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Review of American Fossil Phlebotominae (Diptera: Psychodidae) with a Description of Two New Species

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The subfamily Phlebotominae constitutes a group of insects of importance to public health, because several of its species are vectors of bacteria, viruses, and especially *Leishmania*, protozoans implicated as etiological agents of leishmaniasis worldwide. Thus, motivating biological, ecological, and systematic studies of its various species.

Slightly >900 species or subspecies, inhabiting different ecosystems, have been described, ≈500 of them occurring in the Neotropical region of the world. The great morphological and ecological diversity of the phlebotomines undoubtedly reflects their long evolutionary history, the group having arisen on earth 250–300 million years (myr) ago (Andrade Filho and Brazil 2003). As a consequence of this long evolutionary history, these insects present morphological variations that reflect their adaptation to diverse environments.

Although members of the family Psychodidae are small insects, the fossil record of the group has been documented (Brazil and Andrade Filho 2002), specimens having been found most commonly in amber from the Tertiary period (Azar et al. 1999).

Approximately 48 species of Psychodidae fossils had formally been described by 1994, 6 of them being Phlebotominae. However, with the recent description of more species (Azar et al. 1999; Brazil and Andrade Filho 2002; Andrade Filho et al. 2004, 2006a, b, 2007, 2008; Poinar 2004; Peñalver and Grimaldi 2005), this number has increased to 15.

*Phlebotomites brevifilis* Hennig, 1972; *Phlebotomites longifilis* Hennig, 1972; *Mesophebotomites hennigi* Azar, Solignac, Paicheler, and Bouchet, 1999; and *Libanophlebotomus lutfallahi* Azar, Solignac, Paicheler, and Bouchet, 1999 have been described from Leba-

nese cretaceous amber (Hennig 1972, Azar et al. 1999). *Phlebotomiella tipuliforme* (Meunier, 1905) has been described from Baltic tertiary amber (Meunier 1905). Another species described from the Cretaceous period is *Palacomyia burnensis* Poinar, 2004, found in Burmese amber (Poinar 2004).

The other species of sand fly found in amber belonging to extant genera are *Phlebotomus pungens* (Loew, 1845), a subfossil of the Holocene; *Sergentomyia succini* Stuckenberg, 1975 of the Eocene (Loew 1845, Stuckenberg 1975), both from the Old World; *Microgyomyia pater* (Quate, 1963) from Mexican Oligocene/Miocene amber; *Pintomyia calcararia* Brazil and Andrade Filho, 2002; *Trichopygomyia killickiana* Andrade Filho, Falcão, and Brazil, 2004; *Lutzomyia filipalpis* Peñalver and Grimaldi, 2005; *Lutzomyia succini* Peñalver and Grimaldi, 2005; *Lutzomyia micenawa* Peñalver and Grimaldi, 2005; *Lutzomyia paleopes* Peñalver and Grimaldi, 2005; *Lutzomyia schlesi* Peñalver and Grimaldi, 2005; *Pintomyia braziliara* Andrade Filho, Galati, and Falcão, 2006; *Pintomyia paleotowsensia* Andrade Filho, Falcão, Galati, and Brazil, 2006; *Pintomyia paleotrichia* Andrade Filho, Brazil, Falcão, and Galati, 2007; and *Microgyomyia brandaoi* Andrade Filho, Galati, Falcão, and Brazil, 2008; *Pintomyia dominicana* nov. sp., amber, fossil, Phlebotominae

**ABSTRACT** The objective of this study was to carry out a taxonomic review of fossil American phlebotomine sand flies and describe two new species found in amber in the Dominican Republic. The gonostyle of one of these, *Micropygomyia dorafeliciangeliae* nov. sp., (=*Lutzomyia dorafeliciangeliae*, species group *osvaldii*), has five spines, similar to that of *Microgyomyia pater* (Quate, 1963) (=*Lutzomyia patera*, species group *osvaldii*), but they may be distinguished by the alpha/gamma ratio, which is <1.0 in the new species and >1 in the latter. *Pintomyia dominicana* nov. sp. (=*Lutzomyia dominicana*, species group *verrucarum*) has four spines on the gonostyle and presents a long bristle on the apex of the paramere, which distinguishes it from the other fossil species. With the description of these two new species, a total of 14 species of the American fossil phlebotomine sand flies has been described, 10 of which belong to the genus *Pintomyia*. An identification key for male fossil species is presented.

