

## VIII. The Alagitans-Bocainensis Complex of the Willistoni Group of *Drosophila*

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The *alagitans* species group of *Drosophila* was established by Patterson and Mainland (1944) for *Drosophila alagitans* and *D. capnoptera*, and was located in the subgenus *Drosophila*. Further study showed that the male genitalia of these species were quite similar to members of the *willistoni* group (Hsu 1949), and the group was therefore transferred to the subgenus *Sophophora* (Wheeler 1949). Carson (1954) found that there were three distinct entities involved under the name *Drosophila bocainensis* in Brazil; he identified one of them as *bocainensis*, described the other two under the names *parabocainensis* and *bocainoides*, and designated the complex as the *bocainensis* subgroup of the *willistoni* species group.

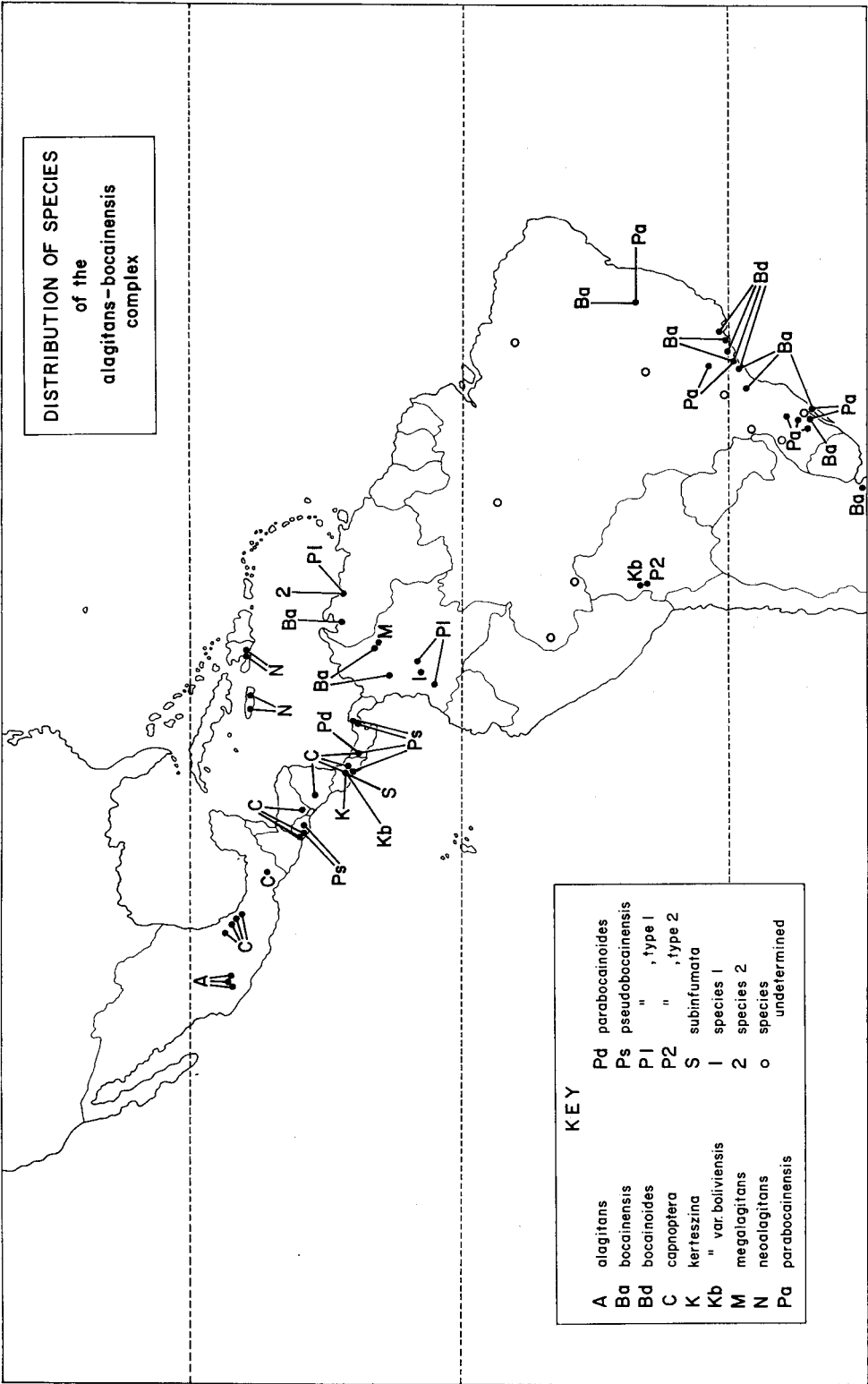
In our collections of Neotropical Drosophilidae we have frequently taken specimens obviously related to *bocainensis* or to *alagitans*, and it is now clear that together they form a natural group of species which could with equal logic be termed a species group or one or two subgroups of the *willistoni* group. Since relatively few of these species have been successfully cultured in the laboratory, we are deferring a decision on the matter of "group" versus "subgroup(s)" until we have more evidence; meanwhile the expression "*alagitans-bocainensis complex*" describes this cluster of species adequately.

With a few exceptions, the species are remarkably similar in their external morphology, but the male genitalia offer numerous useful characteristics. The dissections of the genitalia were done by the junior author (LEM) who also prepared *camera lucida* drawings of the various parts. The final drawings were made by Mrs. Linda Kuich, to whom we wish to express our sincere gratitude. All of the figures are drawn to the same scale; the true sizes are indicated by the 0.1 mm line which has been drawn on several of the figures.

The known distribution of the species of this complex is shown in Figure 1; several of the points in South America are taken from the distribution records of Carson (1954) and Salzano (1955, 1956). Both morphologically and geographically the species fall into two groups—the southern *bocainensis*-like forms and the more northern *alagitans*-like forms. *D. bocainensis*, however, reaches Colombia and thus overlaps the distribution of the "northern" members, while *bocainoides*, clearly a member of the northern group, occurs only in southern Brazil, as far as is known. Although we are not familiar with the species, *kerteszi* Duda, *kerteszi* var. *boliviensis* Duda,<sup>2</sup> and *subinfumata* Duda quite possibly belong to this complex also. The known localities for these three species have also been added to the map.

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<sup>2</sup> We attempted to borrow the type of var. *boliviensis* from the Dresden Museum, but were informed by Dr. Hertel that he was unable to locate the specimen among Duda's type material. The types of *kerteszi* and *subinfumata* are believed to be in the Hungarian Museum, Budapest.



## LECTOTYPE SELECTIONS

Since we had among our material an estimated twelve species belonging to the *alagitans-bocainensis complex*, it has been necessary to establish beyond any doubt the true identity of the described species: *alagitans*, *capnoptera*, *bocainensis*, *parabocainensis*, and *bocainoides*. Patterson (1943) stated that the type of *alagitans*, from Laguna Patzcuaro, Michoacan, Mexico, had been sent to the American Museum of Natural History in New York City. It cannot be found there at the present time and is presumed lost. In The University of Texas collection, however, are specimens from Valle de Huajumbaro and Uruapan, Mich., Mexico, collected by Gordon Mainland within a few days of the time he collected the type material, and which he clearly indicated belonged to the species *alagitans*. We have therefore used these specimens, which agree perfectly with the description, as representatives of the species, and believe that a neotype is not required. The holotype of *capnoptera*, from Perote, Veracruz, Mexico, as well as numerous other specimens from many localities, is in The University of Texas collection.

