

THE RELATIONSHIPS AND CLASSIFICATION OF THE PHLEBOTOMINAE
(Diptera, Psychodidae)

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The position which *Phlebotomus* occupies in the family Psychodidae has been discussed by several previous students, notably Meunier (1905), Alexander (1929), Tonnoir (1935), Enderlein (1937), Parrot (1951) and Theodor (1948). In addition, Edwards (1926) and Crampton (1925), give valuable discussions on the relationships of the Psychodidae as a whole. Recent discovery of related genera (Hertig 1948, Fairchild 1949) has induced me to reexamine the question, taking into consideration the known fossil species as well as the living representatives of the family.

It is now generally accepted that the Diptera are descended from some Mecopteralike ancestor, and it is believed that the genera *Bruchomyia* and *Nemopalpus* are among the most primitive living members of the order (Alexander 1929, Fairchild 1952). A comparison of the wing venation of a species of *Nemopalpus* and a fossil mecopteran belonging to the Suborder Proto-diptera (*Permotipula* sp.) shows their great similarity (Figs. 1 and 4). In any event, *Bruchomyia* and *Nemopalpus* are undoubtedly the least specialized Psychodidae, and I believe are closest to the basic stock from which the other Psychodidae have been derived.

Differentiation from *Bruchomyia*, or a similar progenitor, has followed several pathways, and different structures have developed in an uncorrelated manner. Since wing venation is generally believed best to show relationships among insects, and is the character most likely to be preserved in fossil forms, it will be discussed first. In regard to the correct interpretation of the venation in the Psychodidae, there seems to be some disagreement. The Comstock-Needham interpretation, which Alexander (1929) and Tonnoir (1935) have used, indicates a radius with five branches and a media with four branches. Dampf (1947) however, following Hendel (1936) and others, interprets the venation of *Phlebotomus* as having a four-branched radius and a five-branched media. The problem appears to hinge upon which of the two transverse veins, joining

R_5 of the Tonnoir interpretation to the veins posterior and anterior to it, is a cross vein and which is the true base of the vein. It is generally believed that true primary veins can be told from the secondary cross-veins by the fact that they bear macrotrichiae. However, in the case of most *Phlebotomus* and other Psychodidae, neither of these transverse veins usually bears macrotrichiae. I have examined specimens of three species of *Bruchomyia* and seven of *Nemopalpus*, as well as *Sycorax silacea*, *Hertigia hertigi* and three species of *Warileya*. In none of these does either transverse vein bear macrotrichiae for its full length except in one wing of a specimen of *N. antillarum* Fchld., and in this case it is the anterior vein. In several cases one or both transverse veins bear macrotrichiae on $\frac{1}{2}$ or $\frac{3}{4}$ of their length from R_5 , but there is little consistency as to which vein bears the greater area of macrotrichiae, even in the same specimen. It is to be noted, furthermore, that the base of M_2 and the bases of M_3 and M_4 often also lack macrotrichiae. In the case of M_3 and M_4 , macrotrichiae are usually present at the base where these veins join M in *Nemopalpus* and *Bruchomyia*. In *Sycorax* the bases of M_3 and M_4 are connected by a short transverse vein bearing macrotrichiae, but the transverse veins connecting with M anteriorly and Cu posteriorly are bare. In *Warileya* and *Hertigia*, on the other hand, the transverse vein connecting the bases of M_3 and M_4 is bare, while M_3 joins M evenly with no break in the macrotrichiae, and M_4 joins Cu as if it were a continuation of that vein, a condition also usually true in *Phlebotomus*.

The positions of the various forks of the radial and median systems in relation to the r-m cross vein might be expected to give some clue. In all the genera examined except *Nemopalpus* and *Bruchomyia* the posterior transverse vein (r-m) is proximal to the fork of M_1 - M_2 , but in these genera it may be proximal, at the same level or distal. The case is similar with the anterior transverse vein (base of R_5), which may be proximal, at the same level, or distal to the most basal fork of the radial sector. That the radial sector was originally four-branched would certainly seem to be suggested by the venation of *Permotipula* (Fig. 1), and that the dichotomous condition shown by both R and M in this insect is also a primitive feature seems a reasonable

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²I am greatly indebted to Dr. L. Parrot of the Institut Pasteur d'Algerie and to Dr. G. H. Satchell, of the University of Otago, Dunedin, New Zealand for reading the manuscript of this paper and for making suggestions and corrections which have very greatly improved its content and readability.

assumption, for it is retained in *Bruchomyia*, *Nemopalpus* and *Hertigia*. Since *Permotipula* has no r-m cross vein there seems good reason to suppose that the most posterior vein in its radial field is really R_3 rather than M_3 , and since the venation of *Bruchomyia* and other *Psychodidae* appears to be homologous, it seems best to consider that the vein in question is R_3 rather than M_3 . Dampf's interpretation (1947) of the median veins in *Phlebotomus* also seems open to question. In *Phlebotomus* M_3 and M_4 are separate at their bases or connected by a bare cross vein, but in most other genera of the family they are either stalked, (*Diplonema*, *Eophlebotomus*, *Horaiella*) joined at the base (*Bruchomyia*, *Trichomyia*), or joined by a transverse vein bearing macrotrichiae (*Sycorax*, *Eatonisca*), so that it seems reasonable to suppose that the general reduction of the anal and cubital fields consequent on the narrowing of the base of the wing in *Phlebotomus* may have given rise to the observed condition. It is, of course, possible that M_3 and M_4 have fused into a single vein in *Phlebotomus*, a continuation of the stalked condition in *Eophlebotomus*, and that M_4 is actually Cu_1 , but there is not any very good evidence for this.

The statement that the Trichomyiinae have the veins R_4 and R_5 fused into a single vein, recently repeated by Vargas and Diaz Najera (1953), does not appear to be correct. In no psychodid is there any evidence for this in the form of partial fusion from either the distal or proximal ends. The forking of R_4 and R_5 is always in the basal half of the wing. On the other hand, there is considerable evidence that R_2 and R_3 have fused to form a single vein in the Trichomyiinae, that this fusion has taken place from the base outwards, and that it has been accompanied by a distal migration of the $R_2 + 3 - R_4$ fork. The tendency to a shortening of R_2 and R_3 is marked in many species of *Phlebotomus*, especially in the subgenus *Sergentomyia*, in *Eophlebotomus* and in *Phlebotomiella*. In all these also the $R_2 + 3 - R_4$ fork has moved distally beyond the level of the $R_4 - R_5$ fork. In *Trichomyia* and in *Sycorax*, where R_2 and R_3 have fused, it is quite common to find the tip of $R_2 + 3$ forked or with a short stub (Fig. 12) a clear indication of the originally dual condition of this vein. The venation of *Horaiella* also seems best interpreted on the same basis, though here the $R_2 + 3 - R_4$ fork has remained proximal to the $R_4 - R_5$ fork, as in *Bruchomyia* and *Nemopalpus*.

The vestigial vein present at the extreme base of the wing in many genera does not seem to have been clearly interpreted. In *Permotipula* there appear to be two cubital veins, parallel and close together. In *Bruchomyia*, *Nemopalpus* and a few other genera, there is a vein-like thickening close to and parallel with the basal part of Cu_1 , which may represent the second cubital. In *Phlebotomus* this is represented by a fold in the

wing. *Trichomyia* shows a spur on the cubitus, as does *Bruchomyia*, which may indicate an originally stalked two branched vein different from *Permotipula*. The short vestigial vein present posterior to the Cubitus and its accompanying fold, best seen in *Trichomyia* and *Sycorax*, but clear enough in *Bruchomyia* and *Nemopalpus*, is probably best interpreted as an anal vein, as high magnification indicates it is not connected with the Cubitus at its base.

In *Bruchomyia* (Fig. 2) all four branches of the radial sector are preserved and the branching is dichotomous. R_2 and R_3 fork quite close to their common union with R_1 , so that they are relatively long, the r-m cross vein is close to the fork of $M_1 - M_2$, Cu_1 is long, about half the length of M_4 , there is a short spur upon it which may be a vestige of Cu_2 and there is a single anal vein. In *Eutonnoiria edwardsi* (Tonn.) the venation is the same, except that Cu_1 is considerably shorter and without the short spur. In *Nemopalpus flavus* Macq., (Fig. 3) a further shortening of the cubitus has taken place, so that it is not much more than twice as long as the m-cu cross vein. The remaining species of *Nemopalpus* show several further modifications in venation. There is a tendency for the stalk of $R_2 + 3$ to become longer and at the same time the r-m cross vein moves distally so that R_2 and R_3 are quite short and $M_1 + 2$ forks quite far basally of the cross vein, culminating in the condition found in *N. dampfianus* Alex. and *N. pilipes* Tonn. (Fig. 4). Or the $R_2 + 3$ fork moves distally while the $M_1 + 2$ fork also moves distally, culminating in such species as *N. arroyi* de Leon.

