

NOTES ON THE PHLEBOTOMUS OF PANAMA (Diptera, Psychodidae)

VII. THE SUBGENUS SHANNONOMYINA PRATT¹

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Subgenus *Shannonomyina* Pratt

- Shannonomyina* Pratt, 1947, Proc. Ent. Soc. Washington 49 (3): 86 (new name for *Shannonomyia* Dyar 1929).
Shannonomyia Dyar, 1929 (July), Amer. Jour. Hygiene, 10 (1): 117-118 (monotypic for *Phlebotomus panamensis* Shannon). Costa Lima, 1932, Mem. Inst. Oswaldo Cruz, 26 (1): 18 (no subgenera accepted). Mangabeira, 1942, Mem. Inst. Oswaldo Cruz, 37 (2): 119 (6 species included). Mangabeira and Galindo, 1944, Amer. Jour. Hygiene, 40 (2): 190 (subgenus redefined). Not *Shannonomyia* Alexander, 1929 (January), Dipt. Patagonia S. Chile, 1: 142-143 (Tipulidae).
Psychodopygus Mangabeira, 1941, Mem. Inst. Oswaldo Cruz, 36 (3): 237-238. (Type *Phlebotomus unisetosus* Mang., 1941).

This group has been variously treated. Accepted as a more or less valid subgenus by Mangabeira (1942), most other workers including Root (1934), Costa Lima (1932), Barretto (1947) and Floch and Abonnenc (1944) have admitted that the species form a group, but have refrained from using a name for it. Mangabeira and Galindo (1944) in their recharacterization of the group rely mostly on male characters, but as will be shown below, female characters appear to be more reliable for group separation. *Psychodopygus*, although striking enough in the male sex, has females very similar to typical *Shannonomyina*.

The group may be characterized as follows: *Phlebotomus* with palpal segments II and III long, subequal, IV very short, generally less than one-third of III, and V not more than twice as long as IV. Cibarium with four to eight horizontal teeth and usually with numerous erect teeth some of which are markedly enlarged. Pharynx unarmed. Abdomen usually covered with recumbent scale-like hairs. Spermathecae characteristic, consisting of six to ten or more deeply incised, imbricated rings and a more or less stalked terminal knob. Ducts of spermathecae long or short, arising from a common duct of variable length. Individual ducts, and usually part of common duct, characteristically wrinkled and sclerotized. Male genitalia without basal tuft on coxite, style with two to five spines, some of which may be reduced to fine setae. Lateral lobes usually as long as or longer than coxite, unarmed. Parameres simple to exceedingly complex, often

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with one or more tufts of modified setae and long digitate processes. Aedeagus stout to slender, genital pump and filaments of the usual type for the genus.

Since the spermathecae are of the greatest importance in this group, we give here a somewhat extended discussion of their structure.

Terminal knob.—We use this descriptive but noncommittal term in the absence of any recognized nomenclature based on a study of the histology of the spermathecae. The knob and its radiating "hairs" are constant, conspicuous and often characteristic structures in most groups of *Phlebotomus*. We have observed in a number of species, particularly in freshly caught specimens cleared in phenol, an envelope surrounding the spermathecae and at times the ducts as well. This envelope may be entirely clear or irregularly refractive in whole or in part. In the case of *paraensis* (fig. 16), for example, most of the envelope is perfectly clear, but there is a sharply delimited refractive area surrounding the terminal knob. It is possible that this represents glandular tissue and that the hairs are actually ducts. In some groups there is no knob at all and the hairs form a patch on the distal end of the spermatheca.

Annulations of spermatheca.—The terminal annulation may be indented or deeply incised on one side. In *panamensis* this characteristically gives rise to marked asymmetry, with a terminal knob bent to one side (fig. 13).

The annulations of the spermathecae show a characteristic pattern of sclerotization which is particularly evident in well stained specimens. We have figured this only for *paraensis* (fig. 17) but it also occurs in all the other species of this group which we have seen. This pattern is on the inward-turned portion of each annulation and takes the form of a band with distal projections, recalling the colored glaze of some pottery.

Duct.—The transition between spermatheca and duct may be marked by one or two small but otherwise typical annulations. In reckoning the number of annulations the judgment of different observers will undoubtedly vary as to the inclusion of the smaller ones. It is therefore well to consider the recorded counts as implying "plus or minus one or even two." The smaller annulations may be followed by several small, irregular or abortive annulations, which in turn give way to a series of evaginated pouches which may characterize a considerable length of the duct. These pouches may be greatly compressed and lie at an angle with the duct axis, so that in optical section they give the impression of a "herringbone" pattern (e.g., *squamiventris*, fig. 21). These pouches greatly complicate the task of making drawings. The characteristic appearance under the microscope at times depends on a more or less regular pattern seen at the focal level of the duct axis, which it is relatively easy to represent in a drawing (e.g., *squamiventris*, fig. 21, *paraensis*, fig. 18). In other instances the characteristic appearance is derived from the very confusion of successively superimposed images, with the lumen of the duct not obvious. In such cases we have elected to show in the drawings chiefly the outlines at the higher focal levels, i.e., the external features of the duct (e.g., *geniculatus*, fig. 15). The evaginated pouches sooner or later give way to ridgelike thickenings on the outside of the duct lining, which may or may not form complete rings.

In all the species we have examined, those portions of the ducts with the imperfect annulations, pouches and thickenings, are sclerotized and conspicuous whether in phenol or in stained preparations. In many species the sclerotized portion ends rather abruptly, with the result that the rest of the duct is thin-walled and often very difficult to see, either in phenol or after staining. In *squamiventris* (fig. 21) this transition takes place on the individual ducts, which are relatively long, whereas in all or nearly all the other species, the sclerotized portion includes part of the common duct or may even extend to its base. Thus it is seen that in this group where the spermathecae are strikingly similar, the ducts are very important taxonomically.

For the sake of convenience, we append here an annotated check list of the species of *Shannonomyia*. Only original or especially pertinent references are cited. For fuller reference the reader is referred to Barretto's catalogue (1947). The biological data are mostly from papers by Barretto and colleagues working in Sao Paulo.

CHECK LIST OF THE SPECIES OF *Shannonomyia*

- P. arthuri* Fonseca 1936, Rev. Ent., 6: 324, figs. 1, 2, 6, 8 (♀; Sao Paulo, Brasil); 1939, Mem. Inst. Butantan, 12: 181-184, figs. 1-3 (♂; Sao Paulo, Brasil). The species has been reared from the egg, though only females were secured, so the association of the sexes is not certain, though very probable. It bites man and domestic animals avidly, both by night and by day in the forest. It is attracted to light and enters houses. So far known only from the State of Sao Paulo, Brasil, where it is locally common.
- P. amazonensis* Root 1934, Amer. Jour. Hygiene, 20: 244, figs. 1, 2, 3, (♀; Iquitos, Peru). Known with certainty only from the type material.
- P. ayrozai* Barretto and Coutinho 1940, An. Fac. Med. Univ. S. Paulo, 16 (1): 131-134, plate I, fig. 2, plate II, figs. 6-10 (♂, Sao Paulo, Brasil); 1943, Rev. Brazil. Biol., 3 (2): 183-185, figs. 1-4 (♀; Sao Paulo, Brasil). Male and female taken in copula. Collected at light in several places in the State of Sao Paulo, Brasil.
- P. bispinosus* n. sp. (See this paper for description and discussion.)
- P. carrerai* Barretto 1946, An. Fac. Med. Univ. S. Paulo, 22: 286-291, figs. 8-16 (♂, ♀; Restrepo, Colombia). Taken in copula. Known only from the types.
- P. chagasi* Costa Lima 1941, Acta Medica, Rio, 7 (1): 6, 8, 11, 13-14, figs. 1, 3 and in key (♀; Rio Negro, Amazonas, Brasil). Known only from the inadequately described type.
- P. colas-belcourti* Floch and Chassignet 1947, Inst. Pasteur Guyane, pub. 152, pp. 1-3 and fig. (♂; French Guiana). Known only from the type.
- P. complexus* Mangabeira 1941, Mem. Inst. Oswaldo Cruz, 36: 242-245, fig. 3 and plate 2 (♂; Piratuba, Para, Brasil). Known only from the type.
- P. davisii* Root 1934, Amer. Jour. Hygiene, 20: 242-244, figs. 1, 2, 3, 5 (♂, Fordlandia, Para; ♀, Caravellas, Bahia, Brasil). Mangabeira 1941, Mem. Inst. Oswaldo Cruz, 36 (3): 249 (♂, ♀, Belem, Para, Brasil). Floch and Abonnenc 1944, Inst. Pasteur Guyane, pub. 90, pp. 11-12, fig. 8 (♂; French Guiana). This species has been taken in a number of other localities in Amazonas and Para. The Bahia females discussed by Root as well as females from Sao Paulo reported by others may or may not be properly associated.
- P. geniculatus* Mangabeira. (See this paper for full discussion.)
- P. guyanensis* Floch and Abonnenc 1941, Inst. Pasteur Guyane, pub. 15, pp. 17-20, fig. 6 (♀; French Guiana); *ibid.*, pub. 88, pp. 1-3, figs. 1-2 (♀; French Guiana). Known only from two female specimens from French Guiana.
- P. hirsutus* Mangabeira 1942, Mem. Inst. Oswaldo Cruz, 37 (2): 116-119, figs. 8-13 (♂, Para, Brasil). Known only from the type.
- P. Lloydii* Antunes 1937, Rev. Biol. Hig., 8: 24 (♀; Sao Paulo, Brasil). Coutinho, 1940, Arq. Zool. Est. S. Paulo, 1 (8): 331-333, figs. 1-3 (♂; Sao Paulo, Brasil). Barretto 1943, Observacoes sobre a biologia, em condicoes naturais, dos