The problem of the type specimens of *bocainensis*, *parabocainensis* and *bocainoides* is rather complex, and has been explained in considerable detail by Carson (*op. cit.*). He has recently requested that the senior author (MRW) select and/or designate the types for these species in such a way that they will be valid under the International Code of Nomenclature.

In naming the species *parabocainensis* and *bocainoides* Carson (*op. cit.*) set up a series of ten syntypes for each species; until recently they have been retained in the collection of Dr. Stalker at Washington University in St. Louis, Missouri. In order to clarify the identity of these species, and the new ones in our laboratory, all of these syntypes were sent to us and several of them have been used to prepare the genitalial figures. A lectotype has now been selected for each species, as follows:

*Drosophila bocainoides* Carson 1954: 150. *Lectotype selection.* The specimen selected to be the lectotype is a male in good condition (one damaged antenna), and now bears the following four labels: "D. bocainoides, Vila Atlantica, ♂, VII '51, H. Carson"; "S. P. Brazil"; "bocainoides"; (red label) "Lectotype, D. bocainoides, selected by M. R. Wheeler, 1960". This specimen, as well as four of the remaining paralectotypes, is being deposited in the American Museum of Natural History, New York City, in accord with Dr. Carson's wishes. The remaining five paralectotypes are in The University of Texas collection. These nine remaining paralectotypes are now so marked with a blue label bearing the word "Paralectotype". Some additional specimens, siblings of the original syntype series, are in the collection of the Museu Paulista, São Paulo, Brazil.

*Drosophila parabocainensis* Carson 1954: 49. *Lectotype selection.* The specimen selected as the lectotype is a male in good condition bearing the following four labels: "D. parabocainensis, ♂, VII '51, H. Carson, Feliz, Rio Grande do Sul"; "Brazil"; "parabocainensis"; (red label) "Lectotype, D. parabocainensis, selected by M. R. Wheeler, 1960". This specimen, and four of the remaining paralectotypes, is being deposited in the American Museum of Natural History, New York City. The remaining five paralectotypes are in The University of

Texas collection. These nine remaining paralectotypes are now so marked with a blue label bearing the word "Paralectotype". Some additional specimens, siblings of the original syntype series, are in the collection of the Museu Paulista, São Paulo, Brazil.

The type specimen(s) of *D. bocainensis* Pavan and da Cunha 1947 has apparently been lost. Carson (*op. cit.*, p. 148 ff.) has described his attempts to locate this material. When he discovered that among the wild-caught specimens of this "species" there existed, in fact, three nearly identical species, two of which could be separated only on the basis of cytological differences, he attempted to find the types of *bocainensis* in order to apply the name to the correct member of the complex. He searched the collection in the Museu Paulista, São Paulo and the private collection of Dr. Pavan at the University of São Paulo, but was unable to locate any extant specimens of this species. Furthermore, the original living culture which had been used to describe the species and set up the types was no longer in existence. After examining the evidence he concluded that the species which was found abundantly in coastal São Paulo state was fairly certainly the true *bocainensis*, and supported his conclusion as follows:

"The type material of *Drosophila bocainensis* Pavan and da Cunha 1947 was collected in February 1944 at a remote fazenda called Campos da Bocaina in the extreme northeastern corner of the State of São Paulo, Brazil. This fazenda lies in a tongue of the state which projects eastward into the State of Rio de Janeiro and is approximately equidistant (30 km.) from Queluz, on the railroad Central do Brazil, and the town of Bananal.

"As the laboratory strain from which this species was described is no longer in existence, it is not possible to assign the type material with certainty to one or the other of the species now recognized cytologically, nor has it been possible to make further collections from the type locality. Campos da Bocaina, however, lies in the coastal rainforest of the Serra do Mar, 270 km. (145 miles) north and east of Vila Atlantica, an area south of Santos from which extensive collections of *Drosophila* have been made. Both locations are closely similar ecologically and lie in the same mountain range. At Vila Atlantica, only one of the two sibling species has been found; this same sibling has likewise been found abundantly at two other locations in eastern São Paulo from which *bocainensis*-like flies have been analyzed cytologically. These locations are the Horto Florestal in the Serra Cantareira, near the city of São Paulo, and Mogi das Cruzes.

"For the above reasons, it seems logical to utilize the original name *Drosophila bocainensis* Pavan and da Cunha to designate the particular member of the sibling species pair found abundantly in coastal São Paulo." He stated further that his choice ". . . conforms to the original description of this species by Pavan and da Cunha, 1947, pp. 18-20. . . ."

To represent the species *bocainensis sensu strictu*, he prepared pinned specimens (five males and five females) ". . . from a laboratory strain of flies derived from the offspring of a single wild female collected at Vila Atlantica in July 1951". Not being familiar with the requirements for the selection of neotypes, no single specimen was so designated at that time. This series of ten specimens was recently sent to us by Dr. Carson who requested that the present authors take whatever action seemed desirable to stabilize the name *bocainensis*.

*Drosophila bocainensis* was thoroughly described by Pavan and da Cunha (1947: 18), but it is so similar in its general morphology to *parabocainensis* Carson that their certain identification has been based only on the pattern of chromosomal inversions characteristic of each of them (Carson, *op. cit.*; Salzano, *op. cit.*). Mrs. Marta Breuer, of the University of São Paulo, compared a number of males of the two species and noted a small difference in the genital arch; although the difference was statistically significant there was sufficient overlap that identification on this character alone was not always reliable. We wish to thank Mrs. Breuer for permitting us to use some of her unpublished figures illustrating this character. We have now compared the male genitalia of the two species, using some of the syntypes of *parabocainensis* and some of the male siblings of the pinned series of *bocainensis* prepared by Carson. There are some consistent differences, as described below, but they are small differences and are not easily seen without well-prepared material.

At the present time we feel that the selection of a neotype for *bocainensis* would serve no useful purpose. We are clearly dealing with a complex of closely related species in which Carson (1954), acting as a "first reviser", clearly restricted the name to a certain definable species. A neotype selection would do nothing that Carson's restriction has not already done; furthermore, a neotype, chosen from among the ten specimens from Vila Atlantica (about 145 miles distant from the original type locality), could lead to still greater confusion if it should be found that the species at Campos de Bocaina (Serra de Bocaina) is different than that at Vila Atlantica.

#### MALE GENITALIA IN THE WILLISTONI GROUP

The male genital arch of several species of the willistoni group was described by Hsu (1949), and Malogolowkin (1952, 1958), Nater (1953), and Spassky (1957) described all or part of the genitalia of various species of this group. Since the terminology employed by these various authors is frequently quite different, we feel that it is desirable to describe and illustrate here the nomenclature of the genitalial pieces which we are using in the *alagitans-bocainensis* complex. An interpretation of the origin and homology of the genital parts among the various genera and subgenera of the family is also highly desirable, but we do not feel that we understand these relationships adequately to attempt such a treatment.

