 6.0× the width (figs. 12A–C). . . . . *billheedi*, n. sp. (El Salvador).
9b. Surstylus generally with abundant microtrichia; aedeagus length ca. 6.5× the width (figs. 8, 9) . . . . . *bromeliae* Sturtevant (widespread in Neotropics).

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