In *Hertigia* (Fig. 6) the radius is still dichotomously branched, though R_5 forks quite close to the division of R_4 and $R_2 + 3$, while Cu_1 is still further reduced and the anal vein is little more than a vestigial fold. In *Warileya* (Fig. 7) the radius becomes pectinately branched by the further displacement proximally of the point of junction of R_5 with R_4 . In *Phlebotomus* (Fig. 8) this tendency is carried still further, combined with a great narrowing of the wing and a movement of the $R_2 - R_3$ fork towards the apex of the wing. The culmination is reached in certain species of the subgenus *Sergentomyia* (Fig. 9) where $R_2 + 3$ forks well beyond the apex of R_1 , causing R_2 to be only a fraction of the length of its stalk. Cu_1 is further reduced in *Phlebotomus*, being hardly demonstrable in most species. The fossil *Phlebotomiella tipuliformis* Meun. (Fig. 10) from Baltic amber shows a venation similar to *Phlebotomus*, but has diverged along a slightly different line, since the forks of $R_2 + 3 + 4$ and $M_1 + 2$ have all moved towards the apex of the wing.

In *Eophlebotomus connectans* Coq., a fossil species from Burmese amber, a different line of development can be seen (Fig. 5). In this species all the veins are still preserved as in *Nemopalpus*,

but the wing has become shortened and rounded. The cubitus is short, the forking of R_3 from the radial sector is now proximal to the forking of R_4 , while the fork of $R_2 + 3$ is quite far distal on the wing, so that R_3 is pectinately branched as in *Warileya*. It differs from this genus however, in the shortened R_2 and R_3 , and in having developed a long stalk on $M_3 + 4$.

Sycorax (FIG. 14) seems to be another somewhat different line of development, resembling in some respects *Trichomyia*. Here the fork of R_2 and R_3 has moved out to the wing margin, so that $R_2 + 3$ has become a single vein. Not infrequently, as also in *Trichomyia*, a short vestige of R_3 remains near the apex of the vein. Unlike *Trichomyia*, however, there is no tendency for $M_3 + 4$ to be stalked, and Cu_1 is reduced to a short spur no longer than the m-cu cross vein.

Trichomyia (FIG. 12) and two fossil genera, *Eatonisca* and *Diplonema*, (FIG. 11 and 13) show the same fusion of R_2 and R_3 as *Sycorax*, but have a long and well developed cubitus. *Trichomyia* has M_3 and M_4 joined at or close to their common origin at the base of the wing, in *Diplonema* there is a stalk of appreciable length, while in *Eatonisca* the condition is as in *Sycorax* and *Phlebotomus*.

The peculiar genus *Horaiella* Tonn. (FIG. 15) combines certain features of *Sycorax* and *Trichomyia*. It has the fused $R_2 + 3$ of *Sycorax* and *Trichomyia*, the stalked $M_3 + 4$ of *Trichomyia*, but Cu_1 is reduced to a minute vestige at the base of the wing. Both m-cu and r-m cross veins are absent and $R_2 + 3$ arises from R_3 proximal to R_4 , an arrangement similar to *Nemopalpus*, but unlike *Sycorax* and *Trichomyia*, though approached by *Eatonisca*.³

The more typical Psychodidae represented by such genera as *Psychoda*, (FIG. 16) *Pericoma* and *Telmatoscopus* appear to have developed along somewhat different lines. Here there has been no fusion, shortening, or loss of veins. Instead of a lengthening and narrowing of the wing, there has been, in general, a broadening and shortening, except in the genus *Maruina*. The forks of all the veins have tended to move towards the base of the wing, the cross-veins have tended to disappear and even the bases of veins have become faint or disappeared. In *Maruina* (FIG. 17) the wing has become secondarily narrowed and pointed, R_3 and M_2 have lost their bases and are attached only to the wing margin, while the forks of $R_2 + 3$ and R_4 ; and $M_3 + 4$ are all close to the wing base. The r-m and m-cu cross veins

have been lost, but the wing retains all the original veins, except for great reduction in the subcosta.

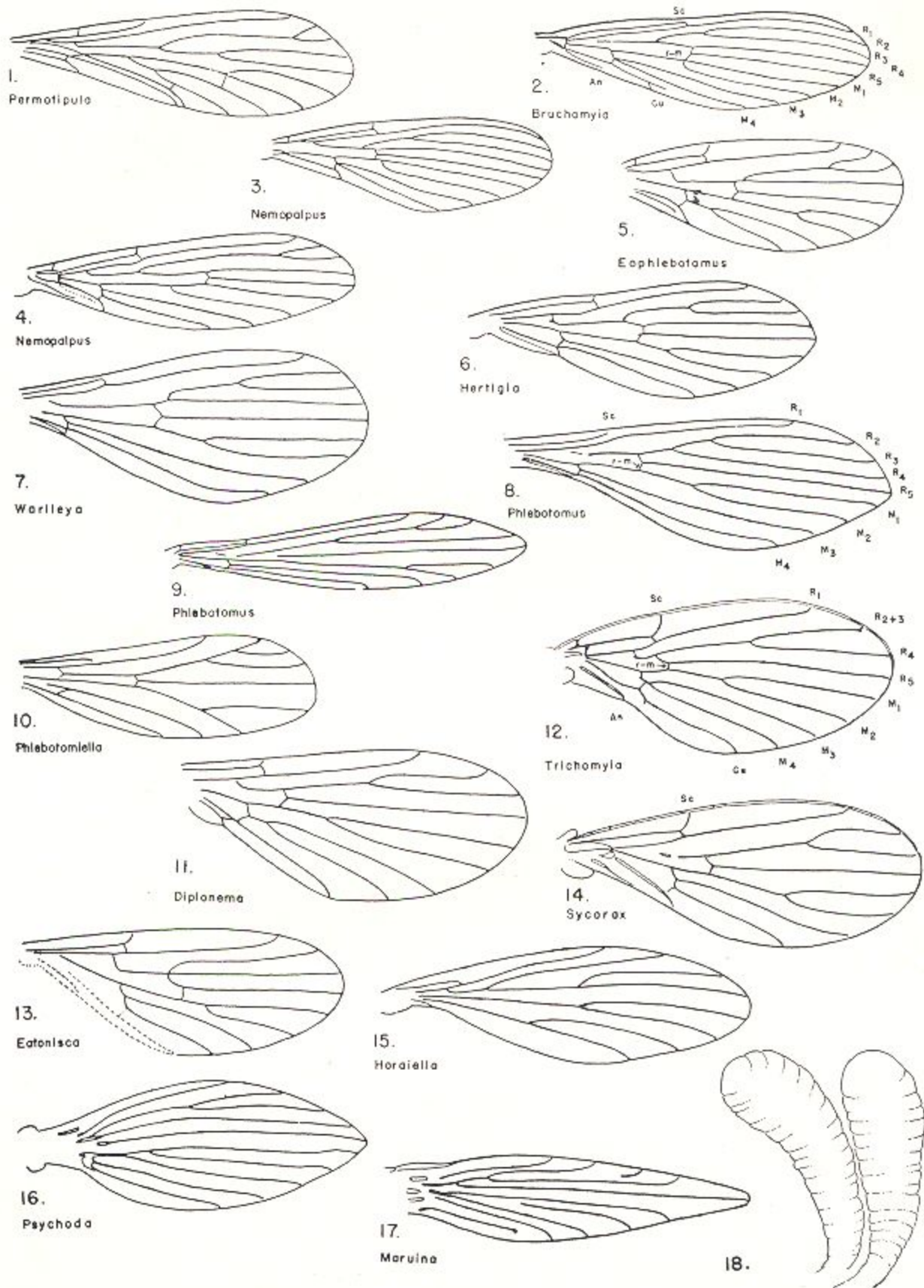
The interpretation of the venation of *Psychoda* given by del Rosario (1936) differs from the one accepted here in considering the media to have but three branches, the two most posterior veins in the wing being Cu_1 and $Cu_2 + 2nd A$. An examination of the wing base of mounted and stained material of *Psychoda* available to me shows the base of the next to last vein attached to M_3 rather than to Cu_1 , much as in my figures of *Warileya* and *Hertigia*. Many of del Rosario's figures of wings; e.g., that of *P. pusilla*, show this condition clearly, while none show the condition illustrated in his diagram (Text FIG. 1, p. 90). It is, of course, possible that the Psychodinae have lost one median vein by the fusion of M_3 and M_4 through a distal migration of the fork to the wing margin, but there seems no strong evidence that this has occurred.