Figure 2 illustrates the individual genital pieces of males of the *alagitans-bocainensis* complex as well as their appearance with different degrees of dissection. The genital arch (A-1) is strongly narrowed dorsally and broadened ventrally; there are three margins: the anterior margin (A-2), in contact with the apical margin of the sixth tergite, the posterior margin (A-3) to which are attached the anal plates (A-8), and, on the ventral side between these two margins, the undermargin (A-4) of Hsu (= *bordo inferior* of Malogolowkin). The angle formed by the anterior and undermargins is termed the heel (A-5) by Hsu, the *angulo anterior-inferior* by Malogolowkin. Hsu described the angle formed by the posterior and undermargins as the "toe"; this is not well marked in the willistoni group (A-7) and is easily confused with a "posterior process" (A-6) which is often more highly developed in the *Sophophora*.

The claspers (A-9; forceps) of each side are connected by the bridge (A-14;

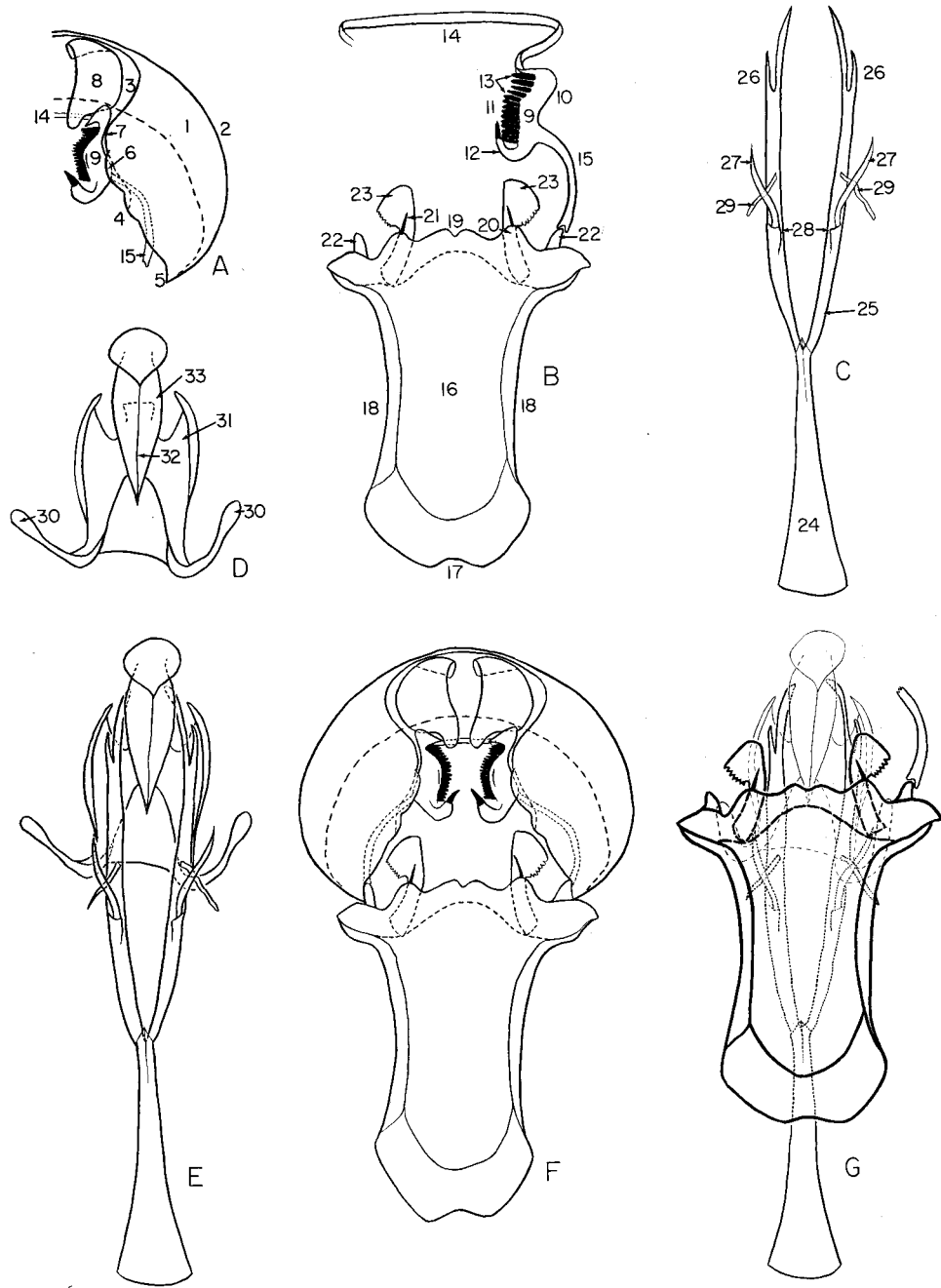


FIG. 2. Diagrammatic representation of the complete male genital (copulatory) structure of an average member of the complex. A, genital arch, clasper, and bridge; B, hypandrium, clasper, and bridge; C, apodeme of the penis and pincers; D, penis; E = C + D; F = A + B; G = B + C + D. See text for key to numbers.

ponte; decasternum of Okada); in this group the clasper is a small plate bearing a row of primary teeth (B-13) along the internal border (B-11), and is elongated below into a hook (B-12). The external border is concave (B-10). From each clasper there is a prolongation of the bridge (B-15) which articulates with the hypandrium (B-16). Secondary clasper teeth are not present in this species complex.

The base of the hypandrium (novasternum plus ventral fragma of Okada) is its anterior margin (B-17); the lateral margins (B-18) are rolled or curved around. The distal (posterior) margin shows many landmarks; the median notch (B-19) may be shallow or deep; to each side is a paramedian expansion (B-20) which usually bear the paramedian spines (B-21), the latter sometimes being absent, sometimes doubled. Near each outer corner is an internal prolongation (B-22) which articulates with the prolongation of the bridge. From the internal wall there also arise two hypandrial appendages (B-23) of varying size and shape. These do not appear to us to be homologous with the anterior gonapophyses (anterior parameres of Okada) of other species. Characteristically, the anterior gonapophyses possess minute sensilla, although Okada (1955) has shown that about 5% of the species of *Sophophora* examined by him lack these sensilla. In some of our macerated preparations we have seen small clusters of sensilla, apparently located on small mound-like masses of soft tissue, sometimes near the caudal border of the hypandrium, and sometimes loosely attached (presumably torn) along the apodeme of the penis. We believe that these masses may represent the extremely reduced anterior gonapophyses.

The apodeme of the penis (C-24) is fused with the base of the pincers (C-25; pincas); the latter are sometimes straight but are more often bent or twisted apically. They may show an apical bifurcation (C-26); they may possess a lateral branch (C-27) and a secondary branch (C-29), the latter often protruding at a more extreme angle than the former. Near the base may be a basal expansion (C-28). The penis (D) is readily detachable from the apodeme and the pincers; from the base, on each side, there arises a ventral prolongation (D-30) the apices of which rest on the posterior margin of the hypandrium. There may also be lateral prolongations, the wings (D-31). On the median ventral line there is a prominence (D-32) and there is another on the back, dorsally (D-33).

In Figure 2, E, is shown the typical position of the penis and the pincer-apodeme complex; F shows the relationship between the hypandrium, genital arch, clasper and bridge; and G shows the appearance of the copulatory apparatus after the genital arch and its associated parts have been removed.