- lebotomos do estado de Sao Paulo; Thesis, Univ. Sao Paulo, pp. 119-120. The species has been taken in fair numbers only in a few localities in south-eastern Sao Paulo. It enters houses occasionally, apparently attracted by light, but shows little inclination to bite man or laboratory animals and cannot be induced to feed on cold-blooded vertebrates. Rearing from eggs laid by captive females has not been successful, nor have matings been observed between the supposed sexes in captivity.
- P. maripensis* Floch and Abonnenc 1946, Inst. Pasteur Guyane, pub. 140, pp. 1-3, fig. 1 (♂, French Guiana). Known only from the type taken in the forest near the Brazilian border.
- P. panamensis* Shannon. (See this paper for full discussion.)
- P. paraensis* Costa Lima. (See this paper for full discussion.)
- P. rooti* Mangabeira 1942, Mem. Inst. Oswaldo Cruz, 37 (2): 112-115, figs. 1-7 (♂; Para, Brasil). Doubtfully distinct from *davisi* Root, as Mangabeira himself admits. Known only from the types.
- P. squamiventris* Lutz and Neiva. (See this paper for full discussion.)
- P. unisetosus* Mangabeira 1941, Mem. Inst. Oswaldo Cruz, 36 (3): 238-242, figs. 1, 2 and plate 1 (♂, Para, Brasil). Known only from the unique type.
- P. sp. no. 780* Floch and Chassignet 1948, Inst. Pasteur Guyane, pub. 170, pp. 1-2, fig. 1 (♀; French Guiana). This unnamed species is closest to *guyanensis* F. & A. and *bispinosus* n. sp. It differs from the first in much shorter individual ducts of the spermathecae and from the last in the much longer common duct. It differs from nearly all other described females in having the common duct completely sclerotized. It is quite likely the female of some known male, as the authors stated when they refrained from naming it.

As can be seen by the above list, the majority of the species are known only in a single sex, and there is some doubt as to the association of the sexes in some of those known in both sexes. Enough is known, however, to show that females with very similar spermathecae, palpi and cibaria may be associated with males of widely different genital structure. Grouping of the males on number of spines on the style or structure of the parameres does not yield groups homogeneous for other characters and is useful only for key purposes. The inclusion of *Psychodopygus* here rests on the finding (in Colombia) of the male of *squamiventris* L. and N., which turns out to be a species very close to *complexus* Mang., and of both sexes of *geniculatus* Mang. in Panama. It is probable also that *maripensis* F. and A. will turn out to be the male of *guyanensis* F. and A. or of "Species no. 780" of Floch and Chassignet.

There are a number of names in this group which appear to us of doubtful utility, but lacking adequate material we hesitate to discard them. It is possible that some may prove useful in a subspecific sense. Thus the differences between *hirsutus* Mang. and *colas-belcouri* Floch and Chass. consist in a slight difference in the position of the basal spine of the style while between *rooti* Mang. and *davisi* Root a slight difference in the relative lengths of the two arms of the paramere seems the only character separating the species. *Ayrozai* B. and C., *paraensis* C. L. and *carrerai* Barr. show a progressive development of the setae and arm of the paramere apparently correlated with geographical factors, but the females of *ayrozai* and *carrerai* are known with certainty, having been taken in copula, and are easily separated by the length of the individual ducts of the spermathecae. The female of *paraensis*, hitherto unknown, is described below.

We give below keys to males and females of the species here placed in *Shannonomyia*. We have studied material of both sexes of *panamensis*, *squamiventris*, *paraensis*, *geniculatus*, and *bispinosus* n. sp.

The other species are placed in the key on the basis of published descriptions, which in some cases have been inadequate. Thus we do not find adequate descriptions of the female cibaria of *chagasi*, *lloydi*, and *arthuri*. The first we have keyed out with *squamiventris*, as the original description seems to us inadequate. Costa Lima separates these two species on palpal measurements. The condition of the erect teeth in the cibaria of *lloydi* and *arthuri* seems not to have been described, so we have assumed they are as in *panamensis*. Should this be an error, they will key out with *amazonensis*, being easily separated by the number of horizontal teeth.

Males and females of the following species have been taken in copula or reared from eggs laid by known females: *carrerai*, *lloydi* and *ayrozai*. A single male of *squamiventris* was taken in an animal-baited mosquito trap with 50 females. No other species were present. Males of *panamensis* have been taken in Panama resting on humans in company with the biting females, in animal-baited mosquito traps as well as light traps, and there is little doubt as to the association of the sexes on morphological grounds as well. We have taken *geniculatus* males and females at light in a Shannon trap on a single occasion and in the absence of other species of this group, while both sexes of *paraensis*, were similarly secured. In the case of *davisi*, there is room for doubt as to the proper association of the sexes, as the male was from Para, while the female came from Bahia.

KEY TO MALES

- | | | |
|----|--|----------------------|
| 1. | Parameres simple. Style with two or four spines..... | 2 |
| | Parameres with modified setae or digitate processes, or style otherwise..... | 4 |
| 2. | Style with two terminal spines..... | <i>bispinosus</i> |
| | Style with four spines..... | 3 |
| 3. | Spines of style grouped closely near the end of the style, which is nearly as long as the coxite..... | <i>arthuri</i> |
| | Spines distributed as follows: two terminal, one subterminal, one near the middle of the style. Style short, hardly half length of the coxite..... | <i>lloydi</i> |
| 4. | Style with a single curved terminal spine and three slender subterminal setae..... | 5 |
| | Style with at least three strong spines. Parameres with strong modified setae and a digitate process..... | 9 |
| 5. | Parameres slender, ending in a slender upturned digitate process, without strongly modified setae or hair tufts. Coxite normal, about as long as style. Lateral lobes shorter than coxite..... | <i>geniculatus</i> |
| | Parameres stout, highly modified. Coxite inflated, constricted in middle..... | 6 |
| 6. | Parameres with a large tuft of long and numerous erect setae on a short, stout upturned arm and with a membranous foliaceous process at its apex..... | <i>unisetosus</i> |
| | Parameres otherwise..... | 7 |
| 7. | Parameres terminating in a long slender arm bent downwards at right angles to the basal part of the parameres and ending in a thin blade-like expansion..... | <i>maripaensis</i> |
| | Parameres otherwise..... | 8 |
| 8. | Parameres with a terminal, slender curved arm bearing a single delicate blade-like spine near its tip ² | <i>complexus</i> |
| | Parameres as above, but the arm bearing two spines ² | <i>squamiventris</i> |
| 9. | Style with five well developed spines. Parameres deeply biramous, the upper arm bearing heavy blade-like spines on its ventral surface..... | 10 |
| | Style with three well developed spines and a fine seta, which is sometimes spine-like, but always markedly slenderer than the other spines..... | 11 |

²These structures are difficult to describe and differentiation must be left to the accompanying figures.

10. Lower arm of paramere markedly longer than spine-bearing arm. *rooti*³
 Lower arm of paramere about equal to spine-bearing arm. *davisi*³
11. Parameres with two distinct tufts of blade-like setae on the upper surface
 and a terminal upturned arm bearing two long setae at its tip. Style
 with seta rather heavy, but more slender than other spines. *panamensis*
 Parameres with but a single tuft of setae. Seta of style very fine. 12
12. Setae of paramere long, numerous and blade-like. Arm long and slender,
 arising quite far towards the base of the paramere. *hirsutus*
 Setae of paramere not blade-like, less densely set. Arm arising at or near
 the apex of the paramere. *colas-belcouri*
13. Setae short, about 20 in number. Arm short, arising nearly terminally. *ayrozai*
 Setae longer, about 30 in number. Arm longer and arising further from
 the apex. *paraensis*
 Setae much longer, about 60, their area of implantation greater. Arm long,
 arising nearly terminally. *carrerae*