The head and its associated structures show several features of possible significance. In *Bruchomyia*, *Nemopalpus*, *Hertigia*, *Warileya*, *Phlebotomiella* and *Phlebotomus* the palpi are five segmented, although the first segment is often poorly demarcated from the second. In all the remaining genera of the family the palpi are four segmented or rarely, three segmented. The mandibles are present and presumably functional in *Hertigia*, *Warileya*, *Phlebotomus*, *Sycorax* and *Horaiella*, the first four of which are known to be haematophagous. (I have been unable to certainly see mandibles in any of the species of *Bruchomyia* or *Nemopalpus* personally examined,

EXPLANATION OF FIGURES IN PLATE I

Plate 1. The figures are derived from various sources and are not to a uniform scale. FIG. 1, *Pernotipula* sp. Redrawn from Tillyard (1937, Nature 139:86) FIG. 2, *Bruchomyia fusca* Barr. Redrawn from Fairchild (1952). FIG. 3, *Nemopalpus flavus* Macq. Redrawn from Becker (1908 Mitt. Zool. Mus. Berlin 4 (1) Pl. 2, fig. 28). FIG. 4, *Nemopalpus dampflanus* Alex. Redrawn from Fairchild (1952). FIG. 5, *Eophlebotomus connectans* Ckll. Redrawn from Edwards (1929 Ann. Mag. N. H. 3 (16): 424). FIG. 6, *Hertigia hertigi* Fehld. Redrawn from Fairchild (1949). FIG. 7, *Warileya phlebotomanica* Hertig. Redrawn from Hertig. (1948). FIG. 8, *Phlebotomus barrettoii* Mang. Redrawn from Fairchild and Hertig (1953, Ann. Ent. Soc. Amer. 46 (1) FIG. 12). FIG. 9, *Phlebotomus dolichobysus* Fehld. Redrawn from Fairchild (1952, Proc. Linn. Soc. N. S. Wales, 77 (3-4): 205 FIG. 70). FIG. 10, *Phlebotomiella tipuliformis* Meun. Redrawn from Meunier (1905, Ann. Mus. Nat. Hung., 3:235). FIG. 11, *Diplonema buceras* Loew. Redrawn from Loew (1845 Dipt. Beitr. 1:7). FIG. 12, *Trichomyia urbana* Hal. Original from specimen in U. S. N. M. FIG. 13, *Eatonisca tertiaris* Meun. Redrawn from Tonnoir (1933). FIG. 14 *Sycorax* sp. Original from an undescribed species from Panamá. FIG. 15, *Horaiella consimilis* Tonn. Redrawn from Tonnoir (1933). FIG. 16, *Psychoda phalaenoides* Linn. Redrawn from del Rosario (1936 Philip. J. Sci., 59 (1) Pl. 1, FIG. 6). FIG. 17, *Maruina lanceolata* Kinc. Original from specimen in U. S. N. M. FIG. 18, *Sycorax silacea* Hal. Spermataecae. Original, drawn in phenol from a specimen from England.

³After completion of the manuscript and figures of this paper, I was enabled to examine the holotype of *Horaiella knautensis* Alex. through the courtesy of Prof. C. P. Alexander. Under high magnification the wing shows a definite though faint r-m cross vein situated between the base of the radial sector and its first bifurcation. There are also connections between the bases of $M_1 + 2$ and $M_3 + 4$, as well as between the latter and the remnants of Cu_1 .



and no reports of their presence, or of biting habits, have been verified for any other Psychodidae.) The antennae have the segments generally long and slender, usually cylindrical, and with the first flagellar segment markedly longer than the succeeding ones in *Bruchomyia*, *Nemopalpus*, *Hertigia*, *Warileya*, *Phlebotomus*, *Horaiella*, *Sycorax* and at least some species of *Trichomyia*. The fossil genera *Eatonisca*, *Eophlebotomus* and *Diplonema* I am unable to check; *Phlebotomiella* has long antennal segments. The remaining genera tend to have the flagellar segments pyriform or flask shaped, and the segments relatively considerably shorter.

The structures of the male genitalia, so extensively used in specific differentiation, also show features of importance in delimiting higher categories. The genitalia of all Psychodidae, except *Sycorax* and possibly *Horaiella*, are rotated through 180° after eclosion, so that the morphologically ventral parts become dorsal in the adult insect. Here again *Bruchomyia* appears to have the simplest structures, consisting of a pair of morphologically ventral clasping organs arising from the ninth sternite and consisting of a fairly simple coxite and style, a median intromittent organ, a simple unmodified ninth tergite, and well developed cerci. In *Nemopalpus* the styles tend to become more complex in structure, while more or less complex periphallal structures may be present. In *Hertigia*, *Warileya* and *Phlebotomus* there are definite parameres, the intromittent organ has become bifid with a tendency to the development of long tubular genital filaments and a concomitant movement of the genital pump from the ninth segment forward into the abdominal cavity. The ninth tergite now bears lateral lobes varying from short thumb-like processes to very long slender structures, occasionally with modified setae at their tips. These lobes, however, are never truly jointed at the base. In *Sycorax* the coxite and styles are much as in *Hertigia*, parameres are present, at least in some species, but the intromittent organ appears to be simple in some species, or with long genital filaments in others, though these appear to be of different structure than those of *Phlebotomus*. The ninth tergite lacks lobes and cerci are present in some species (Tonnoir 1929), while others appear to have cercopods (Satchell 1950). In *Trichomyia* the genitalia are much modified and the homologies difficult to make out from available descriptions and the little material available to me. The coxite and style are well developed in some species, apparently reduced in others. The aedeagus may be simple or complex and surrounded by one or more pairs of paramere-like structures, while the cerci and ninth tergite seem to be involved in the formation of various finger like lobes, though true cercopods do not seem to occur. *Horaiella* seems to have genitalia of the same basic pattern as *Sycorax*, though in two

species small lobes have developed on the ninth tergite. Not enough is known of the genitalia of the fossil genera for conclusions to be drawn, though the figures of *Phlebotomiella* seem to indicate genitalia of the general type of *Phlebotomus* (Fairchild 1951). The genitalia of the remaining genera appear to be characterized by a great development of the lateral lobes of the ninth tergite into true jointed claspers, the cercopods. Since cerci appear to be absent, it is also possible that the cercopods are modifications of these structures rather than of lobes of the ninth tergite. The coxites and styles are present, generally of rather simple structure, sometimes almost vestigial. The aedeagus is usually heavily sclerotized, often complex in structure, not infrequently asymmetrical.

The external female genitalia are quite uniform and simple in *Hertigia*, *Warileya*, *Phlebotomus*, *Sycorax* and *Horaiella*, consisting of a pair of generally short and flattened lobes on the ninth sternite and of fleshy, somewhat flattened, small cerci. There is some variation in shape, but never a modification into a sclerotized ovipositor. In *Bruchomyia* the lobes of the ninth sternite are long and fingerlike and the sternite is completely divided, while in *Nemopalpus* the lobes are fingerlike on the end of an undivided plate, or form part of what may be some sort of ovipositor (*N. dampfianus*). In *Trichomyia* the lobes of the sternite are absent, replaced by a single ridged plate, and the cerci are large, flattened and paddle-like. In the remainder of the genera, the ninth sternite seems to form the ventral piece of a true ovipositor, the cerci being more or less modified to form the lateral plates. These structures do not seem to have been described in sufficient detail for comment in any of the fossil forms.

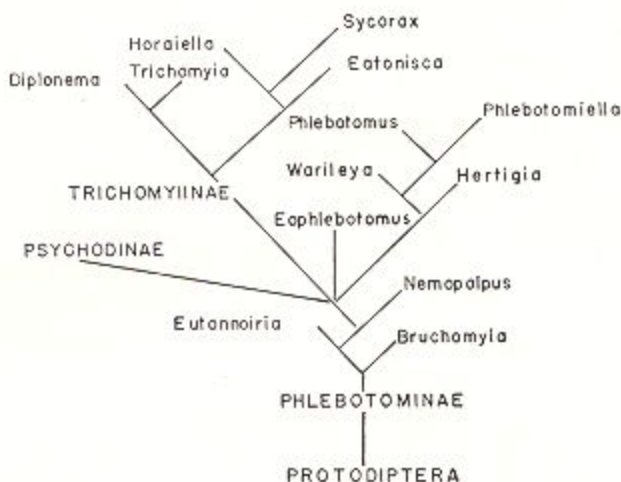
The internal genitalia consist of various sclerotized pieces whose homologies do not seem to have been worked out. The spermathecae are important in the classification of *Phlebotomus*, but have not been much studied in the other groups. They are paired hollow structures of varied shape in *Phlebotomus*, *Warileya*, *Hertigia*, *Sycorax* and *Trichomyia*, opening separately or through a common duct into the vagina. Jung (1954) apparently did not see the true spermathecae in *Sycorax*, and since there appear to be no published figures of these structures, one is included here, drawn from a specimen of *S. silacea* cleared in phenol. (FIG. 18). In the species of *Nemopalpus* and *Bruchomyia* in which they have been seen, they are large single sac-like structures often lined within with setae and opening by a single slender duct. The spermathecae of *Psychoda* according to Satchell (1953) are heavily sclerotized organs of quite different structure. The larvae of the various genera are known to me only from the literature, and there are many gaps to be filled here. That of *Bruchomyia argentina* Alex. has recently been described by

Satchell (1953) who finds it very like the larva of *Phlebotomus*. Both are generalized terrestrial forms. The larvae of *Sycorax* and *Horaiella* have developed a ventral sucker as an adaptation to life in water falls, a modification which, with others, may tend to obscure their relationships. Tonnoir (1933) feels that the larva of *Horaiella* is closer to *Sycorax* than to other Psychodidae. The larvae of *Psychoda* are also modified for aquatic or semi-aquatic life, but in other directions, while *Maruina* seems to show modifications parallel to those of *Horaiella* in response to life in running water. *Trichomyia* larvae are specialized wood borers. Satchell (*l.c.*) states that larvae of *Psychodidae* can be divided into two sections, those with a tubular respiratory siphon, and those without a siphon. He places *Sycorax*, *Trichomyia*, *Phlebotomus* and *Bruchomyia* in the latter group, to which should probably be added *Horaiella*. *Psychoda* and allied genera by inference are placed in the first group.