The species of the *alagitans-bocainensis* complex are mainly distinguished from the other members of the willistoni group by the features of the pincers, showing an apical bifurcation and/or lateral branches and/or secondary branches. (Compare, for example, the comparable figures for *fumipennis*, *nebulosa*, *capricorni* and *sucinea* in Malogolowkin, 1952: 91). The southern group of *bocainensis*-like forms all have the secondary branch of the pincer but lack apical bifurcations and lateral branches; the northern group of *alagitans*-like forms all have the lateral branches of the pincer and may also show the apical bifurcation and the secondary branches. The rather crude drawing of the male of *kerteszi* (Duda

1927: 216) shows clearly the presence of the secondary branch of the pincer, thus leaving no doubt as to its position in this complex.

*Drosophila changuinolae*, the last species described in this report, lacks these features of the pincer (Figure 8) and cannot be included in the complex. It is clearly a member of the willistoni group, however, the male genitalia appearing more similar to those of *mangabeirai* than to those of other species of the group (see Malogolowkin 1958: 444).

#### SPECIES DESCRIPTIONS AND DISTRIBUTIONS

The species of the *alagitans-bocainensis* complex can usually be recognized by the following combination of characters: wings usually darkened, lightly to intensely, the crossveins often strongly clouded; two subequal oral bristles; cheeks quite narrow; eyes with rather bare appearance; body color mostly tan, often with some pleural darkening, at least in males; basal scutellars divergent; only two distinct sternopleural bristles, the posterior one stout and long, the anterior one half as long or shorter; abdomen with dark bands, usually darkest apically on males, less heavily darkened on females.

The two other species of the willistoni group that are most likely to be confused with the members of this complex are *nebulosa* and *fumipennis*. The simplest recognition character for these two concerns the sternopleural bristles; there are clearly three, the two anterior ones weak and approximately subequal, the posterior one long and strong.

#### ***Drosophila alagitans* Patterson and Mainland**

1943. Univ. Texas Pub. 4313: 194.

*Recognition features:* Upper half of pleura brown in both sexes, the lower half contrastingly pale; wings only slightly dusky, the posterior crossvein dark but only slightly clouded. Male genitalia as in Figure 3, A-C.

*Type locality:* Laguna Patzcuaro, Mich., MEXICO. Also known from Valle de Huajumbaro, and Uruapan, Mich., Mexico.

#### ***Drosophila neoalagitans*, new species**

Mesonotum dark tan; acrostichal hairs in six rather regular rows. Pleura of male brownish, darkest on sternopleura; female pleura less brownish, the sternopleura paler than mesopleura. Male abdomen mostly black, the basal 3-4 tergites with yellowish bases; female abdomen paler, the tergites mostly tannish yellow with apical brown bands. Wings rather uniformly grayish, the posterior crossvein a bit more heavily darkened. Costal index 2.4-2.6; 4th vein index 1.8-2.0. Male genitalia as shown in Figure 3, D-F. Body length 2.8-3.0 mm.

Holotype male, allotype, and eleven paratypes (H410.7), Kenscoff, HAITI, June-July 1959, W. B. Heed and H. L. Carson. Additional specimens from Petionville, Haiti, and Hardware Gap, JAMAICA.

#### ***Drosophila capnoptera* Patterson and Mainland**

1944. Univ. Texas Pub. 4445: 47.

*Recognition features:* Pleura of both sexes brown, somewhat mottled above, on



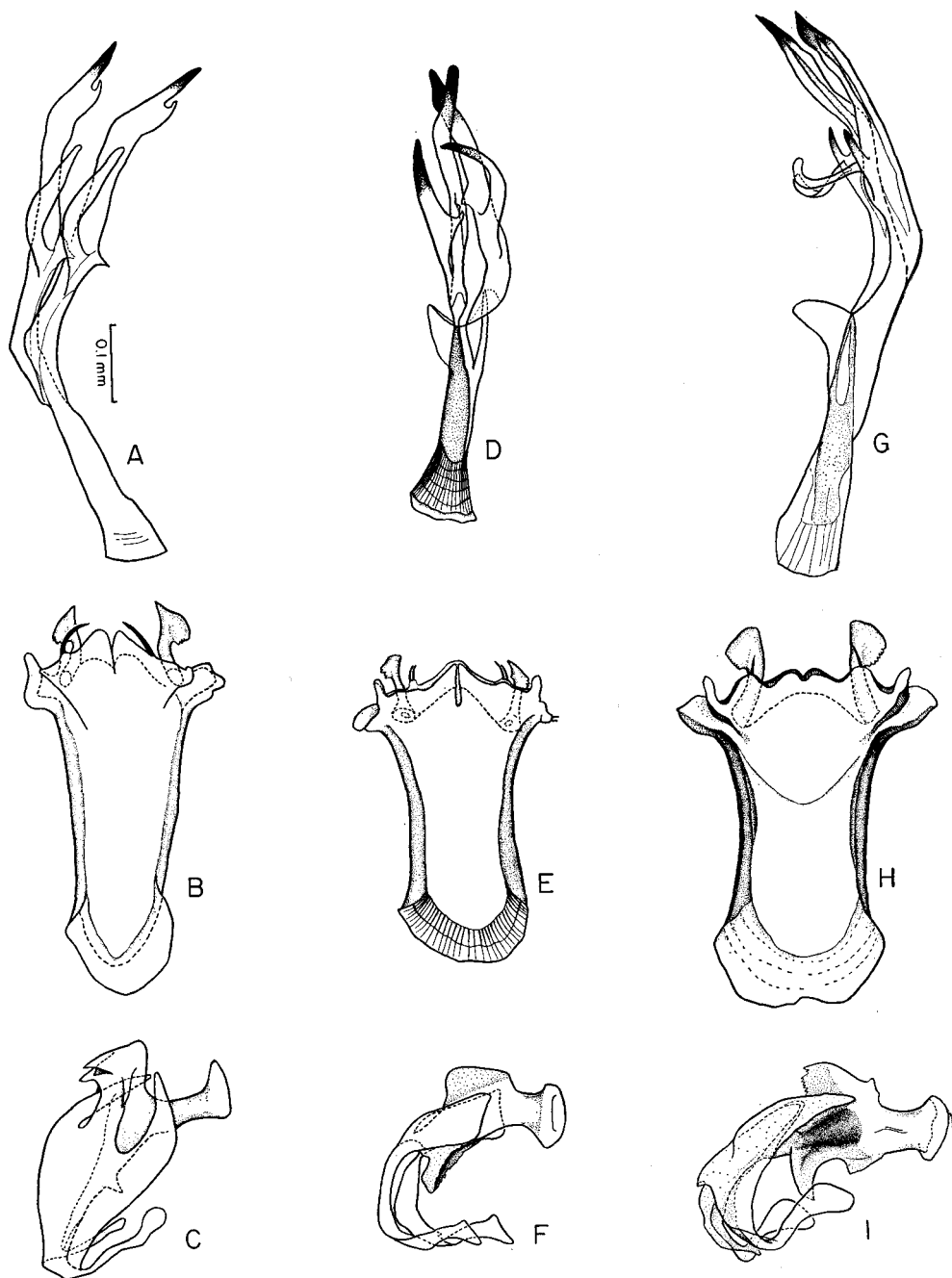


FIG. 3. Apodeme, pincers, hypandrium and penis of: A-C, *alagitans*; D-F, *neolagitans*; G-I, *megalagitans*. Many specimens of *neolagitans* show only a single paramedian spine on each side of the hypandrium, rather than two, as shown.

males becoming intense on lower sternopleura where the color contrasts strongly with the pale fore coxae; wings heavily clouded over both crossveins and over anterior half of wing; large species. Male genitalia as shown in Figure 4, A-C.