KEY TO FEMALES

1. Individual ducts of spermathecae longer than the bodies of the spermathecae. 2
 Individual ducts shorter than spermathecae. 5
2. Common duct of spermathecae much shorter than the individual ducts.
 Spermatheca with 8 annulations. *squamiventris*
 Common duct longer than individual ducts. *chagasi*
3. Individual ducts more than twice as long as spermathecae. Common duct
 very long, three to four times individual ducts and completely annulated.
 Spermatheca with 8 annulations. *guyanensis*
 Individual ducts less than twice as long as spermathecae. Common duct
 shorter, its distal part tenuous and but faintly annulated. Spermatheca
 with 6 annulations. 4
4. Palpal segments IV and V together about two-thirds as long as III. *geniculatus*
 Palpal segments IV and V together only slightly less than III. *ayrozai*
5. Erect teeth in cibarium subequal in size, the median ones not enlarged;
 four horizontal teeth. Spermathecae with about nine rings. *amazonensis*
 A double row of markedly enlarged erect teeth in the cibarium. 6
6. Terminal annulation of spermatheca markedly asymmetrical. 7
 Terminal annulation of spermatheca symmetrical or nearly so. 8
7. Cibarium with six horizontal teeth. *Hoydi*
 Cibarium with four horizontal teeth. Abdomen with scales dorsally.
 Mesonotum strongly infuscated. Palpal segments IV and V together
 about two-thirds as long as III. *panamensis*
8. Cibarium with eight horizontal teeth. Palpal segments IV and V together
 nearly equalling III. *arthuri*
 Cibarium with four horizontal teeth. 9
9. Common duct of spermathecae well sclerotized throughout, with clearly
 visible annular thickenings. Spermathecae with 7 to 8 annulations. 10
 Common duct of the spermathecae well sclerotized for only a short distance
 below the junction of the individual ducts, the rest membranous, poorly
 sclerotized and visible with difficulty even in stained preparations.
 Spermathecae with 9 to 13 annulations. 11
10. Common duct much thicker than individual ducts, about 3.5 times as
 long as the individual ducts. *bispinosus*
 Common duct hardly thicker than individual ducts, about 5.5 to 6 times
 as long as the individual ducts. Sp. No. 780
11. Palpal segments IV and V together equalling III. Mesonotum but slightly
 darker than pleura. *carrerae*
 Palpal segments IV and V less than III. 12
12. Abdomen without flat scale-like setae. Mesonotum hardly darker than
 pleura. Palpal segments IV and V together about five-eighths as long
 as III. *paraensis*
 Abdomen with numerous flat scale-like setae. Mesonotum somewhat
 infuscated. Palpal segments IV and V together about five-sixths as
 long as III. *davisi*

³These two species doubtfully distinct. No material seen.

Phlebotomus (Shannonomyina) panamensis Shannon

Figs. 1, 2, 13, 26, 27, 34, 35, 40, 51

1926, Jour. Washington Acad. Sci., 16 (7): 192-193, fig. 1 (♂, ♀; Cano Saddle, near Gatun, Canal Zone, and other localities in Panama and the Canal Zone). Barretto, 1946, An. Fac. Med. Univ. S. Paulo, 22: 279-282, 2 figs; 1947, Arq. Zool. Est. S. Paulo, 5 (4): 216-217 (complete references). Fairchild, 1949, An. Rep. Gorgas Mem. Lab., 1948, p. 12.

A medium sized sandfly with markedly infuscated mesonotum and the abdomen clothed with flat white recumbent scales. The male genitalia have not previously been adequately figured, the original sketch of Shannon being quite misleading. Stone's sketch in Barretto (1946) shows the proportions, but is admittedly diagrammatic and does not indicate the broad blade-like character of the setae on the parameres. Ascoids simple, not quite reaching the ends of their respective segments, paired on all segments, but absent from the terminal three segments in the female, the terminal six in the male. Terminal three segments in both sexes noticeably shortened, pear-shaped. Newstead's scales scattered sparsely over the distal two-thirds of palpal segment III. Eyes rather large in both sexes. Palpi as figured, those of the male about one-third shorter than the female. Stem of genital fork rather slender and pointed in dorsal view. Gonapophyses of the eighth sternite (Sinton, 1925) short and slender. Spermathecae as figured, the common duct mostly very thin-walled and difficult to see. Annulations of spermathecae variable in number, 10 to 11 in our material, though others show up to 13, the terminal annulation markedly asymmetrical. Cerci rather slender. Cibarium as figured. Pharynx fairly broad and well sclerotized, its posterior end provided with numerous fine transverse wrinkles, apparently beset with minute spinules. Venation as figured, the veins and margin bearing numerous fine long hairs but no scales, though the hairs at the extreme base of the costa are somewhat lorate.

This species is one of the more abundant biting species in Panama, where it attacks both man and domestic animals. We have examined 1075 specimens, of which 19 were males. The great majority of these specimens were taken in horse-baited stable traps, 744 specimens including 3 males; 256 specimens were taken at light, either light traps of the automatic type with fan, or in Shannon traps using a gasoline lantern; 11 of these were males. Sixty-four specimens have been taken biting man, all, with the exception of 5 from the Rio Bayano area which were perhaps taken indoors, secured in the forest. A lot of several species, including a male and female of *panamensis*, were secured in a pigsty and biting pigs; a single female was taken in the ruins of Old Panama; and a lot of 6 males and 2 females were taken in buttresses near Almirante.

From the foregoing it is evident that we know little or nothing of the normal haunts or diurnal resting places of the species. In spite of many hundreds of searches of the usual type of daytime resting places in areas where the females were quite abundant, either biting man in the forest or attracted to lights or animal-baited traps, we have only twice taken the species in such habitats. In the forest it bites readily during the daytime as well as at night. During the course

of recent studies of forest mosquitoes by our colleagues quite a number of *Phlebotomus* have been taken both at ground level and at platforms in the tree tops. *Panamensis* has been quite often taken, but only at ground level. Although we have done little serious collecting in houses, we have records of *Phlebotomus* biting in houses a number of times, but these have all proved to be *gomezi* Nitz. The specimens mentioned above from the Rio Bayano were collected by Dr. H. W. Kunn in 1942 and may have been taken indoors.

The species seems quite widely distributed in Panama, probably more widely than our records indicate, as collecting with light or animal bait has been limited to a relatively few localities. We have specimens from Bocas del Toro, Chiriqui, Colon and Panama Provinces, though the bulk of our material is from animal-baited traps in the Canal Zone and vicinity. We have taken the species in every month save March and April, though our records show a preponderance of specimens in July and August. It is probably a rainy season species.

The literature records the species from Panama, Venezuela, Colombia and Peru, but so far as we are aware, males have been taken only in Panama. Records based on the female alone are open to question due to the difficulty of separating the various species of this group in that sex. In addition, we have seen females of what we believe to be *panamensis* from Mexico and Venezuela.

Phlebotomus (*Shannonomyia*) *paraensis* Costa Lima

Figs. 8-10, 16-19, 30, 31, 37, 41, 42, 52

1941, Acta Medica, Rio de Janeiro, 7 (1): 7, plate 1, figs. 1-3, and text fig. 2 (♂; Ara, Belem, Para, Brasil; taken in a Shannon trap). Barretto, 1946, An. Fac. Med. Univ. S. Paulo, 22: 282-286, figs. 3-7 (♂, Piratuba, Abaete, Para, Brasil). Abonnenc, 1948, Inst. Pasteur Guyane, pub. 177, p. 1-3, fig. 2, A, B (type seen and figured).

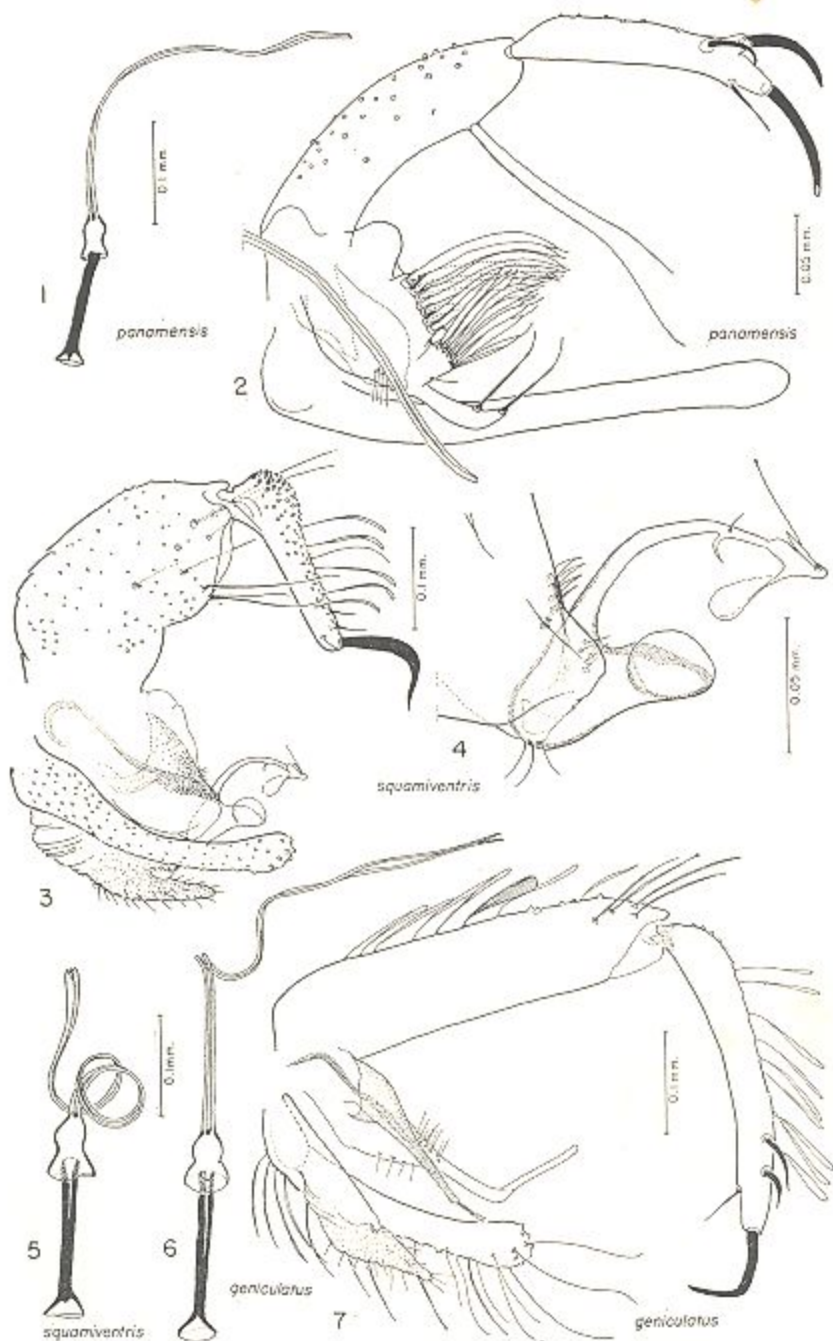
Phlebotomus ayrozai, Barretto and Pessoa, 1946, Livro homenagem a R. F. d'Almeida, p. 79 (in part). Barretto, 1947, Arq. Zool. Est. S. Paulo, 5 (4): 188 (in part).