**KEY WORDS** *Microgyomyia dorafeliciangeliae* nov. sp., *Pintomyia dominicana* nov. sp., amber, fossil, Phlebotominae.
2008, all of these species from Dominican Republic Miocene amber (Quate 1963; Brazil and Andrade Filho 2002; Andrade Filho et al. 2004, 2006a, b, 2007, 2008; Peñalver and Grimaldi 2005). Besides these, Young and Lawyer (1987) recorded 14 fossil specimens from the Dominican Republic belonging to two species, and Antoine et al. (2006) found one species of phlebotomine sand fly from Miocene amber from Peru, but these species were not described by the respective authors.

The objective of this study was to carry out a taxonomic review of these fossils based on data from the literature and on microscopic examination of the phlebotomine fossil material. Descriptions are also provided for two more species from the Dominican Republic.

Materials and Methods

Review of the fossil species of American phlebotomines was based on direct observation under the microscope of specimens deposited in the Phlebotomine collection of the Instituto Rene Rachou. Information on the morphological characteristics of the other species was obtained from Quate (1963) and Peñalver and Grimaldi (2005).

One of the new species was found in a piece of amber measuring 2.5 by 1.2 by 0.3 mm, containing the male holotype and a male paratype. The other new species was found in a concave piece of amber that contained six phlebotomines (five males and a female). These latter phlebotomines were not well preserved, and the form of the amber also impedes more detailed study, so that few structures described in this study have been measured. One of the males was elected as holotype and the other four as paratypes. It was not possible to associate the female with these specimens because of its imperfect state of preservation.

The insects were examined under the microscope and measured using an ocular micrometer calibrated for this purpose. Drawings were made using the same microscope with the aid of a camera lucida and photographs taken with Konica digital equipment with a definition of 8.0 megapixels, the photographs being taken directly through the eyepiece of the microscope. The measurements are given in micrometers.

Some morphological details that help to distinguish fossil from extant species have been provided. A dichotomous key is provided to assist in the identification of the fossil species. The authors have listed species names in accordance with the classification system of Galati (1995, 2003), followed by the corresponding nomenclature of Young and Duncan (1994) in brackets when cited for the first time. The new species will be deposited in the phlebotomine collection of the Instituto René Rachou, Fundação Oswaldo Cruz, Belo Horizonte, Minas Gerais State, Brazil.

Results

Family Psychodidae Newman, 1835

Subfamily Phlebotominae Kertész, 1903

Micropygomyia (Sauromyia) dorafeliciangeliae nov. sp. Andrade Filho, Galati, and Brazil, 2008 (Figs. 1–6) (=Lutzomyia dorafeliciangeliae species group oswaldoi)

Description. Male (holotype. Figs. 1–6). Total length 1,298 μm. The coloration of the insect not was indistinguishable.
Head (Lateral View). Clypeus 83 μm and labrum-epipharynx 118 μm long. Flagellomeres: AIII, 187 μm; AV, 94 μm; AVI, 83 μm; AXVI longer than AXV. Interocular distance was not measured because of the lateral position of the phlebotomine heads. Ascoids visible in AV–AX, simple, inserted at the same level, and very short, not reaching the middle of the segment. Papilla absent on AV and AXIII and present on AIII and AIV. Several papillae on AXIV, AXV, and AXVI. Pulpal formula 1.4.2.3.5; palpomere lengths as follows: first, 30; second, 113; third, 118; fourth, 83; fifth, 250. Newstead’s spines grouped on basal third of third palpomere.

Cervix. Vento-cervical sensillae could not be observed.

Thorax. Median and hind legs lost. Lengths of femur, tibia, basitarsus, and tarsomeres II + III + IV + V of the foreleg 463, 598, 339, and 463 μm, respectively. Wing 1,332 μm long by 294 μm at maximum width. Principal alar indices in micrometers: alpha, 147; beta, 181; gamma, 226; delta, 23; R5, 847.

Abdomen. Gonocoxite 154 μm long by 33 μm wide, without tuft of bristles. Gonostyle 81 μm long, presenting five spines: two apical (one of them smaller and finer than the other), one external superior, one external inferior, and one internal, the last two inserted at the same level, in the middle of the structure. Paramere length 171 μm and shorter than the lateral lobe (184 μm long). The ejaculatory pump, genital filaments, and aedeagus could not be observed.

Etymology. This species was named **Micropygomyia dorafeliciangeliae** nov. sp. in tribute to Dr. Maria Dora Feliciangeli, Senior Lecturer at the Facultad de Ciencias de la Salud, Centro Nacional de Referencia de Flebótomos y Otros Vectores, Universidad de Carabobo, Maracay, Venezuela, who has made a great contribution to our knowledge of the American phlebotomines.

