

Taxonomic revision of phlebotomine sand fly species in the series *davisi* and *panamensis* of the subgenus *Psychodopygus* Mangabeira, 1941 (Diptera: Psychodidae: Phlebotominae)

Gustavo Mayr de Lima Carvalho⁺, Alda Lima Falcão, José Dilermando Andrade Filho

Laboratório de Leishmanioses, Centro de Pesquisas René Rachou-Fiocruz, Av. Augusto de Lima 1715, 30190-002
Belo Horizonte, MG, Brasil

Several species of the subgenus Psychodopygus Mangabeira, 1941 are known to be leishmaniosis vectors in Brazil. Some of them are morphologically similar, which makes their identification quite difficult concerning epidemiological studies. The aim of the current work is to study the morphology of adult specimens of the subgenus Psychodopygus, in accordance with the morphological similarity and still taking into account the epidemiological importance of some species. Thus 11 species have been studied, including four subspecies of adult specimens deposited in the phlebotomine collection of Centro de Pesquisas René Rachou-Fiocruz. Morphological characters found in the literature and new features observed in this study were recorded in a taxonomic discussion format. These characters make it easy to separate such species. Four taxa, previously considered as subspecies, were raised to the category of species.

Key words: *Psychodopygus* - Psychodidae - Phlebotominae

Certain members of the Psychodidae family are notorious vectors of leishmaniosis (Ward 1977), bartonellosis (Schultz 1968), and arboviroses (Tesh et al. 1974), diseases that have brought about many problems for humans living in Neotropical and other regions (Young 1979). The subfamily Phlebotominae includes all the Psychodidae of medical significance. Some authors consider the phlebotomine to be a separate family of their own, the family Phlebotomidae (Williams 1993).

From the perspective of leishmaniosis control, the study of the taxonomy and geographical distribution of species of phlebotomine is of great importance, due to their role in disease transmission, the prevalence of which has increased significantly in the past few decades. This is a result of constant alterations in the natural environment, caused mainly by the increasing process of urbanization, which has generated various endemic sites of concentration in non-forest regions, conferring a new and previously unknown feature on the epidemiology of this parasitosis.

The subgenus *Psychodopygus* Mangabeira, 1941 was named from three species previously described by the author species-type: *Flebotomus unisetosus*. Due to the fact that these species are distinguished by morphological characteristics of the genitalia, it was considered to be an entirely justifiable new subgenus. Thus this subgenus is characterized by variable coloration, completely pale to dark; simple antennal ascoids; very short palpomere 5, shorter than palpomere 3; large eyes; females cibarium

with 4-8 horizontal teeth, few to many vertical teeth, complete or incomplete arch; unarmed pharynx; imbricated spermathecae, i.e., with semi telescoped annulations; individual and apical part of common spermathecae ducts usually rugose or striated. The male genitalia presenting the coxite without persistent setae; style with 1-5 large spines; less developed spines or setae present or not; paramere simple to highly modified; lateral lobe without specialized setae (Young & Duncan 1994).

Species of the subgenus *Psychodopygus* are frequently grouped into three or more series, informally named and based upon morphological characteristics of the males and occasionally of the females (Fairchild 1955, Theodor 1965, Ortiz 1972, Martins et al. 1978, Young 1979, Ryan 1986). Reasons for turning this subgenus into genus were given by Forattini (1971, 1973), Ready et al. (1980), and Galati (2003), but this paper is in accordance with Lewis et al. (1977), Martins et al. (1978), and Young and Duncan (1994), who classify *Psychodopygus* as a subgenus of *Lutzomyia* França, 1924. They group the species of this subgenus in four series: *squamiventris*, males with the style presenting one terminal spine and three sub apical smaller setae; paramere with a sub transverse row of setae, direct upwards, near middle of structure at level of aedeagus and coxite bilobed or not; *guyanensis*, males presenting the style with one large terminal spine and three much shorter sub apical setae or spines; *davisi*, males presenting five spines in the style; *panamensis*, paramere without arched dorsal arm.

The subgenus *Psychodopygus* has a distribution restricted to jungle areas and, with some exception, is rarely found in the human domains. However the species of this subgenus are widespread in the Brazilian territory (Young & Duncan 1994) and some of them present substantial importance as a vehicle for leishmaniosis, since several species are anthropophilic and identified as vectors of this disease (Ryan et al. 1987). Some species in this sub-

Financial support: Pibic/CNPq, Fiocruz

⁺Corresponding author: gumayr@cpqrr.fiocruz.br

Received 3 May 2005

Accepted 15 February 2006

genus share morphological similarities, which bring about errors in their identification, leading, in some areas, to an incorrect epidemiological understanding of the disease. With the aim of helping to correct specific identification of the vectors, which is a pre-requisite for application of opportune strategies of prevention and control, in this paper we review and give new diagnostic characters for the separation of 11 species in this medically important subgenus allocated in the series *davisi* and *panamensis*.

MATERIALS AND METHODS

The material used for the taxonomic revision of species in the subgenus *Psychodopygus* belong to the scientific collection of phlebotomines located at Centro de Pesquisas René Rachou-Fiocruz, Belo Horizonte, state of Minas Gerais.