In view of the considerations discussed above, I believe the Phlebotominae are more closely related to the Bruchomyiinae than to the Trichomyiinae or Psychodinae and that the two groups are best combined into a single subfamily, where they will stand as tribes. I give below a partial key to the subfamilies and tribes, carried to genera in the case of the Trichomyiinae and to subgenera in the Phlebotominae. The classification here suggested and the probable relationships of the groups are shown schematically in the accompanying text figure (FIG. 1) and in the key. An arrangement involving the treating of *Sycorax*, *Horaiella* and *Bruchomyia* and *Nemopalpus* as subfamilies, as has been done by some recent students (Alexander 1953; Jung 1954), seems to me unnecessary. Carried to its logical conclusion, it would necessitate the creation of an additional subfamily for *Eophlebotomus* and probably also for *Maruina* and some other aberrant forms now included in the Psychodinae. This would result in seven or eight subfamilies, most of which would be monotypic, and would, it seems to me, obscure rather than clarify the relationships within the family. Even Enderlein (1937), noted as he was for the erection of new categories, recognized but five subfamilies in the Psychodidae. The tribal category is available for those who feel that the nomenclature should reflect relationships in more detail than the present arrangement.

The fossil genera discussed above have been omitted from the key, as they are as yet too imperfectly known. *Eatonisca* and *Diplonema* seem to belong clearly in the Trichomyiinae and closer to *Trichomyia* than to *Sycorax*.⁴ *Phlebotomiella* I

believe is best placed in the Phlebotominae, while *Eophlebotomus* apparently represents a condition somewhat between the Trichomyiinae, especially *Sycorax*, and the Phlebotominae. Its venation differs from *Sycorax* in retaining R_2 and R_3 as separate veins, though they are short, and in having M_3 and M_4 stalked, as in *Horaiella* and *Diplonema*. It differs from *Warileya* in the Phlebotominae by the shorter R_2 and R_3 , in having M_3 and M_4 stalked, and in the retention of an appreciable cubitus. The genus *Lepria* Enderlein, founded for a recent species from Costa Rica, has also been omitted, as the description is wholly inadequate. *Eubonetia* Vargas and Diaz Najera I believe is a synonym of *Lepria*, differing from the latter only in the presence of a short sub-



Text figure 1. Schematic representation of the phylogeny and relationships of the Phlebotominae and Trichomyiinae.

costal vein, which may well have been overlooked by Enderlein. The distinctness of both these forms from *Trichomyia* is doubtful, and final decision must await more complete information. *Termitodipteron* Holmgren 1905, is also omitted, as I have not seen the description. It is placed by Tonnoir (1929) in the Trichomyiinae with a query. Finally it may be noted that of the recent genera the following are also known as fossils, mostly from the Baltic Amber or Burmese Copal: *Nemopalpus*, *Phlebotomus*, *Trichomyia*, *Sycorax*, *Pericoma* and *Psychoda*.

KEY TO SUBFAMILIES, TRIBES, GENERA AND SUBGENERA

1. Radius with 5 branches. 2
- Radius with 4 branches, R_2 and R_3 fused into a single vein (*Trichomyiinae*). 4
2. Palpi with 5 segments (*Phlebotominae*). 3
- Palpi with but 4, rarely 3, visible segments. (Psychodinae)
3. Mandibles present and functional; bloodsucking. Spermathecae paired, intromittent organ bifid and with lateral lobes on ninth tergite. (*Phlebotomini*). 8

⁴After the preparation of this study was completed, Dr. G. Satchell (*in litt.*) informed me that he believes *Diplonema* Loew to be inseparable from *Trichomyia* Haliday in Curtis, and will place it in synonymy in a forthcoming paper.

- Mandibles absent or rudimentary, not bloodsucking. Spermatheca single, intromittent organ not bifid and no lateral lobes on ninth tergite (*Bruchomyia*) 6
4. Cubitus short, hardly longer than m-cu. Mandibles present 5
- Cubitus long, several times as long as m-cu. Mandibles absent. *Trichomyia*
5. No r-m cross vein. M_2 and M_4 stalked, forking far from base of wing. $R_2 + 1$ branching from the sector proximal to R_4 *Horaiella*
- r-m cross vein present. M_2 and M_4 not stalked, forking at level of m-cu. $R_2 + 1$ and R_4 forking distal to emission of R_5 *Sycorax*
6. Antennae of 16 segments. Vein Cu_1 short, generally not over twice length of m-cu cross vein *Nemopalpus*
- Antennae of more than 16 segments. Vein Cu_1 long, over one third length of M_4 7
7. Antennae of about 30 segments. Ascoids in the form of peltate disks. Coxite with a subapical tuft of modified setae *Bruchomyia*
- Antennae of 113 segments. Ascoids slender and forked. Coxite without a tuft of setae. *Eutonnoiria*
8. Radius dichotomously branched, at least R_3 not forking from R_2 proximal to R_4 . Lateral lobes of ninth tergite very short, shorter than cerci. Cibarium without teeth. Palpal formula 1-4-5-3-2 *Hertigia*
- Radius pinnately branched, R_3 always arising proximal to R_4 . Lateral lobes always longer than cerci. Palpal formula never as above 9
9. Wing broad and rounded, R_3 arising close to R_4 so that gamma is very short. Coxite short and rounded, shorter than style. No pleural setae. Cibarium without teeth *Warileya*
- Wing usually long and slender, often pointed. Gamma never so short. Coxite always considerably longer than wide and at least as long as style. Pleural setae present or absent. Cibarium with or without teeth *Phlebotomus* 10
10. Postspiracular pleural setae absent, except in *P. squamipleuris* which has short broad scales. Fifth palpal segment always the longest. Old World species 11
- Long, narrow or ligulate setae present on upper border of anepisternum and lower border of mesanepisternum. Frequently with third palpal segment the longest. New World species 12
11. Cibarium without teeth, or the teeth rudimentary or few, not forming a comblike row. Abdominal hairs erect, not recumbent or scale-like. Male genitalia and female spermathecae diversified, the latter usually annulate. Usually with fourth palpal segment the shortest (Subgenus *Phlebotomus*)
- Cibarium with well developed teeth, usually numerous and generally forming a comb-like row. Abdominal hairs all or largely recumbent and scale-like. Male genitalia quite uniform, female spermathecae generally smooth, or at least rarely annulate. Usually with second palpal segment the shortest (Subgenus *Sergentomyia*)
12. Third palpal segment the longest, fourth the shortest, very rarely the third and fifth segments subequal. Coxite without a basal tuft of setae. Style with 2 to 5 major spines, not set on long tubercles. Parameres simple or very complex. Cibarium with 4 or more horizontal teeth, numerous erect teeth, a strong chitinous arch and a well marked pigment patch. Pharynx unarmed. Spermathecae annulate, the rings often imbricated and the terminal knob large and conspicuous. Abdominal setae often in part scale-like and recumbent (Subgenus *Psychodopygus*)
- Fifth palpal segment the longest, or if subequal to the third, then the coxites bear a basal tuft of setae or the styles are deeply bifid or the spermathecae quite otherwise 13
13. Third and fifth palpal segments subequal or the fifth longest. Coxite without basal tuft. Style with four spines, deeply bifid. Parameres with modified setae. Spermathecae with heavily sclerotized associated structures (Subgenus *Viannamyia*)
- Fifth palpal segment generally clearly the longest, it subequal to third, the coxites bear a basal tuft of setae or the parameres are modified; styles various, but never bifid. Parameres simple, armed or modified in various ways. Spermathecae various, but never with sclerotized associated structures (Subgenus *Brumptomyia*)

The further classification of the insects now placed in *Phlebotomus* in the broad sense is beset with difficulties of two kinds, nomenclatorial and morphological. On the purely nomenclatorial side the name *Phlebotomus* is now firmly established in the medical as well as entomological literature as the name for the bloodsucking psychodid sandflies. Any attempt to rename or separate off a considerable part of these insects would lead to much confusion, and, in my opinion, would be unjustifiable on practical grounds. From the morphological and taxonomic standpoint, however, the type of the genus *Phlebotomus*, *P. papatasi* Scop., is a rather aberrant form, and were the sandflies of no economic interest, most of the other species would long ago have been placed in separate genera. The case of the genus *Anopheles* among mosquitoes is in many ways parallel. Here a very considerable number of names were proposed for segregates believed to be of generic rank, but through the genius of Edwards (1932) the resulting confusion was clarified and a workable and satisfactory system of classification devised which preserved the economically important name *Anopheles* for the malaria carrying mosquitoes.