A medium sized pale colored sandfly with rather large eyes. Abdominal hairs recumbent or semi-erect, not scale-like. Wing venation as figured, the veins and margins clothed with long hairs, with a few lorate or ligulate scales at base of costa. Palpi as figured, shorter in the male, and with the terminal segments relatively longer in this sex. Ascoids simple, slender, long, but not reaching the ends of their

EXPLANATION OF PLATE I

FIG. 1. *P. panamensis*, pump and genital filaments. FIG. 2. Same, male genitalia, inner aspect; the two long hairs on the coxite are apparently the same as the deciduous hairs on the outer surface, but one or two commonly persist in this position in our series of specimens. FIG. 3. *P. squamiventris*, male genitalia, outer aspect. FIG. 4. Same specimen, paramere. FIG. 5. Same species, pump and filaments. FIG. 6. *P. geniculatus*, pump and filaments. FIG. 7. Same, male genitalia, inner aspect.

All drawings in this and subsequent plates were made by the authors with the aid of the camera lucida from stained copal-balsam preparations, except as noted. Magnifications are indicated on the drawings. With the exception of the male genitalia, each series of the same structure was drawn at the same magnification.



respective segments; absent from the terminal three segments in the female, the terminal six in the male. Newstead's scales scattered sparsely over the distal two-thirds of palpal segment III.

Male genitalia as figured. Genital filaments slender, without modified tips, a little over three times as long as the pump. Female cibarium as figured. Pharynx broad, moderately sclerotized, with short, fine, digitate transverse ridges at its posterior end. Spermathecae as figured. Stem of genital fork long, slender and blunt. Gonapophyses of eighth sternite slender with a flaring membranous tip.

Our material differs in one respect from the descriptions of the two known specimens, both from Para, Brazil. Our specimens are uniformly pale yellowish, while both Para specimens are stated to have the mesonotum strongly infuscated. The position of the seta on the style varies somewhat, our figure showing a specimen with the seta placed quite far distally. Other specimens agree with the figures of Barretto and Costa Lima in this respect.

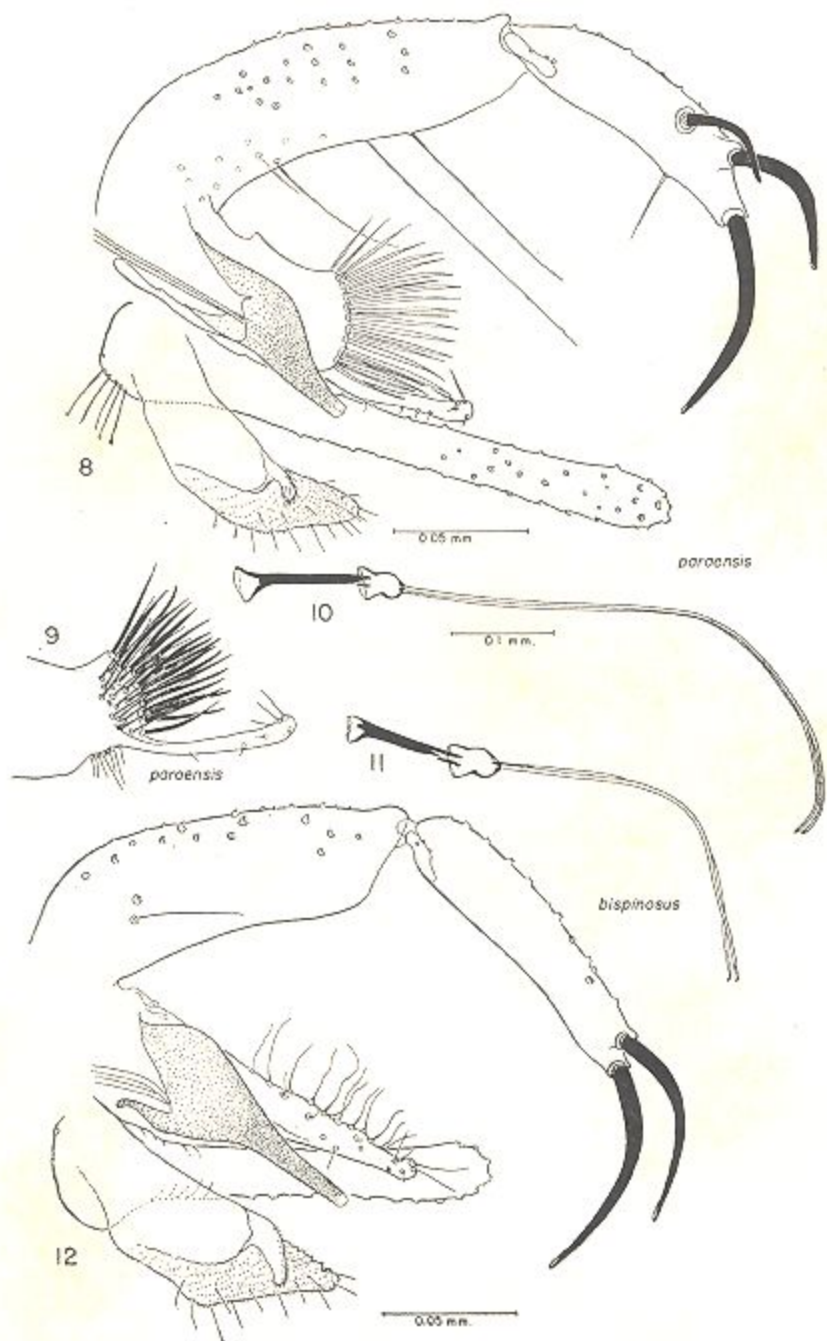
The females which we have associated with this species agree with the males in pigmentation, in lacking scales on the abdomen, and in wing measurements. Females were taken in numbers for some time before males were secured, our attention being attracted by their wholly pale color in contrast to the dark mesonotum of *panamensis*. Later both sexes were taken in Shannon light traps at a locality where the females had been taken abundantly biting man.

We have examined a total of 5 males and 129 females. Four males were taken in a light trap with 2 females, the other male was taken resting on a man, accompanying biting females. A single female was recovered from a lot of miscellaneous sandflies taken in buttresses, animal burrows and rock crevices. The remaining 126 females were all taken biting man in the forest during the daytime and at ground level. All the males and 102 of the females were taken at a single locality, Yellow Fever Station F, located in heavy forest at 1900 ft. elevation on the slopes of Cerro Campana, Panama Province. The remaining specimens were from the following localities in Panama: 2 ♀, Juan Mina, C. Z., 2 Sept., 1949; 1 ♀, 28 Oct., 1949; 1 ♀ Cacique, Colon Prov., 19 Sept., 1949; 1 ♀, upper Rio Pequeni, Panama Prov., 26 March, 1949, in buttresses or other crevices; 1 ♀, Yellow Fever Station X, Chorcha, Chiriqui Prov., 19 June, 1950, and 6 ♀, 19 Jan., 1951; 3 ♀, Yellow Fever Station A, Arraijan, Panama Prov., 5 June, 1950; 18 ♀ Candelaria Hydrographic Station, Rio Pequeni, Panama Prov., 14-23 August, 1950.