In the present work, 11 species were studied, including four subspecies of the subgenus *Psychodopygus*, according to the classification proposed by Young and Duncan (1994) who group them in four series: *squamiventris*, *guyanensis*, *davisi*, and *panamensis*.

The investigation of adult specimens was accomplished with an optical microscope, besides consulting the literature on this species. The priority in this revision was to observe structures proposed by Cipa Group (1991). Based on the analyzed structures, all the observable features in the specimens were noted in the form of a taxonomic evaluation. Thus, a characterization of closely related species was carried out in order to facilitate their distinction, without, nevertheless, specifically describing them in minutia.

The updated geographical distribution of every species involved in this study can be found in the publication of Aguiar and Medeiros (2003).

REMARKS

This research revised and validated 11 species as belong to the subgenus *Psychodopygus*. Three of them, *Lutzomyia (Psychodopygus) davisi* (Root, 1934), *Lutzomyia (Psychodopygus) amazonensis* (Root, 1934), and *Lutzomyia (Psychodopygus) clautrei* Abonnenc, Leger and Fauran, 1979, are allocated in the series *davisi* by Young and Duncan (1994), the other eight belong to the series *panamensis*. Four of these, considered as subspecies, are raised to the category of species: *Lutzomyia (Psychodopygus) hirsuta* (Mangabeira, 1942) (new status), *Lutzomyia (Psychodopygus) nicaraguensis* (Fairchild & Hertig, 1961) (new status), *Lutzomyia (Psychodopygus) carrerai* (new status) (Barretto, 1946), and *Lutzomyia (Psychodopygus) thula* Young, 1979 (new status). Beside these, we include in this review *Lutzomyia (Psychodopygus) ayrozai* (Barretto & Coutinho, 1940), *Lutzomyia (Psychodopygus) paraensis* (Costa Lima, 1941), *Lutzomyia (Psychodopygus) yucumensis* (Le Pont, Caillard, Tibayrenc, Desjeux, 1986), and *Lutzomyia (Psychodopygus) panamensis* (Shannon, 1926). We do not include *Lutzomyia (Psychodopygus) llanosmartinsi* (Fraiha & Ward, 1980) and *Lutzomyia (Psychodopygus) recurva* Young, 1973, which have a paramere with a characteristic arched dorsal arm and are easily distinguished. Moreover, we do not deal with *Lutzomyia (Psycho-*

dopygus) fairchildi Barretto, 1966 and *Lutzomyia (Psychodopygus) nocticola* Young, 1973, because the available material was not enough for comparison. However, new features observed in 11 species studied, which make easy to distinguish them, justify this work. Such characters, with other found in literature are presented in a taxonomic discussion, so that the most similar species are discussed together, thus simplifying the process of distinguishing among them.

TAXONOMIC DISCUSSION

Species in the series *davisi*

Lutzomyia (Psychodopygus) amazonensis

Lutzomyia (Psychodopygus) davisi

Lutzomyia (Psychodopygus) clautrei

In this series are included three species were males show five well developed spines on style. It is possible to distinguish each one by the following features: *L. (P.) amazonensis* shows a lateral-inferior dilation in aedeagus in the shape of "cheeks" (Fig. 1), while in *L. (P.) davisi*, it is not dilated (Fraiha et al. 1980) (Fig. 2). Aedeagus in *L. (P.) clautrei* shows no distinctive characteristics. Genital filaments in *L. (P.) amazonensis* are shorter than those of *L. (P.) davisi* (Fraiha & Ward 1980b). Another morphological feature that is crucial to separate among the three species is the paramere: in *L. (P.) amazonensis*, the lateral arm is thinner and the tuft is practically inserted in its whole extent; in *L. (P.) davisi*, this lateral arm is thicker and the tuft is uniformly inserted in the distal margin; in *L. (P.) clautrei*, the lateral arm is very characteristic and notably stout, as well as the principal lobe, with a more leafy tuft than the two other species (Abonnenc et al. 1979) (Fig. 3).

Another morphological character as thorax pigmentation and disposition of the spines on the style were observed and may help in the distinction of the three species, mainly when analyzed with the other characters mentioned above. However, these features may not be used individually in the distinction of the species of this series, since they present variations in several of the specimens studied. Regarding the thorax pigmentation, the follow-

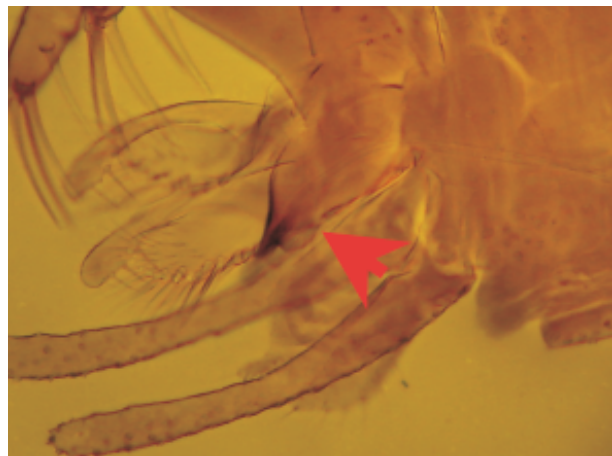


Fig. 1: *Lutzomyia (Psychodopygus) amazonensis*. Arrow showing the lateral-inferior dilation in aedeagus in the shape of "cheeks".