Type Material. HOLOTYPE: one male, Dominican Republic, north of Santiago, specimens in Miocene amber; PARATYPE: one male, same data.

Remarks. The presence of Newstead’s spines inserted together on the basal half of the third palpomere and the absence of the papilla on AV leads us to include the new species in the subtribe Sergentomyiina. The presence of five spines on the gonostyle, gonocoxite without tuft of bristles, and AIII shorter than length of head permit the inclusion of the new species within the genus **Micropygomyia**, subgenus **Sauromyia**, series **oswaldoi** (= genus Lutzomyia, species group **oswaldoi**).

With respect to extant species, **M. dorafeliciangeliae** nov. sp. can be distinguished from **Micropygomyia peresi** (Mangabeira 1942) (=Lutzomyia peresi, species group **oswaldoi**) by the clypeus, which is shorter than the labrum-epipharynx. It can be distinguished from **Micropygomyia quinquefer** (Dyar, 1929) (=Lutzomyia quinquefer, species group **oswaldoi**), **Micropygomyia ferreirana** (Barretto, Martins, and Pellegrino, 1956) (=Lutzomyia ferreirana, species group **oswaldoi**), **Micropygomyia saccai** (Feliciangeli, Ramírez Pérez, and Ramírez, 1989) (=Lutzomyia saccai, species group **oswaldoi**), **Micropygomyia quechua** (Martins, Llanos, and Silva, 1975) (=Lutzomyia quechua, species group **oswaldoi**), **Micropygomyia quechua** (Martins, Llanos, and Silva, 1975) (=Lutzomyia quechua, species group **oswaldoi**), **Micropygomyia rorotaensis** (Floch and Abonnenc, 1944) (=Lutzomyia rorotaensis, species group **oswaldoi**), and **Micropygomyia longipennis** (Barretto, 1946) (=Lutzomyia longipennis, species group **oswaldoi**) by the absence of bristles on the gonocoxite. The R5/wing length ratios, 2.88 in the new species and 3.60 in **Micropygomyia machupicchu** (Martins, Llanos, and Silva, 1975) (=Lutzomyia machupicchu, species group **oswaldoi**), distinguish them from one
another. The species *Micropygomyia pratti* (Vargas and Díaz-Nájera, 1951) (=*Lutzomyia pratti*, species group *oswaldoi*) has the lower external spine of the gonostyle inserted at a more apical level than the internal one, whereas in the new species they are at the same level. In *Micropygomyia zikani* (Barretto, 1950) (=*Lutzomyia zikani*, species group *oswaldoi*), there is a small projection, absent in the new species, on the ventral margin of the paramere. The terminalia of *Micropygomyia villelai* (Mangabeira, 1942) (=*Lutzomyia villelai*, species group *oswaldoi*), *Micropygomyia trinidadensis* (Newstead, 1922) (=*Lutzomyia trinidadensis*, species group *oswaldoi*), *Micropygomyia oswaldoi* (Mangabeira, 1942) (=*Lutzomyia oswaldoi*, species group *oswaldoi*), and *Micropygomyia capixaba* (Días, Falcão, Silva, and Martins, 1987) (=*Lutzomyia capixaba*, species group *oswaldoi*) are longer (>300 μm long) than those of *Mi. dorafeliciangeliae* nov. sp. (<250 μm). The fossil species of *Micropygomyia pusilla* (Días, Martins, Falcão, and Silva, 1986) (=*Lutzomyia pusilla*, species group *oswaldoi*) may be distinguished by its smaller thorax and abdomen, which together measure æ1.140 μm, whereas in *M. pusilla*, they measure 1.648–1.976 μm (n = 5).

Regarding the fossil species, all of them present four spines on the gonostyle, except *Micropygomyia paterna* (Quate, 1963) (=*Lutzomyia paterna*, species group *oswaldoi*), which is found in Mexican amber and is morphologically very similar to the new species (Quate 1963). The drawings in the original description of this species are very rudimentary and provide little morphological information, although the alar indices are sufficient to differentiate them. The alpha/gamma ratio is 0.65 in *M. dorafeliciangeliae* nov. sp. and 1.05 in *M. paterna*.

Figs. 3-6. *Micropygomyia dorafeliciangeliae* nov. sp. (holotype). (3) Terminalia (bar = 100). (4) Third, fourth, and fifth palpomeres (bar = 100). (5) VI antennomere (bar = 100). (6) Wing (bar = 200).
Pintomyia (Pifanomyia) dominicana nov. sp. Andrade Filho, Galati and Brazil, 2008 (Figs. 7–11) (=Lutzomyia dominicana, species group verrucarum)

Description. Male (Holotype, Figs. 6–11). Total length 1,524 μm. The color of the insect was indistinguishable.