The majority of our specimens were taken in August with fair numbers in June and July, a few in September, one in October, 6 in January and one in March. This would indicate an early rainy season form, but too few light trap and biting collections have been made at

EXPLANATION OF PLATE II

FIG. 8. *P. paraensis*, male genitalia, inner aspect. FIG. 9. Same species, paramere of another specimen, outer aspect. FIG. 10. Same, pump and filaments. FIG. 11. *P. bispinosus*, pump and filaments. FIG. 12. Same, male genitalia, holotype.



suitable localities at other seasons for any definite statements to be made. The information available to date on this species indicates habits very similar to those of *panamensis*, but with more restricted habitat preferences.

Phlebotomus (Shannonomyia) bispinosus sp. nov.

Figs. 11, 12, 14, 28, 29, 36, 43, 46, 50

A medium sized sandfly with the mesonotum moderately infuscated and the eyes of average size. Abdomen with the tergites clothed with broad flat striate scales and with longer simple setae on the lateral and posterior margins. Sternites with only long semi-recumbent hairs. Second sternite as figured. Wings with venation as figured, clothed with long slender hairs, except at the base, where there are numerous large striate scales. Palpi as figured, those of the male a little more than half as long as those of the female. Newstead's scales sparse and long, scattered over the distal three-fourths of segment III. Ascoids as figured, absent from the terminal three segments in the female, the terminal six in the male.

Male genitalia as figured. Pump with expansion of plunger rather small (the "pavillon" of Parrot). Genital filaments rather stout, the distal fourth minutely annulate, tips simple, about twice as long as pump. Female cibarium as figured. Pharynx with numerous transverse minutely spinulose ridges at posterior end. Spermathecae as figured. Stem of genital fork broad and bladefike. Gonapophyses of eighth sternite slender and pointed.

Holotype male, slide 2344, La Victoria, Cerro Jefe, Panama, 29 Aug., 1950. Taken at light in a Shannon trap at Yellow Fever Station C, 1200 ft. elevation, in heavy forest. M. Hertig and P. Galindo colls.

Allotype female, slide 2359, same data as holotype.

Paratypes, 9 males, slides 2342-2343 and 2345-2351 and 9 females, slides 2352-2358 and 2360-2361, same data as holotype; 1 female, slide 2055, Juan Mina, Canal Zone, 20 Dec., 1949, in fan-type light trap, H. Trapido coll.; 3 females, slides 2383, 2386-2387, same data as holotype, but taken biting the collectors; 49 males, 33 females in alcohol, same data as holotype.

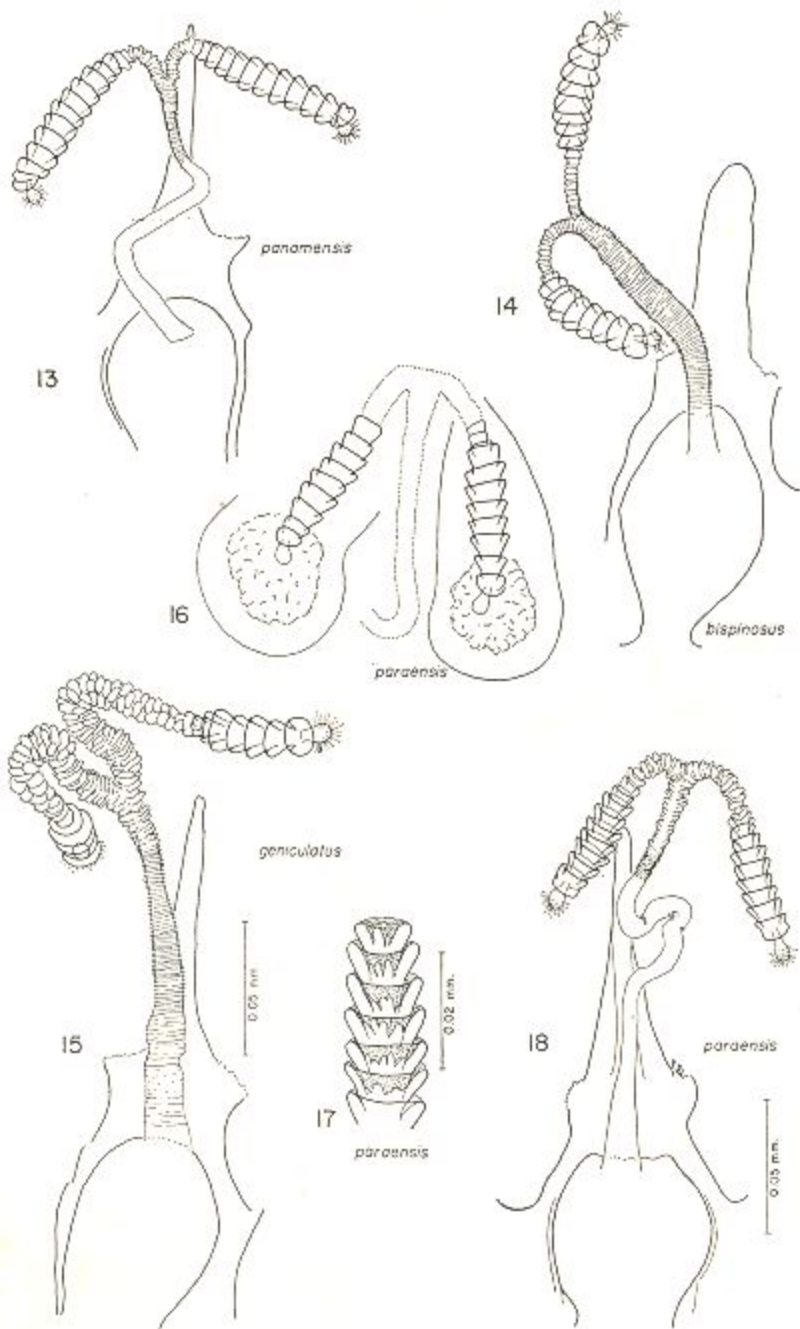
This species seems most closely related to *arthuri* Fons. in the male sex, having simple parameres and the spines of the style both nearly

EXPLANATION OF PLATE III

As will be noted from this plate and from figs. 21-23 of the next plate, the spermathecae of this group are strikingly similar, but the ducts show a number of distinct characteristics which are important taxonomically.

Figs. 13, 14, 15, 18, spermathecae, ducts and genital fork, dorsal aspect, all at the same magnification. FIG. 13. *P. panamensis*; note asymmetrical terminal annulation, terminal knob bent to one side. FIG. 14. *P. bispinosus*; note very broad stem of genital fork. FIG. 15. *P. geniculatus*. FIG. 18. *P. paraensis*.

FIG. 16. *P. paraensis*, freshly killed specimen in phenol; clear envelope surrounding spermathecae, with refractive area (glandular tissue?) surrounding terminal knob. FIG. 17. Same, detail of spermatheca, showing pattern of sclerotization, found also in the four other species figured in this paper.



terminal. In the female it most resembles the unnamed "Species no. 780" of Floch and Chassignet, differing in the shorter and thicker common duct of the spermathecae and in the spines of the cibarium not being laterally placed.

Phlebotomus (*Shannonomyia*) *geniculatus* Mangabeira

Figs. 6, 7, 15, 20, 32, 33, 38, 44, 47, 48

Phlebotomus (*Psychodopygus*) *geniculatus* Mangabeira, 1941, Mem. Inst. Oswaldo Cruz, 36 (3): 245-249 (σ^7 ; Belem, Para, Brasil, in horse-baited Shannon trap). Fairchild, 1943, Amer. Jour. Trop. Med., 23 (6): 571.

Phlebotomus geniculatus Barretto, 1947, Arq. Zool. Est. S. Paulo, 5 (4): 202.