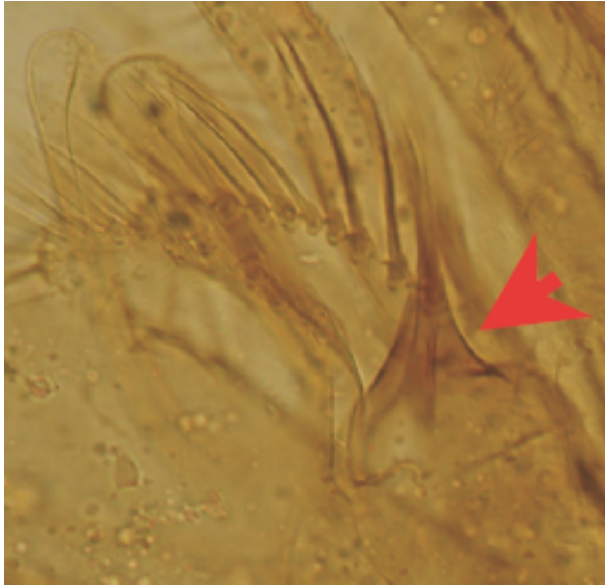


Fig. 2: *Lutzomyia (Psychodopygus) davisi*. Arrow showing the aedeagus without dilation.

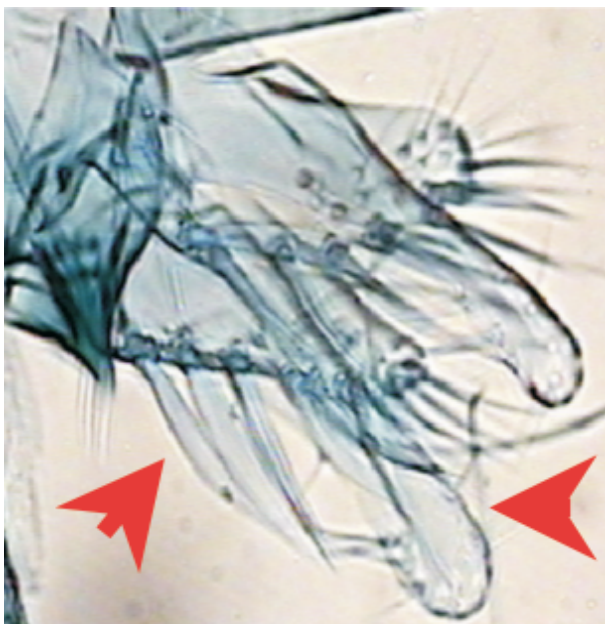


Fig. 3: *Lutzomyia (Psychodopygus) clauserei*. Arrows showing the digitiform appendix of the paramere and the bristles inserted at the principal lobe.

ing tendency was observed: *L. (P.) clauserei* presents scutellum, prescutum, and pronotum pigmented, whereas, in *L. (P.) davisi*, the scutellum is not pigmented and in *L. (P.) amazonensis*, prescutum and pronotum are not pigmented. Thus, in *L. (P.) davisi* the scutellum tends to be pale, though in various specimens this structure seems to be dark brown, but not too pigmented as in the other two species. On females the dark brown scutellum was more frequent. The distinction among the three species based on the position of the more basal spines of the style is

also not to be considered, because variations may occur inclusive at the same specimen. However, some specimens of *L. (P.) clauserei* present the inferior external spine and the internal one, inserted at the same level while in *L. (P.) amazonensis* and *L. (P.) davisi* the internal spine is more basal than the external one.

Females of the three species mentioned may be differentiated by spermathecae, common, and individual sperm ducts. *L. (P.) davisi* may be easily distinguished from, *L. (P.) amazonensis* and *L. (P.) clauserei* by the angle formed at the junction of the individual sperm ducts and by the chitinous area at the beginning of the rough part of the common sperm duct, that is absent in the two other species; furthermore *L. (P.) davisi* shows the common sperm duct longer and more chitinous than those of the two other species; *L. (P.) amazonensis* and *L. (P.) clauserei* show basically the same size of common sperm duct, but they may be distinguished by the number of rings of the spermathecae, being approximately eight in *L. (P.) clauserei* and about ten in *L. (P.) amazonensis*, such as in *L. (P.) davisi*. *L. (P.) amazonensis* and *L. (P.) clauserei* may also be distinguished by the length of the individual sperm ducts and the spermathecae: in *L. (P.) amazonensis*, the formers are approximately as long as the spermathecae and in *L. (P.) clauserei* they are shorter than spermathecae (Le Pont & Pajot 1980, Young & Rogers 1984).