*Type locality:* Perote, V.C., MEXICO. Also known from Jacala, Hid., Tezuítlan and Huauchinango, Pueb., and San Cristobal, Chiap., Mexico; Volcan Santa Ana and Volcan Boqueron, EL SALVADOR; Monte Vyuca near Zamorano, HON-

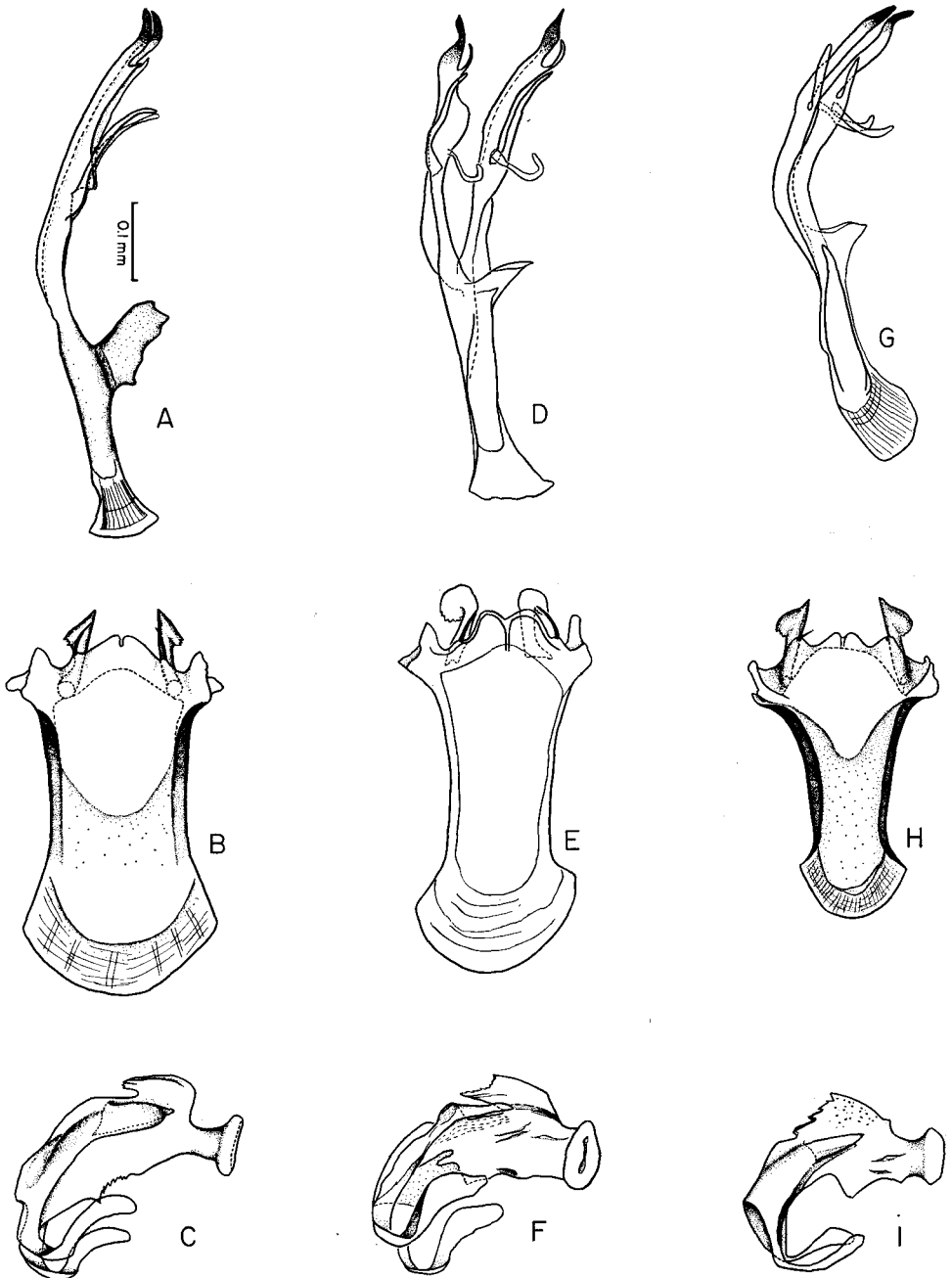


FIG. 4. Apodeme, pincers, hypandrium and penis of: A-C, *capnoptera*; D-F, *bocainoides*; G-I, *parabocainoides*.

DURAS; Santa Maria de Ostuma, NICARAGUA; Volcan Irazu and Heredia, COSTA RICA; Boquete, PANAMA.

***Drosophila megalagitans*, new species**

Holotype ♂: Mesonotum tan, scutellum a little darker; upper half of pleura brown, rather mottled, and the sternopleura with a brown area on upper posterior part surrounding the bristle bases, in front of this all pale. Wings dark, darkest along costal margin; crossveins clouded but the clouding diffuses into the general wing color. Costal index 3.0; 4th vein index 1.4. Male genitalia as shown in Figure 3, G-I. Body length greater than 3.0 mm.

Female paratypes: Two females, taken at the same time and place as the holotype, are not certainly conspecific. The wings are less heavily darkened, and the pleura is much paler.

Holotype male, Cerra de Par Rico, east of Bucaramanga, COLOMBIA, Sept. 1956, H. L. Carson, M. Wasserman and H. Hoenigsberg. Male genitalia of holotype mounted on slide No. 278, The University of Texas collection. Two paratype females, with the same collection data as the male. The collection was made at about 12,000 ft. in the Cordillera Oriental de Andes.

***Drosophila bocainensis* Pavan and da Cunha**

1947. Bol. Fac. Fil. Cien. Letr. Univ. S. Paulo 86: 18.

*Recognition features:* Pale tan, both sexes with poorly defined dull brownish abdominal bands; pleura pale; wings slightly dusky, both crossveins with narrow clouds. Not readily separable from *parabocainensis*.

Mrs. Marta Breuer (personal communication) has observed that on the ventral portion of the genital arch there is a posterior, rather knob-like process that is visible from external view, and which is useful in distinguishing these two sibling species. The "typical" position of this process is shown in Figure 5; in *bocainensis* it usually forms an angle of  $\pm 15^\circ$  with the lower margin, while in *parabocainensis* the upper margin of the process is nearly parallel with the lower margin of the genital arch. However, there is considerable variation in this character in both species, even between sibling specimens, and the degree of overlap is such that certain identification cannot be based upon this feature alone.

The male copulatory organs of the two species are also extremely similar (Figure 6), but a few fairly distinctive features are discernible in good preparations. In *bocainensis* the outer corners of the posterior margin of the hypandrium

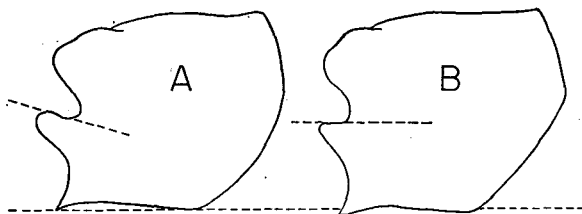


FIG. 5. Ventral portion of genital arch of (A) *bocainensis* and (B) *parabocainensis*, showing the average difference in position and direction of the posterior process of the undermargin.