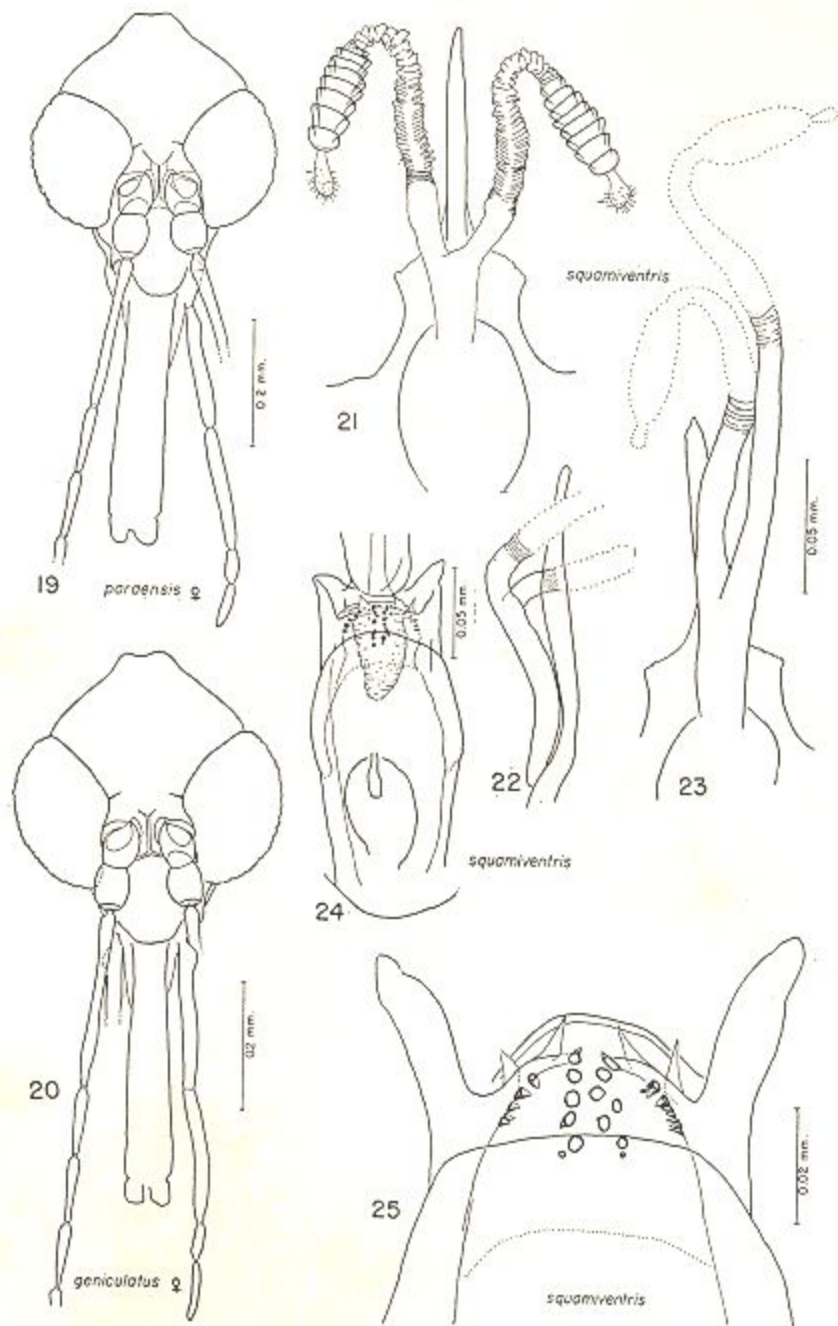
A medium sized sandfly with the mesonotum and abdominal tergites quite strongly infuscated. Eyes of average size for the genus. Tergites mostly clothed with semi-recumbent setae, a few of which, especially on the second and ninth tergites, are lorate or strap-shaped. Sternites with only long semi-recumbent hairs. Wings with venation as figured, clothed with long slender hairs except at the base, where there are numerous large striate scales. Palpi as figured, those of the male about one-fourth shorter than those of the female. Newstead's scales sparsely scattered over the distal three-fourths of palpal segment III. Ascoids as figured, absent from the terminal three segments in the female, the terminal six in the male. Second sternite as figured. Cerci of male quite acutely pointed, of female much less so.

Male genitalia as figured. Dorsal aspect of coxite and style with numerous moderately broad striate scales, and a few such scales scattered along the outer aspect of the lateral lobes. Pump long, the "pavillon" rather small. Genital filaments slender, tips simple, about three times as long as the pump. The genital filaments of this and the following species are sometimes coiled within the base of the genitalia. Female cibarium as figured. Pharynx rather broad and well sclerotized, with fine, transverse, minutely spinulose ridges at its posterior end. Spermathecae as figured. Ninth tergite with numerous ligulate scales mixed with the setae. Stem of genital fork thick and heavy, though not blade-like. Gonapophyses of eighth sternite heavy pointed rods.

The sexes of this species are associated on the basis of colorational and metrical characters and of a single collection of 3 males and 3 females taken at light in a Shannon trap, La Victoria, Cerro Jefe, 1 Sept., 1950, Yellow Fever Station D, 2100 ft. elevation, M. Hertig and P. Galindo colls. The relatively few other *Phlebotomus* taken on this occasion all belonged to unrelated groups. The single specimen previ-

EXPLANATION OF PLATE IV

FIG. 19. *P. paraensis*, head, female. FIG. 20. *P. geniculatus*, head, female. FIG. 21. *P. squamiventris*, spermathecae, ducts and genital fork, dorsal aspect. Note that sclerotized portion ends on individual ducts. FIGS. 22, 23. Same, spermathecae stained in phenol after KOH, showing bifurcation of ducts and termination of sclerotized portion; in fig. 23, ducts have been stretched in manipulating specimen. FIG. 24. Same, entire cibarium, female, showing armature, chitinous arch, pigment patch, salivary pump. FIG. 25. Same, cibarium, different female, showing detail of armature, pigment patch omitted.



ously reported (Fairchild, *l.c.*) as possibly being this species was lost before careful study of it could be made, but in view of the subsequent captures, it is probable that it belonged here. Our males do not differ discernibly from the figures and description of Mangabeira.

Phlebotomus (Shannonomyia) squamiventris Lutz and Neiva

Figs. 3-5, 21-25, 39, 45, 49

1912, Mem. Inst. Oswaldo Cruz, 4 (1): 89 (♀; Rio Trombeta and Para, Brasil). Franca, 1920, Bull. Soc. Portug. Sci. Nat., 8: 225 (♂, ♀; Matto Grosso, Brasil). Costa Lima, 1932, Mem. Inst. Oswaldo Cruz, 26 (1): 23-25, figs. 1, 2, 4, 5, 7, 8, 9, 41, 42, 68, 140, 141. Root, 1934, Amer. Jour. Hygiene, 20: 234-237 (♀; Santarem, Para, Brasil, and Iquitos, Peru). Galvao and Coutinho, 1940, Rev. Ent., 11 (1-2): 434 and figs. Costa Lima, 1941, Acta Medica Rio de Janeiro, 7 (1): 8-14. Ploch and Abonnenc, 1944, Inst. Pasteur Guyane, pub. 88, pp. 3-5, fig. 3. Barretto, 1947, Arq. Zool. Est. S. Paulo 5 (4): 224-225.

No species of American *Phlebotomus* seems to have given rise to as much discussion as this one. We have cited above only the more important references, as there seems no point in repeating here the full treatment given by Barretto (*l.c.*).

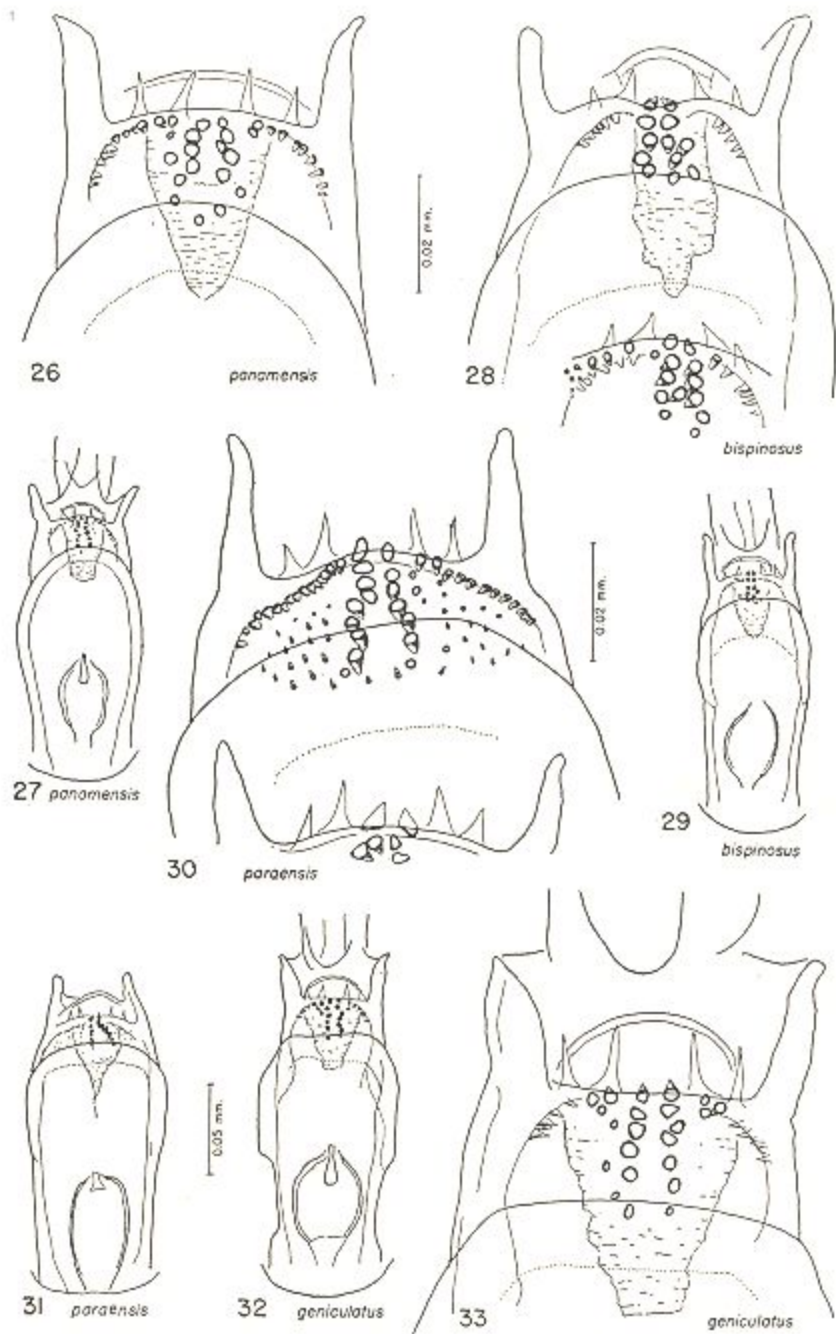
The material on which we base the following discussion consists of a male and about 50 female specimens, some of which we have mounted, the rest examined in phenol. This series was taken in a donkey-baited stable trap in Villavicencio, Intendencia de Meta, Colombia, 10 June, 1948, by Dr. C. Y. Chow. Dr. Chow informed us that these specimens represented the total catch of *Phlebotomus* in that trap for that night.