Regarding the cibarium, the three species may be differentiated, mainly by the vertical teeth. However, it was observed that this character may present variation between specimens of the same species. Even so, this character may be useful to distinguish the females of these species, mainly when observed with other characters. The disposition and length of the vertical teeth present the following tendency: in *L. (P.) amazonensis*, are small and uniformly distributed into one to three transversal rows (Fig. 6); in *L. (P.) davisi*, most of the vertical teeth are small, but with a double longitudinal row with larger vertical teeth (Fig. 5); in *L. (P.) clauserei*, vertical median teeth are remarkably larger than the other ones and they generally form one or two longitudinal rows smaller than those in *L. (P.) davisi* (Fig. 4).

Species in the series *panamensis*

- Lutzomyia (Psychodopygus) ayrozai*
- Lutzomyia (Psychodopygus) paraensis*
- Lutzomyia (Psychodopygus) hirsuta* (New Status)
- Lutzomyia (Psychodopygus) nicaraguensis* (New Status)
- Lutzomyia (Psychodopygus) carrerai* (New Status)
- Lutzomyia (Psychodopygus) thula* (New Status)
- Lutzomyia (Psychodopygus) yucumensis*
- Lutzomyia (Psychodopygus) panamensis*

The species listed above belong to the group, were males show style with three strong spines and an atrophied one and the basal part of the paramere without an arched dorsal arm, but it shows a wide basal lobe, with one or two tufts of long bristles. This lobe shows a lateral digitiform prolongation, also called lateral arm. Females are very similar as for the cibarium and spermathecae (Martins et al. 1978). A taxonomic discussion of this group is yielded below.



Fig. 4: *Lutzomyia (Psychodopygus) claustreri*. Arrow showing the disposition of vertical teeth in the cibarium.

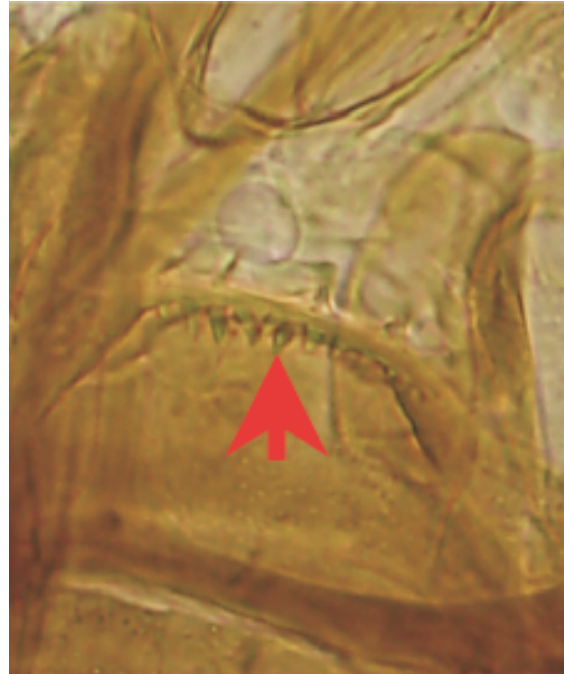


Fig. 6: *Lutzomyia (Psychodopygus) amazonensis*. Arrow showing the disposition of vertical teeth in the cibarium.



Fig. 5: *Lutzomyia (Psychodopygus) davisi*. Arrow showing the disposition of vertical teeth in the cibarium.

L. (P.) ayrozai presents thorax with pigmented mesonotum, contrasting with pale pleura. Clypeus is used to characterize species, which is very short when compared to other species. Males are distinguished from other members of the same group, mainly by the characteristic paramere, which is thick and short, half the length of

gonocoxite, with a round distal end of the principal lobe, covered with few slightly curved and thick bristles (around 20) and turned towards the genitalia apex (Fig. 7). Lateral arm is slightly strangled in its base, covered with straight, curved, and thin bristles, inserted in the superior and external side of the appendix. Still in paramere, just ahead the lateral arm insertion, about five straight, thin and short bristles are inserted on the inferior side of the principal lobe of the paramere (Barretto & Coutinho 1940).

The spines in the style are slightly different displayed when compared to the similar species: one apical; the external superior inserted in the distal end; the external inferior and the atrophied internal inserted in the middle of the structure (Barretto 1966). Genital filaments are thin and very long, with internally dilated ends.

Females may be distinguished mainly by the cibarium (Fig. 8), with four short horizontal teeth inclined towards the center at an angle of 45° and are frequently difficult to be visualized (Christensen & Fairchild 1971). Vertical teeth present approximately the same size and form a regular arch at the base of horizontal teeth. Spermatheca has 10-12 rings, with individual sperm ducts never exceeding the size of spermatheca and common sperm ducts with the apical third having a very visible striation.

The most closely related species of *L. (P.) ayrozai* is *L. (P.) paraensis*. The two males can be easily distinguished: *L. (P.) paraensis* has a very peculiar thorax pigmentation – mesonotum, first urotergite, procoxae, and pleurae just above these latter dark-brown, sharply contrasting with the rest of the body (Costa Lima 1941). Moreover, in the paramere, a little evident pigmented crest may be observed externally on its middle part (Fig. 9), from which three



Fig. 7: *Lutzomyia (Psychodopygus) ayrozai*. Arrow showing the principal lobe of the paramere.