An attempt has been made below to subdivide *Phlebotomus* into subgenera, groups and series. In the case of the Old World species, the system devised by Theodor (1948) has been modified to overcome certain criticisms and to bring it into line with the system proposed here for the New World species. In the case of the New World species, the arrangement suggested below will be subject to considerable revision as the species become better known. The fact that considerably less than half the described species are known in both sexes has greatly hampered the devising of a workable arrangement.

Genus *Phlebotomus*

Subgenus *Phlebotomus*

Group *Papatasi* (= *Phlebotomus* s. s. of Theodor)

Series *Major* (= *Synphlebotomus*, *Larrousius*, *Adlerius* and *Euphlebotomus* of Theodor)

Series *Sergenti* (= *Paraphlebotomus* and *Anaphlebotomus* of Theodor)

Group *Brevifilis* (= *Austrophlebotomus* of Theodor)

Group *Gigas* (= *Speleophlebotomus* of Theodor)

Subgenus *Sergentomyia*Group *Minutus* (= *Sergentomyia* s. s. of Theodor)Group *Hospitii* (= *Sintonius* of Theodor)Group *Mirabilis* (= *Spelaomyia* of Theodor)Subgenus *Psychodopygus* (= *Shannonomyia* Dyar,
Shannonomyia Pratt.)Group *Panamensis* (= *Shannonomyia* Fehld. &
Hertig 1951)Group *Intermedius*Subgenus *Viannomyia*Subgenus *Brumptomyia*Group *Brumpti* (= *Brumptomyia* auct.)Series *Brumpti*Series *Vexator*Group *Vespertilionis*Group *Triacanthus* (= *Pressatia* Mang.)Series *Triacanthus*Series *Fischeri* (= *Pintomyia* C. L.)Group *Anthophorus* (= *Dampfomyia* Addis)Group *Cayennensis*Group *Shannoni*Group *Cruciatus*Series *Cruciatus*Series *Verrucarius*Series *Migonei*Series *Walkerii*Series *Castroii* (= *Catomyia* Mang.)Series *Atrocavalus*Series *Baityi*Series *Longipalpis* (= *Lutzomyia* Franca)Series *Infraspinosus* (= *Evandromyia* Mang.)Series *Castanheirai*Series *Servulolimai*Group *Longispinus*Group *Alphabeticus*

It may be useful to give a key to the groups of both Old and New World *Phlebotomus*, and one is here appended. Keys to the series must await the appearance of very considerably more information, especially in regard to the New World species. Following the key, however, will be found some discussion of the series proposed for the New World species, and a list of the described species placed in subgenera, groups and series.

KEYS TO GROUPS OF PHLEBOTOMUS

Subgenus *Phlebotomus*

1. Style long and cylindrical with five spines, three of which are terminal. Parameres trifid, the dorsal arm long and setose. Lateral lobes with short spines at tip. Spermathecae annulate. Pharynx without spines. Group *papatasi*
- Style with 3 to 5 spines, never more than two of which are terminal. Lateral lobes unarmed. Pharynx usually armed with scale-like or spine-like setae. 2
2. Style with four or five spines, when with five, two are terminal. Spermathecae with ducts and body clearly differentiated, usually annulate and with a discrete terminal knob. Pharynx armed with large or small spines. Group *major*
- Style with three or five spines only one of which is terminal. Spermathecae wrinkled or smooth, the terminal knob poorly defined or absent. 3
3. Style with three spines. Genital filaments short and heavy, little longer than the very large pump. Spermathecae with irregularly wrinkled or smooth ovoid body and slender ducts, the terminal knob small and sunk in a pit. Cibarium with four or more small but discrete horizontal teeth. Pharynx densely armed with short and long hair-like spines. Group *brevifilis*

— Style with five spines, long and cylindrical. Genital filaments several times as long as the rather slender pump, and with a pair of paragenital sclerotized rod-like structure on each side of the pump. Spermathecae membranous, not annulate, consisting of a pair of broad short tubes opening from a wide common duct and tapering irregularly to a slender apex bearing a small tuft of hairs. Cibarium without teeth. Pharynx with a few scale-like teeth. Group *gigas*

Subgenus *Sergentomyia*

1. Abdominal hairs normally all recumbent. Spermathecae tubular or ovoid generally smooth, less often wrinkled or with rows of spines, the terminal knob sunk in a pit or within a terminal funnel-shaped structure. Group *minutus*
- Abdominal hairs not all recumbent. Spermathecae annulate, or if otherwise, lacking a terminal knob. 2
2. Style with four major spines, at least two of which are terminal. Spermathecae generally annulate, sometimes irregularly so and with a discrete terminal knob not sunk in a pit. Aedeagus sclerotized. Group *hospitii*
- Style with two major spines, one of which is terminal. Spermathecae large membranous sac-like structures without terminal knob. Coxite with a tuft of long setae on inner aspect of base. Genital filaments short and heavy, their apices with a lateral process. Aedeagus membranous. Group *mirabilis*

Subgenus *Psychodopygus*

1. Fifth palpal segment very short, never more than twice as long as fourth and generally less than $\frac{2}{3}$ as long as third. Cibarium with four to eight horizontal teeth and usually numerous erect teeth some of which are markedly enlarged. Abdomen usually with recumbent scale-like setae. Spermathecae with deeply imbricated annuli and with their ducts partly or wholly characteristically wrinkled or pleated. Parameres simple or complex. Group *panamensis*
- Fifth palpal segment longer, occasionally subequal to third. Cibarium always with more than four teeth, generally over ten, and with numerous erect teeth and strong pigment patch. Abdomen without scale-like setae. Spermathecae annulate, the annuli not imbricate, ducts smooth or weakly wrinkled. Style with four spines, parameres simple. Group *intermedius*

Subgenus *Brumptomyia*

1. Style of male genitalia with five spines, two of which are terminal. Coxite with a tuft or patch of fine to heavy setae on inner aspect of base. Parameres simple or rarely armed. Cibarium with several rows of weak horizontal teeth (series *Brumpti*) or a single row of four or more horizontal teeth (series *Vexator*). Spermathecae annulate, with usually a sub-globose terminal annulus and a more or less well developed terminal knob, or rarely smooth. Group *brumpti*
- Style of male genitalia with four or fewer spines, or if with five spines, only one is terminal and the coxite lacks a basal tuft. 2
2. Coxite with a basal tuft of hairs or modified setae. Style with four or less spines. 3
- Coxite without basal setae. Style sometimes with five or more spines. 5
3. Individual ducts of spermathecae short and heavily sclerotized, common duct usually wide and membranous. Style with three or four spines and a subterminal seta. Group *triacanthus*
- Individual ducts of spermathecae short or long, not sclerotized. Style as above. 4

4. Spermathecae membranous, smooth or finely wrinkled, often with large bladder-like subterminal expansion or small globular excrescences. Ducts usually short, joining in a wide common duct. Style with three or four spines, the basal ones often reduced to slender setae. Cibarium with four slender horizontal teeth. Group **vespertilionis**
- Spermathecae smooth, wrinkled or annulate, generally small, without bladder-like or globular excrescences, the ducts usually long and slender, opening separately or with a short slender common duct. Style with four spines, rarely with two paired terminally, usually with a subterminal seta. Cibarium with 4-12 teeth. Pharynx rarely armed with spines and transverse ridges. Group **cruciatius**
5. Pharynx armed with slender teeth, or small spines set on tubercles. Style with four spines, two of which are terminal and without subterminal seta. Cibarium with 5 to over thirty fine teeth forming a comb. Group **cayennensis**
- Pharynx unarmed. Style never with terminal spines paired. Cibarium with teeth not forming a comb. 6
6. Ascoids with a long or short posterior prolongation. Style with four spines, generally without subterminal seta. Spermathecae usually smooth, sausage shaped or globose, less often wrinkled or tubular, rarely annulate, the ducts smooth and slender, usually with a short to long common duct. Parameres simple or with modified setae or rarely bifid Group **shannoni**
- Ascoids simple, without posterior prolongation. Style with three to five spines, generally with a subterminal seta. Spermathecae with wide membranous ducts or otherwise modified. 7
7. Style with four spines and a subterminal seta, the basal spine close to base of segment. Parameres bifid or trifid. Spermathecae pear shaped, finely wrinkled, with short smooth individual ducts and wide membranous common duct. Group **longispinus**
- Style with three, five or six spines, with or without a subterminal seta. 8
8. Style with three or five spines and usually a subterminal seta. Parameres with long dorsal articulated setiferous arm. Spermathecae morulate, the slender terminal knob embedded between the segments; ducts membranous, slender or wide. Cibarium with two to six broad, often blade-like horizontal teeth and usually one or more rows of fine lateral teeth. Eyes unusually small. Group **anthophorus**
- Style with five, rarely six spines, one of which is terminal. Parameres simple. Spermathecae annulate with smooth slender ducts. Group **alphabeticus**

In regard to the further subdivision of the Old World species, I do not feel qualified to comment in detail. I have, however, at the suggestion of Dr. Parrot, included two series in the *Major* group, those with five spines on the male style forming the series *Major*, those with four spines forming the series *Sergenti*. Further subdivisions of the *minutus* and *hospitii* groups of *Sergentomyia* may be found useful, but the working out of a suitable arrangement had best be left to those more familiar with Old World species.