Head (Lateral View). The head is 248 μm, clypeus is 79 μm, and labrum-epipharynx is 192 μm long. Flagellomere lengths as follows: AIII, 248 μm; AIV, 112 μm; AV, 112 μm; AXV, AXVI. Interocular distance not measured because of position of the head. Ascoids of AV–X simple, inserted at same level and very short, not reaching middle of segment. Papilla absent on AV–XIII but present on AIII and AIV. Several papillae on AXIV, AXV, and AXVI. Pulpal formula 1.4.2.3.5, flagellomere lengths as follows: first, 33 μm; second, 125 μm; third, 135 μm; fourth, 79 μm; fifth, 293 μm. Newstead’s spines not observed.

Cervix. Ventro-cervical sensillae could not be observed.

Thorax. Legs without special characters. Length of femur, tibia, basitarsus, and tarsomeres II + III +
IV + V on foreleg 621, 756, 406, and 497 μm, respectively. Median and hind legs lost. Wing 384 μm at maximum width. Principal alar indices (μm): alpha, 203; beta, 248; gamma, 260; delta, 11; R5, 982.

Abdomen. Gonocoxite 350 μm long, without tuft of bristles. Gonostyle could not be measured but presents four spines, of which one apical, one upper external, one lower external inserted in middle of structure and one internal implanted at same level as the last. Preapical bristle absent. Paramere curved upward, presenting three small bristles at its apex, two of which are smaller and inclined forward and downward and the third, much better developed than the others, inclined upward. Lateral lobe very long, measuring 452 μm, lateral lobe/gonocoxite ratio 1.29:1. Ejaculatory pump, genital filaments and aedeagus could not be observed.

Etymology. The name *Pintomyia dominicana* nov.sp. derives from that of the country in which the species was found.

Type Material. HOLOTYPE: one male, Dominican Republic, north of Santiago, specimens in Miocene amber; PARATYPE: four males, same data.

Remarks. The combination of a long fifth palpomere (longer than the sum of 3 + 4), short simple ascoids, four spines on gonostyle, gonocoxite without tuft of bristles, and long lateral lobe with pointed apex, as well as the arrangement of the spines on the gonostyle, permit the new species to be included in the genus *Pintomyia*, subgenus *Pifanomyia*, seeing that there is no longitudinal row of spines on the hind femur. We prefer not to include the new species in any of the known series at present, because its characters do not fit any of them. The upwardly curved paramere and presence of a spiniform bristle on its apical region, clearly distinguish the new species from those of the present day.

*Micropygomyia* (*Sauromyia*) *paterna* (Quate, 1963) (*=Lutzomyia paterna*, species group *oswaldoi*)

*Phlebotomus paternus* Quate, 1963: 114, Fig. 2

Palpal formula not given and fifth segment lost. Gonostyle with five spines, two being apical: one external superior close to the apex and one external inferior on the
middle of the structure, at the same level as the internal spine. Gonocoxite with few bristles, although these may also be deciduous (Quate 1963). Paramere long, a little shorter than the lateral lobe.

The original description provides little information on this species, although there seems to be no doubts regarding its inclusion in the genus *Micropygomyia*, as suggested by Galati (1995).

**Pintomyia falcaorum** Brazil and Andrade Filho, 2002 (= *Lutzomyia falcaorum*, species group *verrucarum*)

*Pintomyia falcaorum* Brazil and Andrade Filho, 2002: 501, Figs. 1 and 2

Palpal formula 1.2.4.3.5, palpmere 5 approximately same size as 2 + 3 + 4. Gonostyle with four spines: one being apical, one external superior, one external inferior, and one internal. Preapical bristle absent. Gonocoxite without tuft of bristles. Paramere with spiniform bristle on basal third. Lateral lobe longer than gonocoxite.

In the original description, Brazil and Andrade Filho (2002) reported the presence of a preapical bristle, which in fact seems to be the shadow of the apical spine. In the original description, the presence of longitudinal bristles along the gonocoxite is also reported; however, these are deciduous and of no taxonomic importance.

**Pintomyia (Pifanomyia) killickorum** (Andrade Filho, Falcao, and Brazil, 2004) New Combination [= *Lutzomyia* (Trichopygomyia) killickorum]

*Trichopygomyia killickorum* Andrade Filho, Falcao, and Brazil, 2004: 71, Fig. 1

Palpal formula 1.4.2.3.5, palpmere 5 longer than 3 + 4. Gonostyle with three spines, of which one apical, one external inserted on the apical quarter and one internal, implanted in the middle of the structure. Gonocoxite without tuft of bristles. Paramere with one lobe on its dorsal margin curved downwards and covered by several bristles.