Fig. 8: *Lutzomyia (Psychodopygus) ayrozai*. Arrow showing the cibarium.

spiniform bristles arise almost parallel to the paramere, while in other similar species this region is covered by short, thin, down-turned spiniform bristles. They are in higher number and never inserted in the crest (Martins et al. 1973). The principal lobe of the paramere has three or four thick irregular rows of bristles which apexes exceed the top of lateral arm (Barretto 1946). The lateral arm is broadened and slightly curved at the distal part, where a tuft of short bristles is inserted. In contrast to *L. (P.) ayrozai*, *L. (P.) paraensis* lateral lobe is slightly longer than coxite. Style shows one apical spine, two external

spines and the internal one closely inserted at the distal third (Barretto 1966).

L. (P.) paraensis females: characterized by common sperm duct which presents an sclerotized area as an inverted “V-shape” in the junction between smooth and rough parts (Fig. 10); it is also present in *L. (P.) yucumensis* and *L. (P.) carrerai*, but distinguishable from the latter by thorax pigmentation (Young 1979, Le Pont et al. 1986) which is completely brown, and also by a very peculiar cibarium with four horizontal teeth which are separated by a curved projection that extends until the pigmented area. Those horizontal teeth are a little inclined towards the center or not inclined at all, differently from that of *L. (P.) ayrozai*. Vertical teeth form two longitudinal rows, separated by the equal space among horizontal teeth, which arise at the exact site of their insertion. Each row is followed by other vertical teeth, all of them of the same size (Fairchild & Hertig 1951, Martins et al. 1973).



Fig. 9: *Lutzomyia (Psychodopygus) paraensis*. Arrow showing the pigmented crest of the paramere.

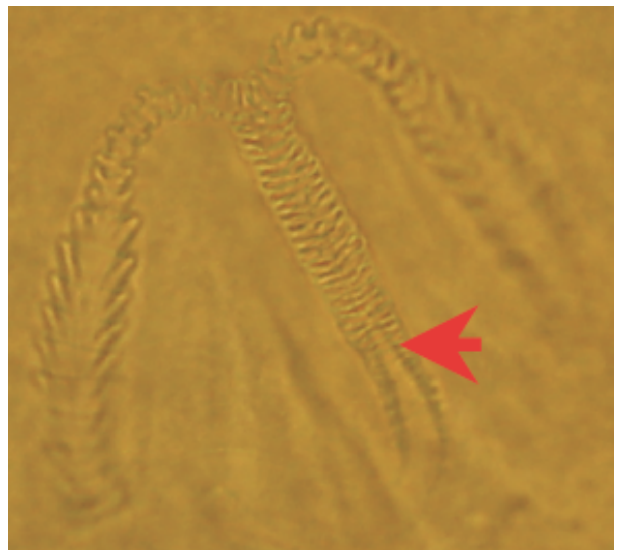


Fig. 10: *Lutzomyia (Psychodopygus) paraensis*. Arrow showing the inverted “V-shaped” in the junction between smooth and rough portions of the common sperm duct.

L. (P.) hirsuta and *L. (P.) nicaraguensis* are two species that belong to the group under discussion and are easily distinguished. Males show a characteristic paramere, where basal lobe shows a row of very wide bristles uniformly inserted in the distal end, and they usually exceed the lateral arm length (Mangabeira 1942). Females present the junction between individual and common sperm ducts wider, with an increasing diameter of the individual duct from the proximal to the distal region (Young 1979). Distinction between males of these species is based on the paramere features, such as the presence of bristles at the principal lobe, inserted on the posterior margin, which are more numerous and not very “spatula-shaped” in *L. (P.) nicaraguensis*. In contrast, *L. (P.) hirsuta*, shows less numerous and “leaf-shaped” bristles (Fig. 11). Only in *L. (P.) nicaraguensis*, at the dorsal-basal region of paramere, there is a strong spine-shaped bristle inserted in a prominent tubercle (Fairchild & Hertig 1961). A ventral tuft, inserted in a more basal region of paramere is also different in both species, consisting of more numerous bristles in the latter species.

The lateral arm in *L. (P.) nicaraguensis* is external and straight, with a thin spine at the distal region and a bristle inserted in its implantation. In *L. (P.) hirsuta*, however, it is more internally inserted with no bristle in its implantation. Style in *L. (P.) nicaraguensis* shows the external inferior spine inserted in a median position, while, in the other species this same bristle is inserted at the distal third (Barretto 1966).

Females may be easily separated by procoxae pigmentation, which is as dark as the mesonotum and the other coxae are pale in *L. (P.) nicaraguensis* and, in *L. (P.) hirsuta*, all coxae are pale (Young 1979) (Fig. 12). The cibarium is very similar in both species, however vertical teeth may distinguish them: in *L. (P.) nicaraguensis*, they form two longitudinal rows, and in *L. (P.) hirsuta* are more irregular. Common sperm duct is also very similar between these two species, however, it is partially rough in *L. (P.) hirsuta* and presents incomplete lines, while in *L. (P.) nicaraguensis* it is formed by distinct punctuations.