(near 22, Figure 2) are not so regularly curved toward the internal prolongation, the paramedian spines are usually larger, the apex and body of the penis are of slightly different shape, and the dorsal prominence shows some degree of a serrated edge.

*Type locality:* Campos da Bocaina, Est. São Paulo, BRAZIL. Also known from several localities in the states of São Paulo, Minas Gerais, Paraná, and Rio Grande do Sul, Brazil; Medellin and Rionegro, COLOMBIA; Merida, VENEZUELA; and from El Destino, ARGENTINA.

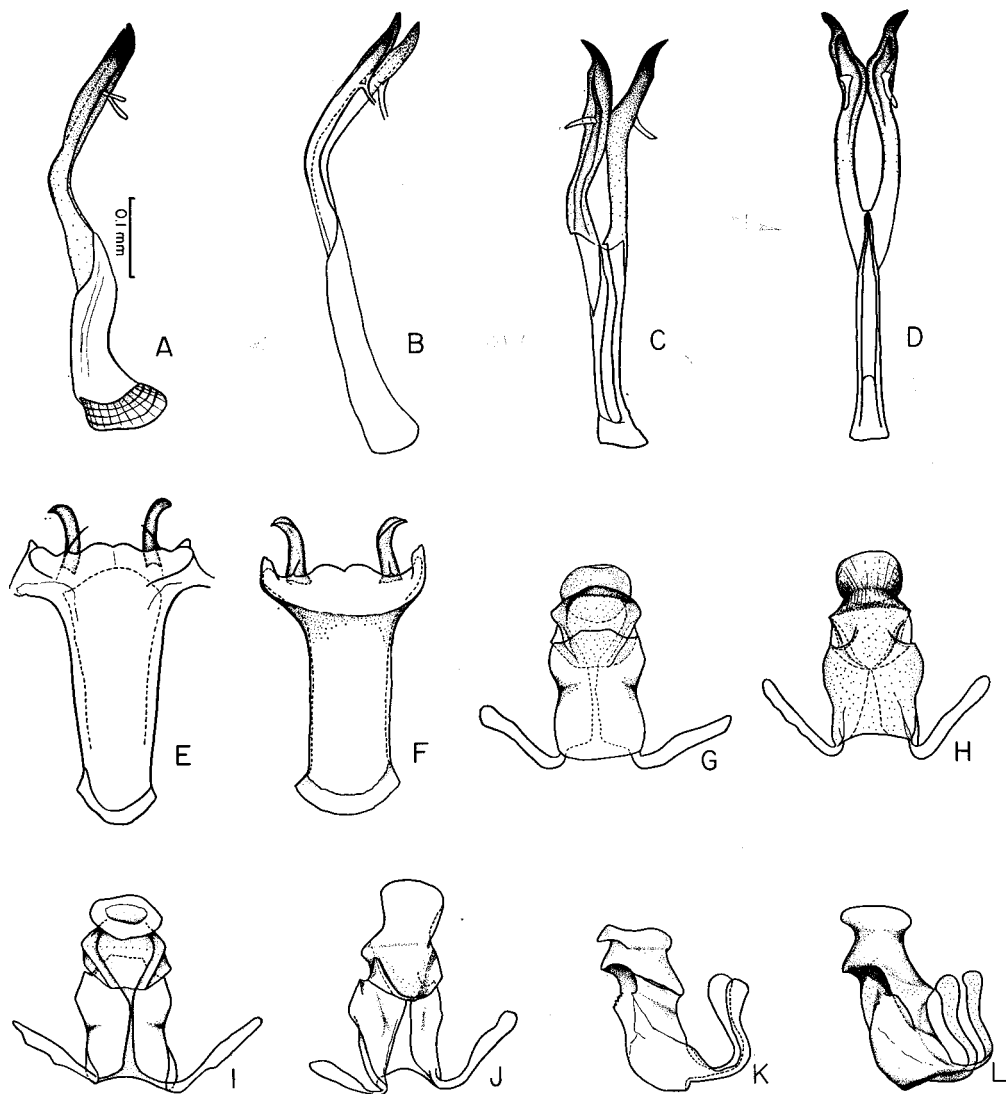


FIG. 6. Apodeme, pincers, hypandrium and penis of *bocainensis* (A, C, E, G, I, K) and *para-bocainensis* (B, D, F, H, J, L). G, H—dorsal view; I, J—ventral view; K, L—lateral view.

***Drosophila parabocainensis* Carson**

1954. *Evolution* 8: 149.

1952. *Science* 116: 518; *nomen nudum*.

*Recognition features:* Identical to *bocainensis* in gross morphology. The male genitalia are shown in Figure 6, and are discussed under *bocainensis*, above.

*Type locality:* Feliz, Est. Rio Grande do Sul, BRAZIL. Also reported from Ponta Grossa, Emboaba, and Muitos Capoes, R.G.S., Pirassununga and Serra Cantareira, Est. São Paulo, and Montes Claros, Est. Minas Gerais, Brazil.

***Drosophila bocainoides* Carson**

1954. *Evolution* 8: 150.

1952. *Science* 116: 518; *nomen nudum*.

*Recognition features:* Pleura of male brown, the fore coxae sometimes darkened; otherwise quite similar in appearance to *bocainensis*. Female pleura pale, rarely the mesopleura a trifle darkened. Male genitalia as shown in Figure 4, D-F.

*Type locality:* Vila Atlantica, Est. São Paulo, BRAZIL. Also known from Serra Cantareira and Mogi das Cruzes, S.P., and Angra dos Reis, Rio de Janeiro, Brazil.

***Drosophila parabocainoides*, new species**

Male. Tan; dark abdominal bands heavy; pleura mostly tan, but with a distinctive brown area on pteropleura just anterior to base of haltere. Wings moderately dark on anterior half, gradually becoming paler behind; posterior crossvein with distinct cloud. Costal index 2.5–2.6; 4th vein index 1.5–1.6. Body length about 3.0 mm. Male genitalia are shown in Figure 4, G-I. Female unknown.

This is possibly the same species as *subinfumata* Duda, described from Costa Rica.

Holotype male and two paratype males, Boquete, Chiriqui Pr., PANAMA, June–July 1959, W. B. Heed and H. L. Carson. Six paratype males, same locality, August 1958, W. B. Heed and M. Wasserman.

***Drosophila pseudobocainensis*, new species**

Tan, the scutellum a little darker; pleura mostly pale, the mesopleura a trifle grayish. Basal abdominal segments with prominent yellow basal bands, more apical tergites increasingly darker. Wings only slightly dusky, the posterior crossvein with a narrow cloud. Coastal index about 2.8; 4th vein index about 1.7. Body length 2.5–2.8 mm. Male genitalia as shown in Figure 7, A, B, D, F, I.

This is possibly the same species as *kerteszina* Duda, described from Costa Rica.