In the original description, Andrade Filho et al. (2004) stated that this species bears four spines on the gonostyle, including one (the external inferior) less developed than the others. However, on re-examining this material, the latter was found to be a deciduous bristle, without taxonomic value. Thus, this species presents only three spines on the gonostyle, a configuration similar to that presented by some species of the series *serrana*.

This species can be distinguished from the others by the dorsal lobe present on the middle of the paramere. Another two species of the series *serrana*, i.e., *Pintomyia boliviana* (Velasco and Trapido 1974) and *Pintomyia torresi* (Le Pont and Desjeux, 1991), which have branched parameres, can be distinguished from *P. killickorum* by the aspect of the dorsal branch of this latter and also by the fact that the present-day species bear a group of bristles in the interlobular region (Galati 2003), absent from the fossil species.

**Pintomyia (Pifanomyia) filipalpis** (Peñalver and Grimaldi, 2005) New Combination [= *Lutzomyia* (Micropygomyia) filipalpis]

*Lutzomyia* (Micropygomyia) filipalpis Peñalver and Grimaldi, 2005: 180, Figs. 2–4 and 7

Palpal formula 1.4.3.2.5, palpmere 5 longer than 3 + 4. Gonostyle with four spines; gonocoxite without tuft of bristles; paramere with slight dorsal curvature in its median region and lateral lobe longer than gonocoxite.

This species was described by Peñalver and Grimaldi (2005), who included it within the subgenus *Micropygomyia*, based on the size of the palpal segments, short ascoids, simple parameres, and presence of four spines on the gonostyle; however, these features are not exclusive to this group. Based on the description and drawing (Fig. 3a), the second palpmere is slightly longer than the fourth, which would exclude *Pi. filipalpis* from the subtribe Sergentomyiina of Galati (2003) and consequently from the genus *Micropygomyia*. It is impossible to observe the point of insertion of the internal and external inferior spines, which precludes a more detailed analysis. However, the general aspect of the terminalia, principally of the paramere, indicates that this species is closer to the genus *Pintomyia*.

In the original description, Peñalver and Grimaldi (2005) stated that the hind femur has a distal spur. However, if there were a longitudinal row of spines on the hind femur, these would be between the base and median region of the appendage. Thus, the femur can be considered unarmed, and this species is included in the subgenus *Pifanomyia*. The presence of four well-developed spines on the gonostyle excludes it from the series *pia* (with five spines) and *serrana* (with three). The absence of tuft (s) on the gonocoxite excludes it from the series *verrucarum* and *townsendi*; species of the series *monticola* also have highly developed mouthparts, unlike this fossil species.

Thus, it seems that it is most closely related to species of the species *evansi*. It can be distinguished from *Pintomyia maranonensis* (Galati, Cáceres, and Le Pont, 1995) and *Pintomyia ovalesi* (Ortiz, 1952) by the absence of a tuft on the gonocoxite. The curvature on the dorsal margin of the paramere shown by *Pintomyia filipalpis* distinguishes it from the other two species of the series, *Pintomyia evansi* (Nuñez-Tovar, 1924) and *Pintomyia necesi* (Damaceno and Arouck, 1956).

**Pintomyia (Pifanomyia) succini** (Peñalver and Grimaldi, 2005) New Combination (= *Lutzomyia succini*, species group *pilosa*)

*Pintomyia succini* Peñalver and Grimaldi, 2005: 181, Figs. 3 and 4
Palpal formula 1.4.2.3.5, palpomere 5 longer than 3 + 4. Gonostyle with three spines: one apical, one external on the basal third, and the other internal implanted close to the external; gonocoxite without tuft of bristles; paramere simple and lateral lobe longer than the gonocoxite.

*Lutzomyia succini* is included in the group *pilosa* of Young and Duncan (1994) by Peñalver and Grimaldi (2005), and in their identification, description, and Fig. 4b, the authors do not mention the presence of bristles, characteristic of species belonging to the group, on the median or distal regions of the structure. However, these authors justify its inclusion in the group *pilosa* based on its having a gonostyle with three highly developed spines and a small median bristle, despite the length of the lateral lobe's being different from that presented by other species of the group. Based on our observations, the lateral lobe is incompatible with that of other species of the series *pilosa*, as are the entire terminalia.