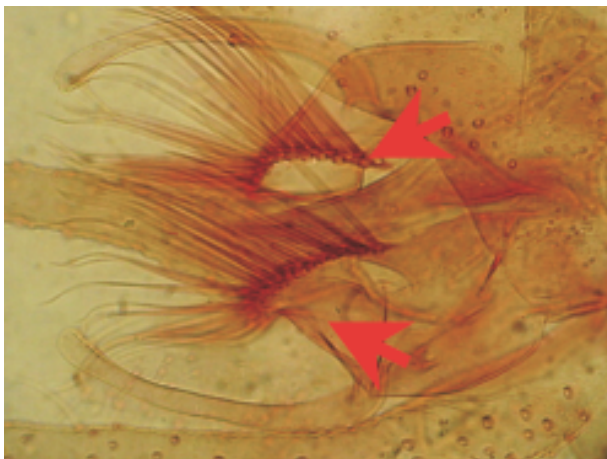


Fig. 11: *Lutzomyia (Psychodopygus) hirsuta*. Arrow showing the paramere features.



Fig. 12: *Lutzomyia (Psychodopygus) hirsuta*. Arrow showing the pigmentation in the thorax.

According to Lane (1988), the use of the subspecies concept would mirror a more philosophical part of the specialist than a biological particularity of the sand fly. The concept of subspecies refers to a differently known geographical population (Futuyma 2002); nevertheless, it is quite difficult or, yet, impossible, to know if those populations would mate in case of contact among them, so that such concept is strictly arbitrary, once many subspecies are taken into account with no biological evidence to support such fact (Lane 1988).

Thus, we believe that there are no biological and ecological data that prove the hypothesis of *L. hirsuta* and *L. nicaraguensis* as subspecies. Moreover, morphological differences between both species are very clear, mainly in males, which would be enough for a reproductive isolation between them, in case of sympatry.

L. (P.) carrerai and *Lutzomyia (P.) thula* are easily distinguished from the other species of the same series. Males show paramere with thin bristles displayed in numerous rows and thorax pigmentation completely pale. Females are separated from others of the same group by a combination of cibarium and spermatheca features together with a pale yellowish thorax. Distinction between males of these species has only been possible by comparing them with females and observing their geographical distribution, since they are morphologically similar, with no peculiar feature for distinction. However we believe that such as *L. (P.) hirsuta* and *L. (P.) nicaraguensis*, *L. (P.) carrerai*, and *L. (P.) thula* present no biological and ecological data that prove the hypothesis of subspecies.

To distinguish females an association of features can be used: the length of the labrum with the combination of the length of the pedicel and the first flagellomere. In *L. (P.) carrerai* the labrum is shorter than the sum of the pedicel and the first flagellomere. In contrast, the labrum of *L. (P.) thula* is much longer and is greater than the sum

of the pedicel + flagellomere I (Young 1979). As for the common sperm duct, in *L. (P.) thula* there is no inverted "V", formed by striation in the junction between the smooth and rough portions, which is normally observed in *L. (P.) carrerai*. This inverted "V" weakly extends towards the apex of the sperm common duct, becoming Y-shaped, which separates *L. (P.) carrerai* from *L. (P.) yucumensis* and *L. (P.) paraensis* (Le Pont et al. 1986). Another feature that may be used for distinction of these species is maxillary palpus length: much longer in *L. (P.) thula* than in *L. (P.) carrerai*, but for the males, morphometry is needed or further studies to detect possible differences.

L. (P.) yucumensis is easily distinguished from others of the same group by the paramere. Bristles inserted in the margin of the principal lobe are curved and leaf-shaped, not exceeding the lateral arm, form a posterior tuft, becoming "paint-brush-shaped". Lateral arm is long and thin, with a low number of bristles inserted both at the distal part and at the appendix base. Another feature used for distinction is the lateral lobe, which is very long, exceeding coxite length. Aedeagus is long and the distal part is dark. Females are more closely related to the species *L. (P.) carrerai*, being easily separated by thorax pigmentation, which shows a dark mesonotum in *L. (P.) yucumensis*, contrasting with a pale colored mesonotum of *L. (P.) carrerai*. Concerning common sperm duct, it has already been distinguished in the discussion above on *L. (P.) carrerai*.

Cibarium shows four horizontal teeth, the two median ones are larger and distant from each other. In the space between median horizontal teeth two longitudinal and irregular rows of vertical teeth arise, becoming divergent in the anterior position. On each side of the cibarium, anterior to the horizontal teeth, there is a thick row of short vertical teeth (Le Pont et al. 1986, Young 1979).

L. (P.) panamensis is the only species of the subgenus *Psychodopygus* in which the males show the basal lobe of paramere with a double tuft of bristles (Fig. 13): one proximal tuft with long, strong, and curved bristles and another distal one with short and thin bristles. Lateral arm, which arises from the basal region of the distal lobe, is curved towards the coxite with two subterminal strong spines, thorax with a very dark mesonotum, contrasting with the pleura, style shows an apical spine, an upper external and a lower external spine inserted at the distal third and the internal-atrophied spine implanted between the apical and the upper external spines.

Females are distinguished among other characteristics by a very characteristic cibarium, with four long horizontal teeth. The distance between the two median horizontal teeth is greater than that from the median to the lateral ones. Vertical teeth are large and irregular (Fig. 14). Spermatheca shows an asymmetric distal segment and 12 nearly overlapping rings, longer than the individual sperm ducts (Shannon 1926, Barretto 1946, 1966, Fairchild & Hertig 1951).