So far as the New World species are concerned, some further comments may be made. The subgenus *Psychodopygus* includes species with a short fifth palpal segment. It seems to be quite well set off from other New World *Phlebotomus* on the basis of the characters in the key, but there

are a few species placed in other subgenera which may have a single character in common with *Psychodopygus*, such as a quite short fifth palpal segment, similar style, or similar spermathecae, while not having the combination of characters shown by *Psychodopygus*. The two groups into which the subgenus has been divided are for the most part clear cut, but *P. Lloydi* Antunes appears to form a connecting link, if the sexes have been properly associated. In this species the male clearly belongs to the *intermedius* group, while the female has spermathecae typical of the *panamensis* group. We included it in *Shannonomyia* (Fairchild & Hertig, 1950), since the name is based on the female. The subgenus as a whole is distributed widely from southern Mexico to Northern Argentina, though the Amazon valley appears to be near the center of distribution. Many of the species are known to bite man and the larger domestic animals, and the subgenus probably contains more man-biting species than any other in the New World, including several possible or probable vectors of human leishmaniasis. The *panamensis* group includes those species placed in *Shannonomyia* by us in 1950, though *Psychodopygus* is the prior name and should have been used. The *intermedius* group includes the following species as well as several undescribed forms: *intermedius* Lutz & Neiva, *whitmani* Antunes & Coutinho, *andusei* Rozeboom, *apicalis* Floch & Abonnenc, *trapidoi* Fairchild & Hertig, *ylephiletor* Fairchild & Hertig, all known in both sexes; *flaviscutellatus* Mangabeira, *elongatus* Floch & Abonnenc, known in the male sex only, and *machicouensis* Floch & Abonnenc, known only in the female.

The subgenus *Vianuamyia* includes a small group of species previously known only as males. We have recently come to the conclusion that certain females described by Floch and Abonnenc, and of which we have material also from Panamá, in reality belong with these males. The characters of both sexes are so distinctive that it has seemed best to maintain the group as a separate subgenus. The species appear to be uncommon and the known range is from the Amazon basin to Panamá. The included species are as follows: *tuberculatus* Mang., *furcatus* Mang., *fariasi* Damasceno, Causey & Arouk, known from males only, *arborealis* F. & A. and an unnamed species of Floch and Abonnenc known from females only. The material from Panamá consists of a considerable series of both sexes, the males close to *furcatus*, the females close to *arborealis*, so that we suspect that *arborealis* may be the female of *furcatus*.

I have included the remainder, and largest portion, of the New World *Phlebotomus* in the subgenus *Brumptomyia*, as I have been unable to find non-sexual characters or marked and correlated sexual characters which can be used to clearly separate them. Some of the groups,

e.g., the *cayennensis* group and the *anthophorus* group, might possibly be better as subgenera, but the most marked characters of the former, the armed pharynx and comb-like cibarial teeth, are found in other apparently unrelated species, while the unusual structure of the spermathecae and cibarium of the *anthophorus* group is also approached by other forms. Several rather bizarre species, now known only in one sex, may prove to warrant the erection of further subgenera when they become more completely known.

Because of the lack of associated females of many species, and of information on ascoids and certain other structures, I have had to rely unduly on male characters in dividing the *Brumptomyia* into groups. I feel this to be a serious defect, for, with some exceptions, the female structures have proven generally more stable. Among these male characters, the number and relative positions of the spines on the style seem to offer the best clues to relationship.

The style with five spines, of which two are paired on the distal end, seems to be the type from which most of the others appear to have been derived. The first step in this process would seem to be the reduction of one of the terminal spines to a small seta, and its eventual disappearance. Where there are but four spines and two of these are terminal, as in the *cayennensis* group, there is no subterminal seta. In the *alphabeticus* group, which is probably not homogeneous, the subterminal seta has been lost in all but one (undescribed) species, and the five-spined condition appears to be due to the permanent acquisition of a supernumerary spine, *alphabeticus* itself showing this tendency by often having six spines on one or both styles.

The *brumpti* group includes those species placed in *Brumptomyia* by Mangabeira and Galindo (1944) plus their "vexator group." The basis for combining these somewhat divergent species is the presence of five spines on the style, a basal tuft on coxite and usually annulate spermathecae. The quite homogeneous *brumpti* series is separable from the *vexator* series on the elongate styles, several rows of horizontal teeth in the cibarium and by the larvae having but two caudal setae in all stages. This combination of characters, if subsequently proven to hold throughout the series, may warrant raising to group or possibly subgeneric level. The *vexator* series is less homogeneous, consisting of species with the male style five-spined and with a terminal pair, though the style is not as elongate as in the *brumpti* series. A basal tuft is commonly present on the coxite, reduced to a few lax setae in some species or rarely absent. The cibarium has a single row of horizontal teeth, sometimes displaced laterally and occasionally with a comb of teeth as in the *cayennensis* group. The spermathecae are usually slender with relatively long and slender ducts, mostly with few to many annuli on the

basal portion of the spermathecal body, rarely the spermathecae quite smooth, but all with a terminal knob. The larva of only *noguchii* seems to be known; it has four caudal bristles except in the first instar. *P. battistinii* Hertig is placed in this series provisionally. It differs from the others in having the parameres armed, though agreeing in other characters, including annulate spermathecae. The *brumpti* series occurs from Mexico to Paraguay, the species being locally abundant, especially in animal burrows. There seem to be no records of their biting man or large animals. The *vexator* series ranges from Eastern United States and California south into Southern Brazil, with a preponderance of species in Mexico. Two species, *peruensis* and an undescribed species will bite man; *vexator* feeds on reptiles and *noguchii* on mice, while information is lacking on the others, though they probably bite man rarely if at all.

The *vespertilionis* group includes species with four or fewer, generally three spines on the style, nearly always a subterminal seta and a basal tuft of setae on coxite. The lateral lobes in most species are considerably to greatly inflated. The cibarium usually has four horizontal teeth and some vertical teeth, often also fairly prominent lateral teeth and usually a strong chitinous arch. The spermathecae have a short broad membranous common duct and usually short individual ducts. The body of the spermatheca is variously modified, cylindrical, pear-shaped or often with a large lateral bladder-like expansion, sometimes finely annulate basally. The group is mainly Central American, with two species in French Guiana and two in the West Indies. None have been taken biting man, but one probably feeds on bats and others may do so.

The group *triacanthus* includes species placed in *Pressatia* by Mangabeira (1942 p. 131) and *Pintomyia* by Costa Lima (1932) p. 44). The style bears three or four spines and a subterminal seta and the coxite has a basal tuft of setae. The cibarium usually bears four horizontal teeth. The spermathecae are subcylindrical or oval, thin walled, often with the terminal knob broad and flattened, and with the individual ducts almost always heavily sclerotized and smooth. The common duct is wide and membranous. The series *triacanthus* has three spines on the style and the hind femora without modified setae, while the series *fischeri* has four spines on the style and the hind femora armed with a row of short heavy spines. *Pilosus* D. & C. and *chassigneti* F. & A. are placed here provisionally on the structure of male style. They lack a basal tuft on coxite, and the spermathecae of *chassigneti* are simpler, the individual ducts but weakly sclerotized and the common duct practically absent. The group as a whole ranges from Panama to southern Brazil, with the center of distribution apparently

in the Amazon region. Two species, both in the *fischeri* series, bite man avidly in Southern Brazil, *fischeri* and *pessoai*. The former is the most important domestic species in Sao Paulo and has been experimentally infected with *Leishmania brasiliensis*, while *pessoai* is also common and has been found naturally infected with *Leishmania* in Brazil. Nothing appears to have been recorded as to the host preferences of the other species.

The group *anthophorus*, for which Addis (1944) proposed the subgenus *Dampfomyia*, is in many ways quite aberrant, and might with considerable justice be retained as a full subgenus. Two species have been described and we have material of four or five additional species. The male genitalia have generally three spines on the style, in one case five. There is no basal tuft on the coxite, but the paramere bears a long dorsal setose arm, apparently with a pseudo-articulation at its base. The cibarium has two or more horizontal teeth, but these appear to be partially fused into a plate-like structure, and there are usually one or more rows of lateral teeth. The spermathecae have rather short broad membranous ducts, while the spermathecal bodies are variously modified, usually morula-like, the terminal knob buried in the mass of bubble-like expansions. The eyes in both sexes are unusually small and the wings quite narrow. *P. anthophorus* Addis, the only species on which information is available, feeds on rabbits but refuses man in the laboratory. All the species so far seen have been taken in Panama or northwards. The two groups of *vespertilionis* and *anthophorus* seem to be somewhat related, showing a tendency towards reduction of the number of spines on the style to three or two, and general similarity in the spermathecae.