The gonocoxite, gonostyle, paramere, and lateral lobe of *L. succini* are 0.23, 0.10, 0.16, and 0.34 mm long, respectively (Peñalver and Grimaldi 2005), whereas those of *Micropygomyia mangabeirana* (Martin, Falcão, and Silva, 1963) measure 0.18, 0.10, 0.14, and 0.18 mm (holotype number 23383) and of *Micropygomyia pilosa* (Damasceno and Causey, 1944) measure 0.17, 0.10, 0.17, and 0.17 mm (specimen from Venezuela).

This information, principally in relation to the gonocoxite and lateral lobe, clearly excludes *L. succini* from the series *pilosa* of Young and Duncan (1994) and approximates it to the subtribe Lutzomyiina, genus *Pintomyia* (Pifanomyia), series *serrana*, in which some species present three spines on the gonostyle. The arrangement of these spines is different from that presented by the other present-day species, given that, on them, the external spine is inserted close to the apical one. In the fossil species, it is inserted in a median position.

**Pintomyia (Pifanomyia) miocena** (Peñalver and Grimaldi, 2005) New Combination (= *Lutzomyia miocena*, species group *pilosa*)

*Lutzomyia miocena* Peñalver and Grimaldi, 2005: 181, Figs. 3 and 4

Palpal formula 1.4.3.2.5, palpomere 5 equal to 3 + 4. Gonostyle with three spines: one apical, one external on the basal third, and the internal inserted proximal to the external one; gonocoxite without tuft of bristles; paramere simple and lateral lobe long. The same line of reasoning used for *Pi. succini* can be applied to *Pi. miocena*, given that the two species are closely similar and do not present a bristle on the gonostyle. According to Peñalver and Grimaldi (2005), the two fossil species can be distinguished by the difference between the overall size of the two insects, palpal formula, and variation in the wing venation (gamma). However, these characteristics could be caused by intraspecific variation or to a distorted orientation of the structure of the phlebotomine within the amber affecting the measurement. The difference between the paramere of the two species may also be caused by the position in which the insect was trapped within the resin, something that occurs frequently in modern phlebotomines when mounted between slide and coverslip. We consider this species to be valid, although the material needs to be examined to settle any further doubts.

**Pintomyia (Pifanomyia) paleopestis** (Peñalver and Grimaldi, 2005) New Combination (= *Lutzomyia paleopestis*, species group *verrucarum*)

*Lutzomyia paleopestis* Peñalver and Grimaldi, 2005: 182, Figs. 1, 3, and 4

Palpal formula 1.4.2.3.5, palpomere 5 as long as 3 + 4; ascoids short and simple. Gonostyle with two spines, one apical and other internal, inserted on apical third; preapical bristle present. Gonocoxite with longitudinal tuft of bristles. Aedeagus straight and long. This species, placed in the group *verrucarum*, series *serrana* of Young and Duncan (1994) by Peñalver and Grimaldi (2005), would correspond, in the classification of Galati (2003) to *Pintomyia (Pifanomyia) paleopestis*. A preapical bristle is represented in Fig. 4d, although nothing is said about it in the diagnosis of the species to justify its inclusion in the series. Peñalver and Grimaldi (2005) mentioned that the aedeagus of this species is bifurcate. The phlebotomine aedeagus is a paired structure, however, and based on Fig. 4d, this bifurcation seems to be caused by misalignment of the right and left sides.

Nevertheless, its long, fine aspect may be used as a diagnostic criterion for *Pi. (Pi.) paleopestis*. Alternatively, the representation of the aedeagus as bifid and atypical may be because of the points of the genital filaments extruding from the aedeagus, as is frequently seen in slide-mounted phlebotomines. However, without studying the species under the microscope, such deductions remain purely speculative.

**Psathyromyia (Forattiniella) schleei** (Peñalver and Grimaldi, 2005) New Combination [= *Lutzomyia (Trichophoromyia?) schleei*]

*Lutzomyia (Trichophoromyia?) schleei* Peñalver and Grimaldi, 2005: 183, Figs. 3–5

Palpal formula 1.4.5.2.3, palpomere 5 shorter than 2 or 3. Ascoid apparently simple and short. Gonostyle with four spines, of which one is apical, one external superior, one external inferior (insertion not clear from Fig. 4e), and one internal, inserted in the middle of the structure. Gonocoxite with two tufts of bristles on the apical half. The two tufts of bristles of the apical half may be deciduous, a common configuration in phlebotomines, or caused by an overlapping of the gonocoxites, each bearing a single tuft. However, this cannot be confirmed without studying the material under the microscope.
The authors who described this species confused the names of the subgenera *Trichopygomyia* Barretto, 1962 and *Trichophoromyia* Barretto, 1962, adopted by Young and Duncan (1994). In the original description of the species, it is named *Lutzomyia* (*Trichopygomyia*) schleei, but in the discussion, it is treated as *Lutzomyia* (*Trichophoromyia*) schleei. It seems that these authors were confused with regard to the figures, because morphologically the two subgenera are very different. We assume that the authors intended to include this species within the subgenus *Trichophoromyia*, given that the size of the fifth palpal segment is incompatible with that of the *Trichopygomyia* species. This characteristic alone is sufficient to exclude the fossil species from the latter subgenus.