This taxonomic revision presents the difficulties of distinguishing some species of the subgenus *Psychodopygus* due to their morphological similarities, mainly concerning females. However using the main morphological features described in the literature as well as adding

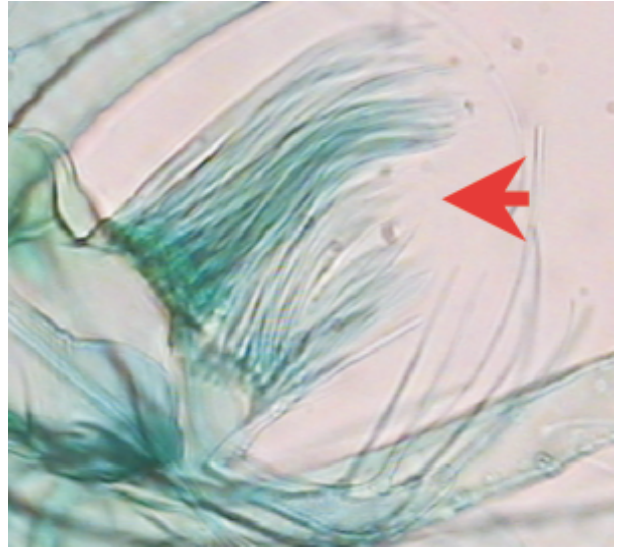


Fig. 13: *Lutzomyia (Psychodopygus) panamensis*. Arrow showing the double tuft of bristles in the paramere.



Fig. 14: *Lutzomyia (Psychodopygus) panamensis*. Arrow showing the vertical teeth of the cibarium.

some new characteristics it was possible to distinguish them, providing an accurate and specific identification. Nevertheless, not all species of the subgenus *Psychodopygus* were studied in this work, but virtually all species reviewed here are present in several places in Brazil, and many of them are part of the fauna of endemic regions for leishmaniosis, making necessary and important to accurately and specifically identify these species.

REFERENCES

- Abonnenc E, Léger N, Fauran P 1979. Sur deux nouveaux phlébotomes de la Guyane Française: *Lutzomyia yuilli pajoti* n. s. sp. et *Lutzomyia clautrei* n. sp. *Bull Soc Path Exot* 72: 75-86.