In studying preparations of male genitalia from specimens from all parts of the range, three types were found. We are considering the form found in Central America to be the "typical" one. The differences between the types are at least as great as those between *bocainensis* and *parabocainensis*, but since there is at this time no information on possible genetic isolation, hybridization, either natural or forced, or on other characteristics of the natural populations, we do

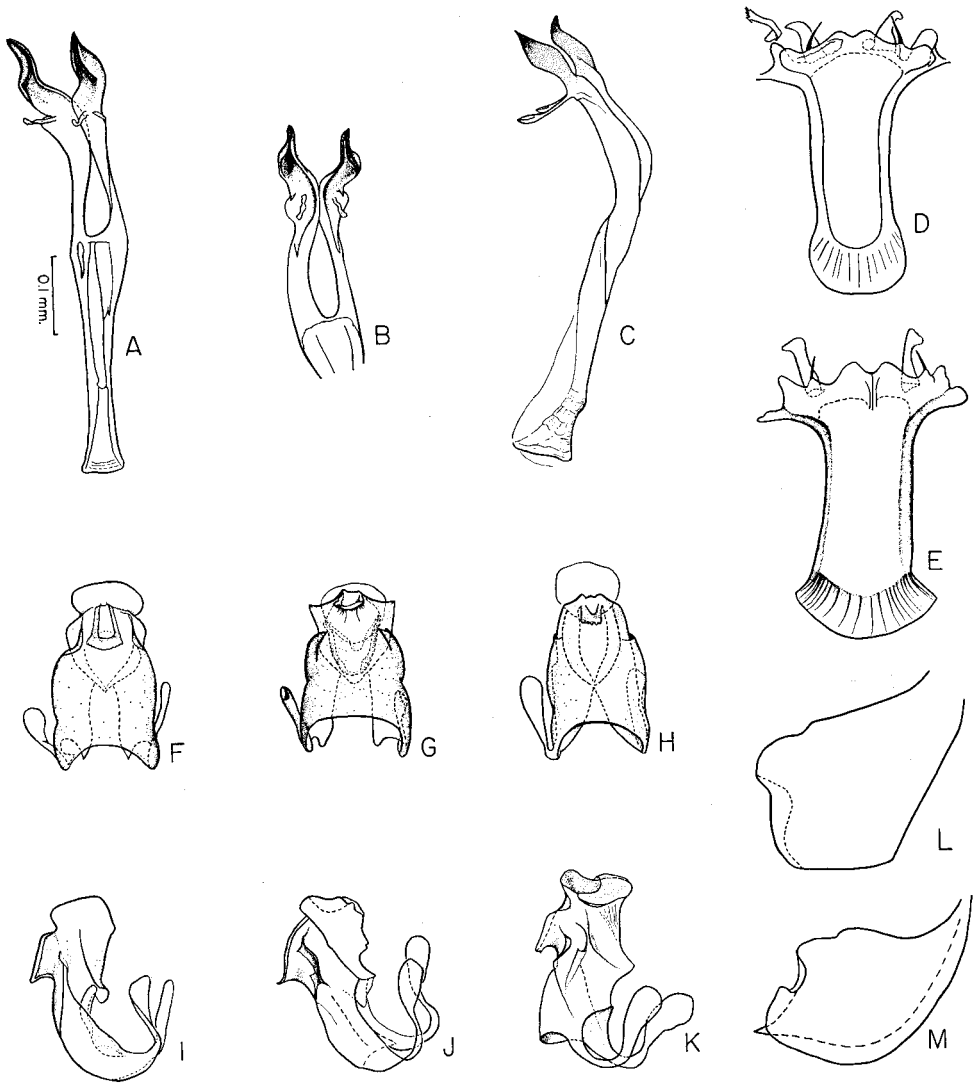


FIG. 7. Apodeme, pincers, hypandrium and penis of *pseudobocainensis*. Typical form (Boquete, Panama): A, B, D, F, I; variant from Popayan, Colombia: G, J; variant from Coroico, Bolivia: C, E, H, K. L, M—lower margin of genital arch of typical form (L) and of variant from Popayan (M).

not feel that it is advisable to designate these variants as distinct species. The male genitalia of type 1, characteristic of northern South America, are shown in Figure 7, G, J, M; type 2, from Bolivia, is shown in Figure 7, C, E, H, K.

Holotype male, allotype and ten paratypes, Boquete, Chiriqui Pr., PANAMA, June–July 1959, W. B. Heed and H. L. Carson. Also known from Cerro la Campana, Panama; Barro Colorado Is., CANAL ZONE; Volcan Santa Ana and Laguna Alegria, EL SALVADOR; and San José, COSTA RICA.

Type 1: Popayan, Colombia; 65 klm. southeast of Bogota, Colombia; Maracay,

Venezuela. Type 2: Coroico, Bolivia. The latter is possibly the same as *kerteszina* var. *boliviensis* Duda.

### Unnamed species 1

A single male, from near Melgar, about 30 klm. west of Girardot, Colombia, collected Nov. 1955 by W. B. Heed, is clearly different from the other known members of the complex. This male was teneral, showing little color. The genitalia are illustrated in Figure 8, A-C.

### Unnamed species 2

A single male, from Maracay, Venezuela, collected Nov. 1956 by M. Wasserman, has rather unique genitalia (Figure 9). The specimen was found among rather numerous individuals of *pseudobocainensis*, type 1, among which it was not recognized as being different until the male genitalia were examined.

### *Drosophila changuinolae*, new species

Mesonotum dull, dark tan, becoming distinctly more brownish on scutellum. Pleura browner than disc of mesonotum, especially on mesopleura, the sternopleura often a bit paler. Acrostichal hairs irregularly 6-rowed. Front dull tan, the orbits dull grayish yellow, the ocellar area blackish. Arista with 6 dorsal and 3 ventral branches basal to the terminal fork. Head bristles stout and black. Anterior reclinate orbital about  $\frac{1}{4}$  length posterior; face tan; carina rather large; 2nd oral bristle not quite as strong as first.

Two anterior sternopleurals thin, subequal, the posterior one long and stout.

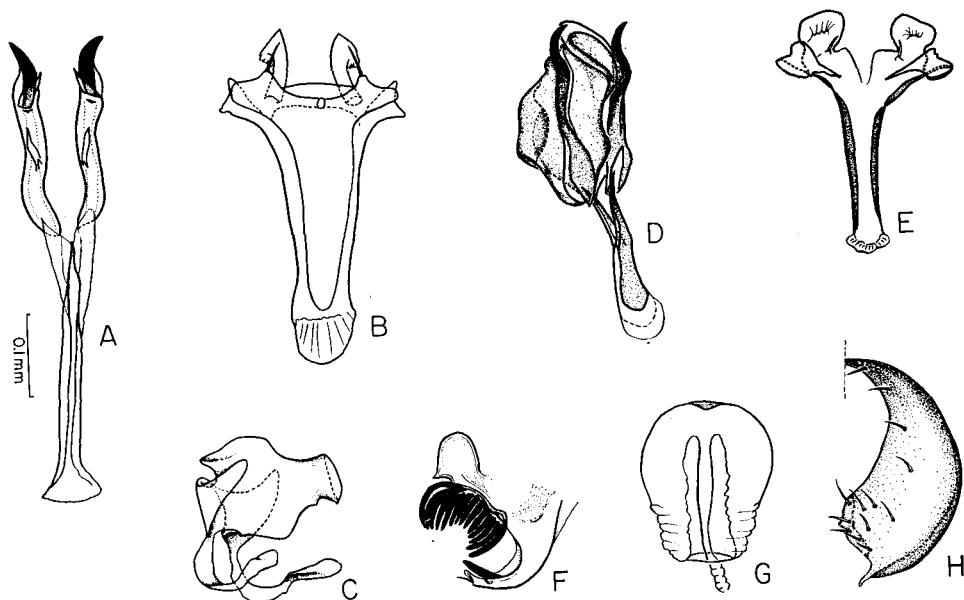


FIG. 8. Apodeme, pincer, hypandrium and penis of unnamed species from Melgar, Colombia: A-C. D-H, *D. changuinolae*.