The palpal formula and genitalia allow this species to be included in the subtribe Psychodopygina, although based on the description of the ascosids, it could be included in any of the extant groups, the terminalia, palpal formula, and wings being most similar to those of the genus *Psathyromyia*, subgenus *Forattiniella*. Peñalver and Grimaldi (2005) described the ascosids as short and simple. Given the difficulty of observing these structures in fossil phlebotomines, there may be a posterior prolongation that is difficult to see; thus, we prefer to call this species *Psathyromyia* (*Forattiniella*) schleei. Where there are two tufts of bristles on the apical half of the gonocoxite, this may be used to distinguish this species from the other present-day species of this group. The form of the paramere is another distinguishing character.

*Pintomyia* (*Pifanomyia*) brazilorum Andrade Filho, Galati, and Falcão, 2006 (=*Lutzomyia* brazilorum, species group verrucarum)

*Pintomyia* (*Pifanomyia*) brazilorum Andrade Filho, Galati, and Falcão, 2006: 141, Figs. 1 and 2

Palpal formula 1.4.2.3.5, palpmere 5 longer than the sum of 3 + 4; ascoad short and simple. Gonostyle with four spines, of which one apical, one external superior, and one external inferior implanted at a different level from the internal one, these last two being atrophied. Gonocoxite without tuft of bristles, paramere with small extension on its dorsal margin.

Because of the position of the terminalia, few details can be observed, and thus it is impossible to measure the length of the lateral lobe, although it seems to be of approximately the same size as the gonocoxite (Andrade Filho et al. 2006b). The presence of four spines on the gonostyle, two of them atrophied, is sufficient to distinguish this species from the modern ones.

*Pintomyia* (*Pifanomyia*) paleotownsendi Andrade Filho, Falcão, Galati, and Brazil, 2006 (=*Lutzomyia* paleotownsendi, species group verrucarum)

*Pintomyia* (*Pifanomyia*) paleotownsendi Andrade Filho, Falcão, Galati, and Brazil, 2006: 57, Figs. 1–3

Palpal formula 1.4.2.3.5, segment 5 longer than 3 + 4. Gonostyle with four spines, of which one apical, one external superior implanted on the apical third, one external inferior implanted in middle of the structure, and one internal implanted on the basal third. Gonocoxite with basal tuft of five bristles, paramere curved upward, with group of apical bristles and a more highly developed spiniform bristle on its basal third.

The position of the terminalia and the quality of the amber permit the observation of several morphological structures of this fossil (Andrade Filho et al. 2006a), although there are doubts regarding its inclusion within the series *townsendi* of the subgenus *Pifanomyia*.

*Pintomyia* (*Pifanomyia*) paleotrichia Andrade Filho, Brazil, Falcão, and Galati, 2007 (=*Lutzomyia* paleotrichia, species group verrucarum)

*Pintomyia* (*Pifanomyia*) paleotrichia Andrade Filho, Brazil, Falcão, and Galati, 2007: 901, Figs. 1–6

Palpal formula 1.4.2.3.5, palpmere 5 longer than 3 + 4. Gonostyle with four spines, of which one apical, one external superior implanted on apical third, one external inferior implanted in middle of the structure, and one internal implanted on the basal third. Gonocoxite with basal tuft with ≈13 bristles, paramere curved dorsally, with groups of setae at its apex and spiniform ones in its median region.

The terminalia of this species overlap, impeding visualization of all the bristles of the gonocoxite and their point of implantation (Andrade Filho et al. 2007), although ≈13 bristles can be seen. The apical spine of the gonostyle of this species is highly developed, as that found on the present-day species *Pintomyia spinacrassa* (Morales, Osorno-Mesa, Osorno, and Hoyos, 1969), both being easily distinguished (among other characters) by the paramere of the fossil species, which presents a group of setae on its apex.