The original description of *squamiventris* by Lutz and Neiva (1912) is, as might be expected, inadequate by present standards, but the types are preserved at the Instituto Oswaldo Cruz. These specimens, all females, were collected on the Rio Trombeta, above Obidos in the State of Pará, by José Diniz and Adolpho Ducke, and another lot of many females was taken in Pará by Dr. Peryassu. The description based on this material was drawn up in December, 1911. Later Lutz and Neiva received additional material from northern Matto Grosso, in part labelled Salto Augusto, and collected by Dr. Murillo de Campos. These specimens consisted of many females and two males, the latter mouldy. Lutz and Neiva identified these as "*squamipennis*," an obvious misprint for *squamiventris*, in an appendix to their paper dated October, 1912, but gave no recognizable description of the male.

In 1919 Bonne-Wepster and Bonne reported the species from Surinam, but we have not seen this publication. Franca (1920) discussed the species and described the male from specimens sent him

EXPLANATION OF PLATE V

Female cibarium entire, showing armature, chitinous arch, pigment patch, salivary pump; detail of armature at higher magnification. The central rows or patch of very heavy erect teeth are characteristic of most of the group. Figs. 26, 27. *P. panamensis*, two different females. Figs. 28, 29. *P. bispinosus*, two females, with detail of armature of a third. Figs. 30, 31. *P. paraensis*, three females. A pair of erect teeth sometimes project so that there may appear to be six horizontal teeth, as in detail of armature forming part of fig. 30; pigment patch omitted in latter figure. Figs. 32, 33. *P. geniculatus*, same female.



by Lutz. This male appears to have been one of the two from Matto Grosso mentioned by Lutz and Neiva in the appendix to their paper. We have not seen this publication, but Costa Lima (1932) has discussed it and reproduced Franca's figure of the style.

Dyar (1939) in discussing the species claimed that the females studied by Franca were *rostrans* Summers, and only the male was *squamiventris*. He claimed to have seen specimens from Venezuela, sex not stated, but presumably males, and states that the fifth palpal segment was very long.

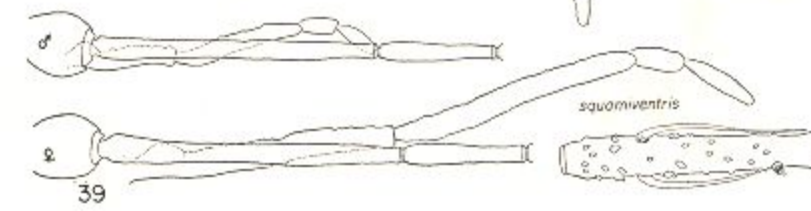
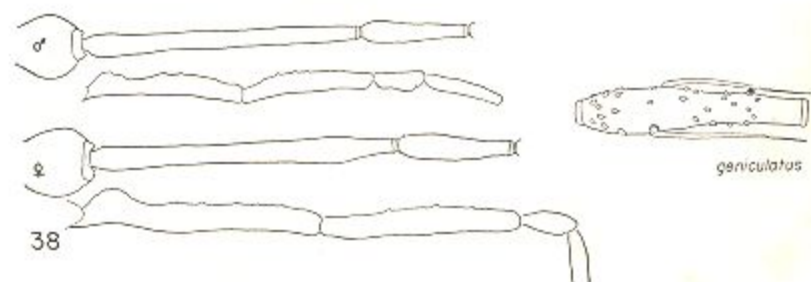
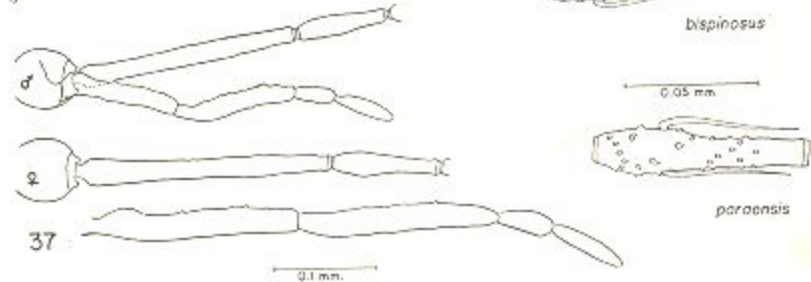
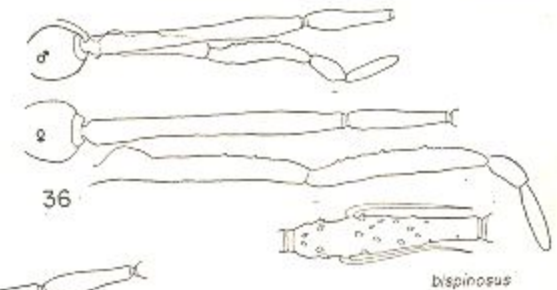
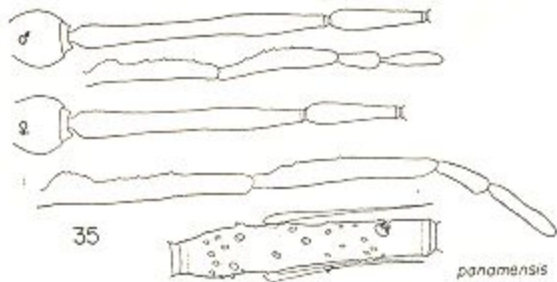
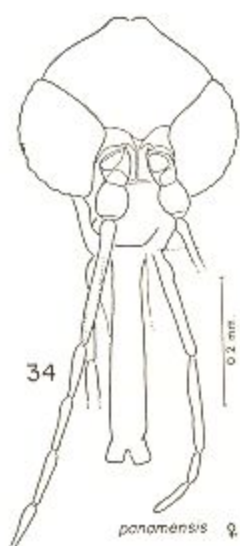
Pinto (1930) reproduced an unpublished figure by Lutz of the male terminalia of *squamiventris* which we have not seen, but which Costa Lima (1932) said agrees with Franca's figure.

In 1932 Costa Lima discussed the species at length after an examination of Lutz and Neiva's material and some additional material from Brasil and Venezuela. He concluded that all the material studied by Lutz and Neiva and by Franca, together with additional material from the Rio Negro collected by Carlos Chagas and from Venezuela, collected by Lutz, appeared to belong to a single species. Dyar's Venezuelan material Costa Lima believed to be *P. evansi* Tovar. He gave figures and measurements of the palpi of females from Matto Grosso, Para, Rio Negro and Venezuela, of the wings of Para and Matto Grosso specimens, and photomicrographs of the spermathecae of two Matto Grosso specimens. These photographs, especially figure 141, show that the sclerotized portion of the individual duct ends abruptly, with the evaginated pouches much compressed, giving the "herringbone" appearance characteristic of all our specimens (our fig. 21). So far as we are aware, in all other species of this group, with the possible exception of Root's species mentioned in the next paragraph, the sclerotization includes the entire length of the individual ducts and usually some of the common ducts as well.

Root (1934), treating the *Phlebotomus* with short fifth palpal segment, notes that the male described by Franca has palpi very different from the female and doubts that they are conspecific, but unlike Dyar, he realized that the name must be based on the female. He determined as *squamiventris* a female from Santarem, Para, and 8 females from Iquitos, Peru. He gave figures of palpi, cibarium, pharynx and spermathecae, unfortunately not stating whether they were made from the Para or Iquitos specimens. He was unable to see the bifurcation of the spermathecal ducts. This fact strongly indicates that the sclerotization did not extend to the bifurcation, a striking and uncommon character in this group. However, the rather slender ducts and their irregular coarse annulations do not correspond with the "herringbone" pattern of Costa Lima's and our specimens.

EXPLANATION OF PLATE VI

FIG. 34. *P. panamensis*, head, female. FIGS. 35-39. Antennal segments II-IV and palps, male and female, drawn to same scale; antennal segment IV with ascoids enlarged: fig. 35, *P. panamensis*; fig. 36, *P. bispinosus*; fig. 37, *P. paraensis*; fig. 38, *P. geniculatus*; fig. 39, *P. squamiventris*.



Galvao and Coutinho (1940) gave keys to males and females of the species of *Phlebotomus* then known from Brazil. The characters for the male appear to be those used by Franca (1920) and Costa Lima (1932), while the characters for the female were based on material presumably from Sao Paulo. The spermatheca of the female is figured in both a drawing and a photomicrograph.