- Aguiar GM, Medeiros WM 2003. Distribuição regional e habitats de flebotomíneos do Brasil. In EF Rangel, R Lainson R (eds), *Flebotomíneos do Brasil*, Fiocruz, Rio de Janeiro, p. 207-255.
- Barretto MP 1946. Uma nova espécie de flebotomo da Colômbia e chave para a determinação das espécies afins (Diptera, Psychodidae). *Ann Fac Med Univ São Paulo* 22: 279-293.
- Barretto MP 1966. Estudo sobre flebotomíneos americanos. I. Notas sobre espécies de *Lutzomyia* França, subgênero *Psychodopygus* Mangabeira, 1941, com a descrição de uma nova espécie (Diptera, Psychodidae). *Pap Avul São Paulo* 18: 133-146.
- Barretto MP, Coutinho JO 1940. Contribuição ao conhecimento dos flebotomos de São Paulo II. Descrição do macho de *Phlebotomus limai* Fonseca, 1935 e de duas novas espécies: *Phlebotomus ayrozai* e *P. amarali* (Diptera, Psychodidae). *Ann Fac Med Univ São Paulo* 16: 127-139.
- Christensen HA, Fairchild GB 1971. *Lutzomyia tintinnabula* n. sp. (Diptera: Psychodidae) from Panamá. *J Med Ent* 8: 301-303.
- Costa Lima A 1941. Um novo *Flebotomus* da Amazônia e considerações relativas as espécies afins (Diptera: Psychodidae). *Acta Med* 7: 3-19.
- Fairchild GB 1955. The relationships and classification of the Phlebotominae (Diptera: Psychodidae). *Ann Entomol Soc Am* 48: 182-196.
- Fairchild GB, Hertig M 1951. Notes on the *Phlebotomus* of Panama (Diptera, Psychodidae). VII. The subgenus *Shannonomyia* Pratt. *Ann Ent Soc Amer* 44: 399-421.
- Fairchild GB, Hertig M 1961. Three new species of *Phlebotomus* from Mexico and Nicaragua (Diptera: Psychodidae). *Proc Ent Soc Wash* 63: 22-28.
- Forattini OP 1971. Sobre a classificação da subfamília Phlebotominae nas Américas (Diptera: Psychodidae). *Papéis Avulsos*, São Paulo, 24: 93-111.
- Forattini OP 1973. *Entomologia Médica*, Edgard Blucher, São Paulo, 658 pp.
- Fraiha H, Ward RD 1980. Caracterização do macho de *Psychodopygus amazonensis* (Root, 1934) (Diptera, Psychodidae, Phlebotominae). *Rev FSESP* 15: 15-19.
- Fraiha H, Ward RD, Quintana J 1980. Taxonomia de *Psychodopygus amazonensis* (Root, 1934) (Diptera, Psychodidae, Phlebotominae). *Rev FSESP* 15: 5-9.
- Futuyma DJ 2002. *Biologia Evolutiva*, Sociedade Brasileira de Genética, Ribeirão Preto, 631 pp.
- Galati EAB 2003. Classificação de Phlebotominae. In EF Rangel, R Lainson R (eds), *Flebotomíneos do Brasil*, Fiocruz, Rio de Janeiro, p. 23-51.
- Grupo Cipa - Bermudes H, Dedet JP, Falcão AL, Feliciangeli D, Ferro C, Galati EAB, Gomes EL, Herrero MV, Hervas D, Lebbe J, Morales A, Oguzuku E, Perez E, Rangel EF, Sherlock IA, Torres M, Vignes R, Wolff M. 1991. Proposition of a standard description for Phlebotomine sand flies. *Parasitologia* 33 (Suppl.): 127-135.
- Lane, RP 1988. Geographic variation in Old World phlebotomine sandflies. In MW Service, *Biosystematics of Haematophagous Insects*, Oxford, p. 77-90.
- Le Pont F, Caillard T, Tibayrenc M, Desjeux P 1986. Bolivian phlebotomines. II. *Psychodopygus yucumensis* n. sp., a new man-biting phlebotomine sandfly from subandean region (Diptera, Psychodidae). *Mem Inst Oswaldo Cruz* 81: 79-85.
- Le Pont F, Pajot F-X 1980. Description de la femelle de *Lutzomyia clautrei* Abonnenc, Léger et Fauran, 1979 (Diptera, Psychodidae). *Cah ORSTOM Ser Ent Med Parasit* 18: 61-65.
- Lewis JD, Young DG, Fairchild GB, Minter DM 1977. Proposals for a stable classification of the phlebotomine sandflies (Diptera: Psychodidae). *Syst Entomol* 2: 319-332.
- Mangabeira O 1942. Contribuição ao estudo dos *Flebotomus* (Diptera: Psychodidae). Descrição dos machos de 24 novas espécies. *Mem Inst Oswaldo Cruz* 37: 226-240.
- Martins AV, Falcão AL, Silva JE 1973. Sobre *Lutzomyia* (*Psychodopygus*) *paraensis* (Costa Lima, 1941) e algumas espécies afins (Diptera, Psychodidae, Phlebotominae). *Rev Brasil Biol* 33: 411-418.
- Martins AV, Williams P, Falcão AL 1978. *American Sand Flies* (Diptera: Psychodidae, Phlebotominae), Acad Bras Ciên, Rio de Janeiro, 195 pp.
- Ortiz I 1972. Revision de los flebotomos Americanos del subgênero *Psychodopygus* Mangabeira, 1941 (Diptera: Psychodidae). *Rev Inst Nac Hyg Caracas* 5: 221-249.
- Ready PD, Fraiha H, Lainson R, Shaw JJ 1980. *Psychodopygus* as a genus: reasons for a flexible classification of the phlebotomine sand flies (Diptera: Psychodidae). *J Med Entomol* 17: 75-88.
- Ryan L 1986. *Flebotomos do Estado do Pará, Brasil* (Diptera: Psychodidae: Phlebotominae), Tech. Doc. No. 1, Instituto Evandro Chagas, Belém, 154 pp.
- Ryan L, Shaw JJ, Braga RR, Ishikawa EAY 1987. Leishmaniasis in Brazil. XXV. Sandfly vectors of *Leishmania* in Pará State, Brazil. *Med Vet Entomol* 1: 383-395.
- Schultz MG 1968. A history of bartonellosis (Carrion's disease). *Am J Trop Med Hyg* 17: 503-515.
- Shannon RC 1926. The occurrence of *Phlebotomus* in Panama. *J Wash Acad Sci* 16: 190-193.
- Tesh RB, Chaniotis BN, Peralta PH, Johnson KM 1974. Ecology of viruses isolated from Panamanian phlebotomine sandflies. *Am J Trop Med Hyg* 23: 258-269.
- Theodor O 1965. On the classification of American Phlebotominae. *J Med Entomol* 2: 171-197.
- Ward RD 1977. New World leishmaniasis: a review of the epidemiological changes in the last three decades. *Proc XV Int Congr Entomol Washington*, p. 505-522.
- Williams P 1993. Relationships of phlebotomine sand flies (Diptera). *Mem Inst Oswaldo Cruz* 88: 177-183.
- Young DG 1979. *A Review of the Bloodsucking Psychodid Flies of Colombia* (Diptera: Phlebotominae and Sycoracinae), Tech. Bull. 806, Agric. Univ. Florida, Gainesville, 226 pp.
- Young DG, Duncan MA 1994. *Guide to the Identification and Geographic Distribution of Lutzomyia Sand Flies in Mexico, the West Indies, Central and South America* (Diptera: Psychodidae). *Mem Am Entomol Inst* 54, Associated Publishers, 881 pp.
- Young DG, Rogers TE 1984. The phlebotomine sand fly fauna (Diptera: Psychodidae) of Ecuador. *J Med Ent* 21: 597-611.