Legs all tan. Abdominal tergites with dull brown apical bands, those of more posterior segments becoming larger and blacker.

Wings darkened, more so on anterior half; posterior crossvein with a narrow cloud. Costal index about 1.5; 4th vein index about 2.2. Body length about 2.0 mm.

The male genitalia and female spermatheca are shown in Figure 8, D-H.

Holotype male, allotype, and eleven paratypes, Changuinola, PANAMA, June-July 1959, W. B. Heed and H. L. Carson. Also known from Leticia, Amazonas, COLOMBIA.

*Relationships.* Belongs to the *willistoni* species group, within which it shows affinities in both external and genitalial characteristics with *D. mangabeirai* Malogolowkin. It is clearly not a member of the *alagitans-bocainensis* complex.

### ECOLOGY

Very little is known about the ecology of the species discussed here. Heed (1957) has made the most extensive ecological study of Central American *Drosophilidae* (principally in El Salvador), a study which included two species of this complex: *capnoptera* and *pseudobocainensis* (= *alagitans*-like of Heed). He reported on the composition of several micropopulations, defined as that group of flies collected over a definite, localized feeding site. Such sites were sometimes quite small, such as a single fallen fruit, or a single flower or fungus. On Volcan Santa Ana at an elevation of about 5000 feet, *capnoptera* and *pseudobocainensis* were elements of four of the seven micropopulations studied. The following table, extracted from his Table 9, shows the feeding sites involved and the number of individuals encountered:

	On acorns	On flowers	On figs	On drupes
Total no. flies	283	100	189	219
Per cent <i>capnoptera</i>	30%	3%	30%	---
Per cent <i>pseudobocainensis</i>	28%	---	---	20%

(Acorns: *Quercus skinneri*; flower: unidentified; figs: *Ficus* sp.; drupes: *Citharexylum donnell-smithii*).

The preponderance of *capnoptera* and *pseudobocainensis* over acorns is quite interesting in view of the fact that *pseudobocainensis*, type 2, from near Popayan, Colombia, was quite common in an oak grove; several hundred specimens were taken in less than an hour simply by sweeping with a net beneath the trees. Heed (*op. cit.*) felt that acorns, as such, were not actually used for egg deposition and larval development. However, *Chymomyza amoena* has been reared from acorns in eastern and central United States, so there is no reason to doubt that larvae of other species might not be similarly adapted to this food source.

### LITERATURE CITED

- Carson, H. L. 1954. Interfertile sibling species in the *willistoni* group of *Drosophila*. *Evolution* 8: 148-165.
- Duda, O. 1927. Die südamerikanischen *Drosophiliden* (Dipteren) unter Berücksichtigung auch der anderen neotropischen sowie der nearktischen Arten. *Arch. f. Naturg.* 91 A 11-12: 1-228.
- Heed, W. B. 1957. Ecological and distributional notes on the *Drosophilidae* (Diptera) of El Salvador. Univ. Texas Pub. 5721: 62-78.



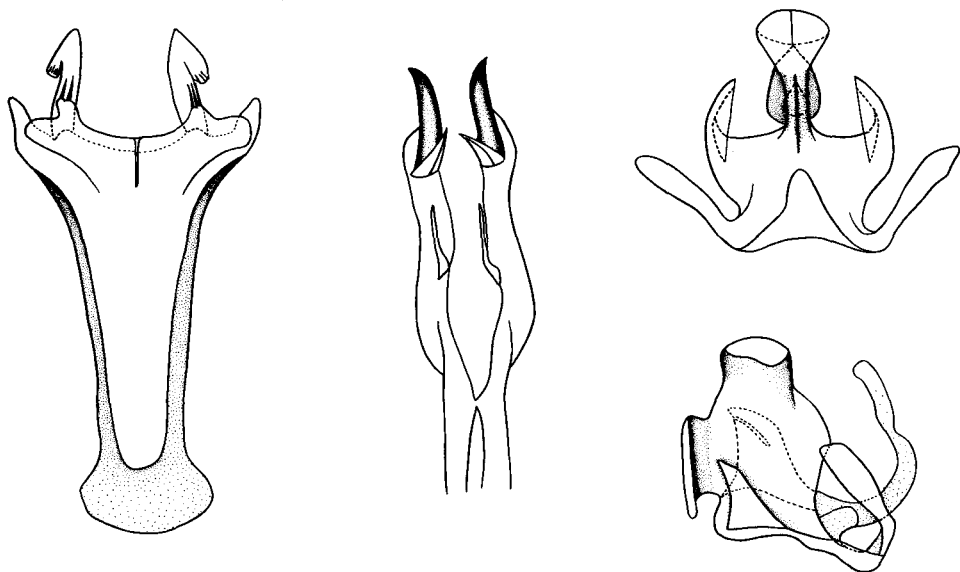


FIG. 9. Male copulatory apparatus of unnamed species from Maracay, Venezuela.

- Hsu, T. C. 1949. The external genital apparatus of male *Drosophilidae* in relation to sytematics. Univ. Texas Pub. 4920: 80-142.
- Malogolowkin, C. 1952. Sobre a genitalia dos *Drosophilidae* (Diptera): III. Grupo willistoni do genero *Drosophila*. Rev. Brasil. Biol. 12: 79-96.
- . 1958. Sobre a genitalia dos *Drosofilideos*. V. A genitalia masculina em "*D. mangabeirai*" (Diptera, *Drosophilidae*). Rev. Brasil. Biol. 18: 443-445.
- Nater, H. 1953. Vergleichend-morphologische Untersuchung des äusseren Geschlechtsapparates innerhalb der Gattung *Drosophila*. Zool. Jb. (Syst.) 81 (5-6): 437-624.
- Okada, T. 1955. Comparative morphology of the *Drosophilid* flies. II. Phallic organs of the subgenus *Drosophila*. Kontyu 23: 97-104.
- Patterson, J. T. 1943. The *Drosophilidae* of the Southwest. Univ. Texas Pub. 4313: 7-216.
- , and G. B. Mainland. 1944. The *Drosophilidae* of Mexico. Univ. Texas Pub. 4445: 9-101.
- Pavan, C., and A. B. da Cunha. 1947. Especies brasileiras de *Drosophila*. Bol. Fac. Fil. Cien. Letr. Univ. São Paulo 86: 3-46.
- Salzano, F. M. 1955. O problema das especies cripticas estudos no sub-grupo bocainensis (*Drosophila*). Boletim Inst. Ciencias Nat. 4 (Porto Alegre, Brasil): 1-88.
- . 1956. Chromosomal polymorphism and sexual isolation in sibling species of the bocainensis subgroup of *Drosophila*. Evolution 10: 288-297.
- Spassky, B. 1957. Morphological differences between sibling species of *Drosophila*. Univ. Texas Pub. 5721: 48-61.
- Wheeler, M. R. 1949. Taxonomic studies on the *Drosophilidae*. Univ. Texas Pub. 4920: 157-195.