The group *cayennensis* is also quite well marked, showing a style with four spines, two of which are paired at the apex, no subterminal seta and no basal tuft on the coxite. The spermathecae are similar in all, with a rounded head, annulate body and relatively slender ducts. The cibarium is quite characteristic, bearing a comb of from 5 to 30 fine horizontal teeth and lacking a complete chitinized arch. All the species bear spines on the pharynx also. The group comes the closest of any New World *Phlebotomus* to the subgenus *Sergentomyia* of the Old World, but the presence of pleural setae and structure of the spermathecae indicate that the resemblance is probably coincidental. The cibarial comb and armed pharynx are exceptional in the New World, but not unique, as *P. chiapanensis* of the *vexator* group has both, while *P. trinidadensis* of the same group also has an armed pharynx. It is possible that the *cayennensis* group was derived from a form like *chiapanensis* having five spines on the style. The group is limited to the Caribbean area, from the Guianas to Mexico and the West Indian Islands. Although direct observations seem to be lacking,

the occurrence of freshly engorged members of this group in localities where mammals are practically absent and birds rare, suggests that they may feed on lizard blood.

The *shannoni* group contains species with four spines on the style, one of which is terminal and without a subterminal seta or basal tuft on coxite. The parameres are frequently armed. The cibarium usually bears four horizontal teeth, though up to 12 may be present, and there are generally numerous small erect teeth and often a few fine lateral teeth. The pharynx is unarmed, the chitinized arch usually present though often poorly developed. The spermathecae are variable, tubular, cylindrical, ovoid or globose, generally smooth, sometimes wrinkled, rarely annulate, but always with slender ducts. Both sexes have the ascoids with a posterior prolongation, which may be very long, extending beyond the base of the segment, or a short rounded spur. Several series are perhaps definable here, but grouping on any one character brings together species heterogeneous for other characters. Thus species with spermathecae like *shannoni* may have short or long prolongations on the ascoids or armed or unarmed parameres, while species with globose spermathecae like *aragaoi* may have quite dissimilar males. Similar males, such as *runoides* and *barrettoi* have females with quite different spermathecae. Since hardly a third of the species are known in both sexes, it seems best to postpone the further division of the group. *P. shannoni* has a very wide range, from Southern U. S. to Paraguay. There have been a few reports of *shannoni* biting man in the U. S. and Brazil, and it appears to do so regularly in Campeche, Mexico (Biagi 1953) but although an abundant species in Panama, we have never taken it biting man nor in animal baited mosquito traps here. There is no information on hosts of other species.

The group *longispinus* contains species with four spines on the style, one of which is terminal and one on the basal third of the segment. A subterminal seta is present and generally a row of very long hairs on the ventral aspect of the coxite, but there is no basal tuft. The parameres are divided into two or three branches and the aedeagus may also be modified. The cibarium has four short horizontal teeth, a few weak lateral and vertical teeth and a chitinous arch. The spermathecae have pear shaped finely annulate or wrinkled bodies, large terminal knobs, and smooth ducts which are usually short and slender, but may have the common duct enlarged and membranous. The fourth stage larva has four caudal setae. The group has a limited distribution, from the Amazon Valley to Panama, and most of the species have been taken from animal burrows. They are not reported as biting man.

The *cruciatas* group contains a large assemblage of rather diverse species, some of which will

probably be segregated into separate groups with increasing knowledge. The males have a style with four spines, with or without a subterminal seta and a basal tuft or group of setae on coxite. The parameres are simple or variously modified, and the lateral lobes may be armed with terminal spines. The females of only a small proportion of the species are known, and show considerable diversity of cibarial and spermathecal structure, though a single row of horizontal teeth is almost always present in the cibarium and the spermathecae almost always have relatively slender ducts and simple bodies, either smooth, wrinkled or annulate. Both sexes have usually simple ascoids, occasionally with a short posterior prolongation. The division into series is based largely on male characters.

The series *cruciatus* has the parameres simple, no subterminal seta on style and the spermathecae generally annulate. It ranges from Texas to Paraguay and at least three species bite man readily.

The series *verrucarum* is similar to the *cruciatus* series, but the style has the subterminal seta and the spermathecae are usually finely wrinkled. The series seems to be limited to Northwestern South America and Central America, from Venezuela and Peru to Costa Rica. At least three species bite man avidly, and one is the vector of bartonellosis in Peru.

The series *migonei* consists of but a few species. The style has a subterminal seta, and the parameres are simple, except in *edwardsi*, which is placed here on style and spermathecae. Four species have the spermathecae globose, two have them sausage-shaped, in both cases smooth and with fairly long smooth ducts. The range is from Argentina to French Guiana. One species, *cortezii*, has been taken biting chickens, while *migonei* bites man as well as many domestic animals and has been found infected with *Leishmania* in nature in Brazil. *P. delposoi* is included here, though the cibarium is aberrant.

The series *walkeri* consists of species with a subterminal seta, the style rather long and slender and the coxite with a patch of lax hairs in the middle as well as the basal tuft. The presumed female of one species has smooth subconical spermathecae with a long terminal knob; of another, the spermathecae are like those of the *triacanthus* group and the sexes may be wrongly associated.

The series *castroi* has styles similar to the *walkeri* series, but the parameres have one or two strong setae arising from a tubercle on the dorsobasal aspect. Mangabeira (1942 p. 185) erected the subgenus *Castromyia* for these species. Females are unknown as yet.

The series *atroclavatus* consists of but three species. The style has a subterminal seta, the pharynx is armed with spines and strong transverse ridges and the spermathecae are smooth,

ovoid or pear shaped. *Atroclavatus* ranges from Trinidad to Panama and in the West Indies it occurs on Guadeloupe and on St. Croix in the Virgin Islands. The other two species are from Venezuela and may be the sexes of a single species.

The series *awaensis* contains species without the subterminal seta and with simple parameres. Several species have median setae or spines on the coxite in addition to the basal tuft. No females are known. The series is probably not homogeneous. The range is from French Guiana to Southern Brazil, with the bulk of the species Amazonian. Nothing is known of the food habits.

The *longipalpis* series includes the species for which the subgeneric name *Lutzomyia* was created. The styles have a subterminal seta and the parameres are armed with heavy dorsal spines. The basal tuft on the coxite is also formed of heavy spines. The spermathecae are cylindrical and wrinkled. *P. vexillarius* F. & H. has more in common with *longipalpis*, though the spermathecae are quite similar to *cruciatus*. *Longipalpis* ranges from Mexico to Argentina and bites man readily. The other species are known from Panama, Brazil and Uruguay.

Series *baityi* includes but three species, two as yet undescribed. The spines of the style are so crowded at the tip that two have become paired terminally, although the subterminal seta is retained. The coxites have median setae as well as the basal tuft, while the parameres are simple and unusually broad and flat. The cibarium has four horizontal teeth and the spermathecae are exceedingly small, sausage shaped and practically without ducts. One species each from the Amazon, Peru and Panama.

The *infraspinosus* series (subgenus *Evandromyia* Mang.) has a subterminal seta and the parameres are deeply divided into two branches, and in one case the upper branch is again forked and the aedeagus modified. Some species also have the lateral lobes with terminal spines. The female of but one species has been described; it has an annulate spermathecae and four spines in the cibarium. French Guiana to Minas Geraes, Brazil covers the range and nothing is known of the feeding habits.

The series *castanheirai* differs from the *infraspinosus* series in lacking the subterminal seta on the style and in having the upper branch of the parameres bearing usually a dense tuft of heavy setae where the upper branch would arise. The two known females have annulate spermathecae with slender ducts, similar to those of *intermedius* and allies, and with cibaria with more than four horizontal teeth. One species occurs in Panama, the remainder in French Guiana and the Amazon basin. Nothing is known of host relationships.

The series *servulolimai* differs from the *walkeri* series in lacking a subterminal seta on the style. Females are unknown and the species are known

to me only from the descriptions, which contain no mention of the ascoids, and in which the presence of a small subterminal seta may have been overlooked. All are from the Amazon basin.

The group *alphabeticus* contains species with five or more spines on the style, but without paired spines terminally and without a basal tuft on coxite. The female of only *alphabeticus* is known; it has a curious spermathecae of four large annuli, the first and last larger than the intermediate ones. The cibarium and ascoids have not been described. The group is probably highly artificial.

There remains a single species described in both sexes which I am unable to place, *P. nordesinus* Mang. The genitalia agree more or less with the *shannoni* group, as do the spermathecae, but the ascoids are simple and the cibarium as in *trinidadensis*, with strong lateral teeth.

Unplaced species known in the male only are as follows, *cerqueirai* D. & C., has a style like *baityi* but lacks a basal tuft and has the parameres forked and lateral lobes armed with heavy clubbed terminal spines. *Rangelianus* Ortiz, with a four spined style and subterminal seta, the basal spine reduced and seta-like and no basal tuft, would go easily into the *vespertilionis* group had it a basal tuft on coxite, or perhaps the *shannoni* group, were the ascoids not simple. The four species *minasensis* Mang., *micropygus* Mang., *quadrispinosus* F. & A. and *venezuelensis* F. & A. share small size, four spined styles without subterminal seta, lack of basal tuft on coxite and simple parameres. They have so few outstanding characteristics that I have found it impossible to place them in any group in the absence of the females.