*Micropygomyia* (*Micropygomyia*) brandaoi Andrade Filho, Galati, Falcão, and Brazil, 2008 (=*Lutzomyia* (Micropygomyia) brandaoi)

*Micropygomyia* (*Micropygomyia*) brandaoi Andrade Filho, Galati, Falcão, and Brazil, 2008: 14, Figs. 1–4

Palpal formula 1.4.2.3.5, palpmere 5 longer than 3 + 4. Gonostyle with four spines, of which one apical, one external superior, one external inferior, and one internal, the last two being implanted at the same level. Terminalia small, gonocoxite without bristles.

This species has been described on the basis of 56 males and is the most abundant fossil species in the Dominican Republic (Andrade Filho et al. 2008). It belongs to the *cayennensis* complex and can be separated from other modern species on the basis of the α/β ratio and by the lateral lobe, which is longer than the gonocoxite and paramere.
**Key for the Identification of American Fossil Phlebotomines**

1. Gonostyle with five highly developed spines ........................................ 2
   Gonostyle with two, three, or four highly developed spines ........................ 3

2. Alpha clearly shorter than gamma. ......................................................... 4
   Gonocoxite with basal tuft of bristles ............................................. 11
   Alpha practically as long as gamma. .............................................. 12
   Palpomere 5 longer than 3 + 4 ......................................................... 4

3. Terminalia short, lateral lobe being longer than the gonocoxite and practically as long as the paramere ................................. 10
   Paramere without spiniform bristle in this region ............................... 6

4. Palpomere 5 shorter than 3 + 4 ........................................................ 5

5. Gonostyle with two or three highly developed spines, with or without other atrophied spines ........................................... 7

6. Gonostyle with two highly developed and two atrophied spines .......... 6
   Conostyle with four highly developed spines ........................................ 9

7. Paramere elongated, simple on its dorsal margin ............................... 10
   Paramere with lobe or highly-developed bristle on dorsal margin .......... 13

8. Palpomere 5 shorter than 3 + 4 ........................................................ 5

9. Terminalia long, lateral lobe longer than gonocoxite. Palpomere 5 longer than 3 + 4 ......................................................... 4

10. Gonostyle with five highly developed spines; aedeagus longer than the paramere .......................... 13

11. Palpomere 5 shorter than 3 + 4 ........................................................ 5

12. Palpomere 5 longer than 3 + 4 ........................................................ 5

13. Paramere elongated, simple on its dorsal margin ............................... 10

**Discussion**

Of the 14 sand fly American fossil species, 13 are from the Dominican Republic. This is a strong indication that the local sand fly fauna during the Miocene was highly diversified, with a predominance of species belonging to the *Pintomyia* genus. According to Péñalver and Grimaldi (2005), the extinct fauna of the Dominican Republic may be as many as two to three times more than those already found, thus amounting to a total of between 24 and 36 species. However, new fossil species of sand flies may yet be described and thus increase that estimate further.

Besides the fossil adult sand flies described by him, Poinar (2007) found two phlebotomine larvae in Burmese amber of ~100 million years old. They were associated with fungi that might have served as food for them. Close to these larvae were found monogenetic trypanosomatids that might have been among the ancestors of today’s digenetic trypanosomatids.

Another fossil monogenetic trypanosomatid is *Paleoleishmania proterus* Poinar Jr. and Poinar, 2004, found parasitizing the species *Palaemomyia burnensis* Poinar Jr, 2004. This species of phlebotomine may be the vector of *Leishmania* between primitive vertebrates of the Cretaceous period (Poinar 2004, Poinar and Poinar 2004).

The *Pintomyia* genus presents some species responsible for the transmission of *Leishmania* in some countries of the Americas, and it may be that some of these fossil species were involved in the transmission of parasites. The current *Psathyromyia* species are commonly found in areas of the Amazonian and Atlantic forests, which would seem to confirm the hypothesis that the Dominican Republic was covered by dense tropical forests 20 million years ago (Allen 1956).

The other genus found in the Dominican Republic, *Micropygomyia*, includes the only species of phlebotomine sand fly fossil registered outside the country, having been found in amber in Chiapas, Mexico. The current species of *Micropygomyia* are not anthropophilic and feed on several cold-blooded animals; therefore, they have no epidemiological significance (Young and Duncan 1994, Andrade Filho et al. 1998).

Several morphological structures could not be visualized because of their small size and the impossibility of their observation at an increase of ×400 because of the thickness of the amber. Moreover, during the process of fossilization, all the sand flies’ heads remained in a lateral position, which prevented the morphological and morphometric study of some structures, such as interocular distance, length and width of the head, and interocular suture. The lack of more information makes a further comparison with existing species impossible.

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