Floch and Abonnenc (1944) gave descriptions and figures of what they considered *squamiventris*, based on females from French Guiana.

Costa Lima reviewed the problem again in 1941 and came to the conclusion that the types of *squamiventris* must be restricted to Lutz and Neiva's specimens from Para, that some of their females from Matto Grosso may be small specimens of *squamiventris*, but that those labelled "Salto Augusto" are a different species. The specimen from Rio Negro formerly (1932) considered by him to be *squamiventris*, he believed in the later paper (1941) to be different and named it *P. chagasi*, while Root's *squamiventris* he also believed to have been based on one or more different species. The Venezuelan specimen referred to *squamiventris* in 1932 he later considered to be *panamensis*. Costa Lima placed great emphasis on the lengths, both actual and relative, of the palpal segments and gave charts of palpal lengths of various specimens. It should be noted that the figures for palpal segments IV and V in this paper (1941) are reversed. The explanation of the figures would result in IV being longer than V, which is never so in this group.

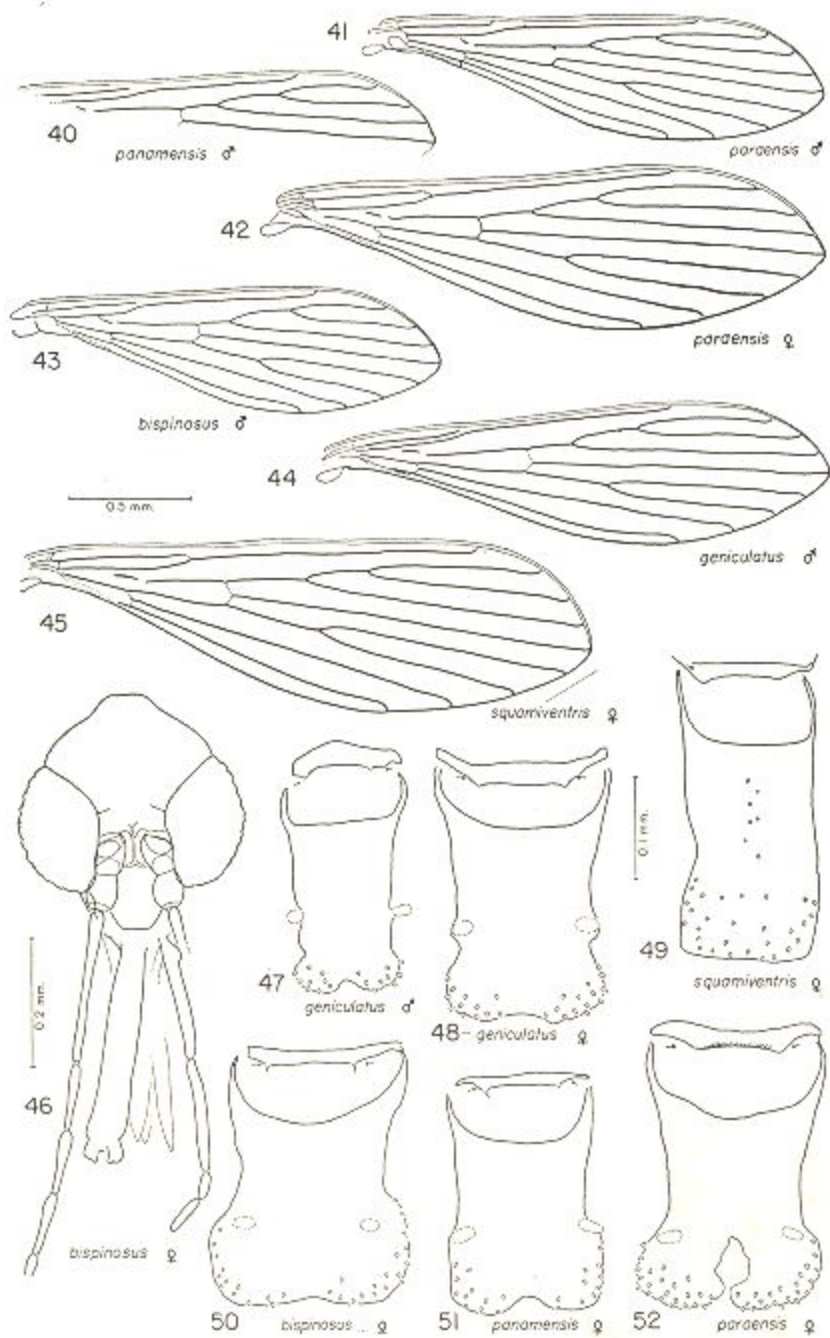
We have compared our female specimens with all the foregoing descriptions and figures and have concluded that they agree only with the specimens from Matto Grosso discussed by Costa Lima and considered by him to be probably small specimens of *squamiventris*. The palpi of our material range in total length, excluding the first segment for comparison with Costa Lima's measurements, from 522 micra to 586 micra. He gave 535 micra for the Matto Grosso specimens and 645 micra for those from Para. The length and character of the spermathecal ducts and the structure of the cibarium seem to us of utmost importance in this group, but unfortunately adequate descriptions or figures of these structures have not been given for true *squamiventris* from Para, for *chagasi* or for the other material discussed by Costa Lima. Root also was unable to make out the non-sclerotized parts of the ducts in his material. The portions of the ducts which he did see, however, are quite different from the comparable parts in our material. Root also stated that the pigmented patch in the cibarium of his specimens was faint or absent, while it is quite strongly marked in ours.

EXPLANATION OF PLATE VII

FIGS. 40-45. Wings: fig. 40, *P. panamensis*, male, costal portion; figs. 41, 42, *P. paraensis*, male and female; fig. 43, *P. bispinosus*, male; fig. 44, *P. geniculatus*, male; fig. 45, *P. squamiventris*, female.

FIG. 46. *P. bispinosus*, head, female.

FIGS. 47-52. Sternites I and II: figs. 47, 48, *P. geniculatus*, male and female; fig. 49, *P. squamiventris*, female; fig. 50, *P. bispinosus*, female; fig. 51, *P. panamensis*, female; fig. 52, *P. paraensis*, female.



The species whose spermathecae are figured by Galvao and Coutinho (1940) is obviously quite different, with much shorter, entirely sclerotized, individual ducts. Their figures, especially the photograph, show both spermathecae and ducts in their general form, proportions and sclerotization, to be very closely similar to *geniculatus* (our fig. 15). Floch and Abonnenc's (1944) figures are unfortunately printed on such poor paper that it is difficult to be sure of the character of the sclerotization of the ducts or of the number and arrangement of the erect spines in the cibarium. The measurements of the palpi and wing which they gave fit well with *squamiventris* and we believe it quite probable that they were dealing with true *squamiventris*.

The associated male we place here on the basis of the collecting data, the similarity of coloring and palpal formula, and the possession of an equally long delta. The only other species of American *Phlebotomus* with similar palpi, coloring, and wing venation are *unisetosus* Mang. and *complexus* Mang., both known only in the male sex. Our male is exceedingly close to *complexus*, differing only in details of the parameres. It is quite possible, of course, and indeed very likely, that *complexus* is in reality the male of *squamiventris*, since both were from near Belem, Para, and that our species is a closely allied form, perhaps *chagasi* C. L. In view of the close similarity of the females of this group it may prove impossible to find characters to differentiate the females of *complexus*, *unisetosus* and *squamiventris*. Lacking material of either *complexus* or *squamiventris* from near the type locality, and in view of the differences in our single male from the description of *complexus*, we hesitate to synonymize the two species. Although realizing that our male is distinct from any described species, the close correspondence of the associated females with *squamiventris* make it seem undesirable to erect a new name until the related species are better known. For purposes of comparison we give here a description and figure of our material.

A medium sized sandfly with conspicuously infuscated mesonotum. Eyes of average size for the genus. Tergites and sternites, except margins, apparently clothed largely with broad striated scales. Margins clothed with semi-recumbent setae. Wings with venation as figured, clothed with long hairs and at least some lorate striate scales at base. Palpi as figured, those of the female nearly twice as long as those of the male. Newstead's scales sparsely scattered over nearly the whole dorsal aspect of the third segment. Ascoids as figured, absent from the terminal three segments in the female, not certainly visible in the unstained male.

Male genitalia as figured. Dorsal aspect of style with numerous non-deciduous lorate scales, not all shown in our figure, a few of which appear to have been present on the coxite also. Pump large, the filaments slender, twice coiled within the base of the genitalia, their tips not clearly visible, but apparently somewhat inflated and annulate just before the tip. Filaments twice or somewhat less the length of the pump. Female cibarium as figured. Pharynx rather broad, with weak digitate processes at the posterior end. Spermathecae as figured. Ninth tergite with mixed lorate scales and setae. Gonapophyses of eighth sternite slender with somewhat falcate tips. Stem of genital

fork slender but blunt. Cerci of male rather slender and pointed, of female broader but quite acute.

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