P. bursiformis F. & A., *falciformis* F. & A., *pescei* Hertig and *oppidanus* Dampf., are known in the female only. The first two are aberrant forms with peculiar spermathecae unplaceable without knowledge of the males. *Pescei* may belong either in the *brumpti* group or the *cruciatu*s group, while *oppidanus* probably belongs near *vexator* in the *brumpti* group.

Finally there are several species whose descriptions are so incomplete that they cannot be placed. Five of these are females, *P. osornoii* Rist. & Dao Van Ty, *imperatrix* Alex., *singularis* C.-L., *fouseci* C.-L. and *cavernicolus* C.-L. Some of these may be the same as better described species. *Maracayensis* Nuñez Tovar, described from a male, is unrecognizable. *Rostrans* Summers, described from both sexes, is also probably unrecognizable. I have seen the types of *rostrans*, which are uncleaned and broken, 1 ♂ 3 ♀ mounted on a single slide and the sexes probably not conspecific. The male lacks wings and fifth palpal segments. The style has four spines but no subterminal seta and a large loose tuft of heavy setae on base of coxite. The females do not show spermathecae or cibarium, and the single specimen with complete palpi shows the fifth seg-

ment short, about one-half length of the third. The male probably belongs in the *cruciatu*s group and seems closest to *auruensis* Mang. or *octavianus* Vargas (= *affinis* Mang.), but remounting and careful comparison will be necessary for certainty. The female is probably a *Psychodopygus*, but without clearing and remounting cannot be certainly determined.

The New World species are listed below, placed in the subgenera, groups and series in which I believe they belong on present evidence.

Subgenus *Psychodopygus*

Group *panamensis*

amazonensis Root, *arthuri* Fons., *ayozai* B. & C., *bispinosus* F. & H., *carrerei* Barr., *chagasi* C.-L., *colas-belcouri* F. & Chass., *complexus* Mang., *davisi* Root, *geniculatus* Mang., *guyanensis* F. & A., *hirsutus* Mang., *Lloydii* Ant., *maripaensis* C.-L., *rooti* Mang., *squamiventris* L.&N., *unisetosus* Mang.

Group *intermedius*

anduzei Rozelb., *apicalis* F. & A., *cauchensis* F. & A., *elongatus* F. & A., *flaviscutellatus* Mang., *intermedius* L. & N., *machicouensis* F. & A., *sylvicolus* F. & A., *trapidoi* F. & H., *whitmani* Ant. & Cout., *ylephiletor* F. & H.

Subgenus *Viannamyia*

arboREALIS F. & A., *fariasi* D., C. & A., *furcatus* Mang., *tuberculatus* Mang.

Subgenus *Brumptomya*

Group *brumpti*

Series *brumpti*

amarali B. & C., *avellari* C.-L., *brumpti* Larr., *cardosoi* B. & C., *cunhai* Mang., *galindoi* F. & H., *guimaraesi* B. & C., *hamata* F. & H., *leopoldoi* Rodr., *mangabeirai* B. & C., *nitzulescui* C.-L., *pentacanthus* Barr., *pinto* C.-L., *spinosis* F. & A., *travassosi* Mang., *trigolodytes* Latz.

Series *vexator*

battistinii Hert., *chiapanensis* Dampf., *durani* Vargas & Najera, *longipennis* Barr., *noguchii* Shann., *oswaldoi* Mang., *peresi* Mang., *peruensis* Shann., *pratti* V. & N., *quinquefer* Dyar, *rickardi* C.-L., *rorotaensis* F. & A., *stewarti* Mang. & Gal., *trinidadensis* Newst., *vexator* Coq., *vindicator* Dampf., *zikani* Barr.

Group *vespertilionis*

beltrani V. & N., *christophe*i F. & T., *deleoni* F. & H., *orestes* F. & T., *pinealis* F. & A., *saulensis* F. & A., *vesiciferus* F. & H., *vespertilionis* F. & H.

Group *triacanthus*

Series *triacanthus*

camposi Rodr., *chassigneti* F. & A., *choti* F. & A., *dysponetus* F. & H., *equatorialis* Mang., *pilosus* D. & C., *triacanthus* Mang., *trispinosus* Mang.

Series *fischeri*

damasceni Mang., *fischeri* Pinto, *peessoai* Cout., & Barr., *spinosus* F. & A.

Group *anthophorus*

anthophorus Addis, *dodgei* Vargas & Najera.

Group *cayennensis*

cayennensis F. & A., *ctenidophorus* F. & H., *cubensis* F. & T., *duppyorum* F. & T., *hardisoni* V. & N., *wirthi* V. & N.

Group *shannoni*

abonnenci F. & Ch., *aragoi* C. L., *barretto* Mang., *brasiliensis* C. L., *campbelli* D. & C., *carpenteri* F. & H., *continho* Mang., *dendrophylus* Mang., *digitatum* D. & A., *dreisbachi* D. & C., *heckenrothi* F. & A., *inflatus* F. & A., *lanei* B. & C., *lichyi* F. & C., *lutianus* C.-L., *oliverioi* B. & C., *pascualei* B. & C., *pestanai* B. & C., *punctigenicalatus* F. & A., *runoides* F. & H., *shannoni* Dyar, *souza-castroi* D. & C., *texasus* Dampf., *undulatus* F. & H., *volcanensis* F. & H.

Group *cruciatu*Series *cruciatu*

antunesi Cout., *bourrouli* B. & C., *cruciatu* Coq., *diabolicus* Hall, *fluvialilis* F. & A., *gomezi* Nitz., *monticolus* C.-L.

Series *verrucarum*

colombianus Rist. & Van Ty., *evansi* N.-T., *verrucarum* Towns.

Series *migonei*

cortelezzii Brethes, *del-pozo* V. & N., *ferrera* C. & D., *migonei* Franca, *pacia* F. & A., *sallei* Galvao & Coutinho, *edwardsi* Mang.

Series *walkeri*

aurensis Mang., *basispinosus* B. & C., *brachipygus* Mang., *carvalhoi* D. & C., *evandroi* C.-L., & Ant., *flochi* Aboon. & Chass., *marajoensis* D. & C., *microps* Mang., *octavianus* Varg., *sericeus* F. & A., *ubiquitatis* Mang., *walkeri* Newst.

Series *castroi*

castroi B. & C., *costalimai* Mang., *deanei* D. & C., *tupynambai* Mang.

Series *atroclavatus*

atroclavatus Knab, *ovallesi* Ortiz, *zuliaensis* F. & A.

Series *baityi*

baityi D. & C.

Series *longipalpis*

cruci Mang., *gaminarai* Cord., Vog., & Coss., *longipalpis* L. & N., *vexillarius* F. & H.

Series *infraspinosus*

brachiphallus Mang., *infraspinosus* Mang., *lenti* Mang., *monstruosus* F. & A.

Series *castanheirai*

aclydiferus F. & H., *castanheirai* D. & C., *dunhami* C. & D., *inini* F. & A., *lopesi* D. & C., *melloi* C. & D.

Series *servulolimai*

meirai C. & D., *servulolimai* D. & C., *williamsi* D., C. & A., *wilsoni* D. & C.

Group *longispinus*

dasydodegeton Castro, *longispinus* Mang., *trichopygus* F. & A., *triramulus* F. & H., *wagleyi* C. & D.

Group *alphabeticus*

alphabeticus Fons., *brevipectus* Barr., *sordellii* Shann. & Del Ponte.

SUMMARY

On the basis of the wing venation of fossil genera and wing venation and other structures of recent genera, it is concluded that the Psychodidae are best divided into three subfamilies, the Psychodinae, Trichomyiinae and Phlebotominae. The Psychodinae are not further considered here.

The Trichomyiinae studied consist of three recent and two fossil genera, *Trichomyia*, *Horaiella* and *Sycorax*, and *Diplonema* and *Eatonisca*. This subfamily is connected with the Phlebotominae by the fossil genus *Eophlebotomus*. Keys for the separation of the recent genera and figures of wing venation of all genera are given.

The Phlebotominae are divided into two tribes, the more primitive Bruchomyiini, consisting of three recent genera, *Bruchomyia*, *Nemopalpus* and *Eutonnoiria*, and the Phlebotomini, consisting of three recent and two fossil genera, *Hertigia*, *Warileya* and *Phlebotomus*, and *Eophlebotomus* and *Phlebotomiella*. Keys to recent genera and figures of wing venation of all genera are given.

The genus *Phlebotomus* is considered further in some detail. It is proposed to divide the genus into five subgenera, two for Old World species, *Phlebotomus* and *Sergentomyia* and three for New World species, *Psychodopygus*, *Viannamyia* and *Bramptomyia*. The subgenera are tentatively further divided into groups, and keys to both subgenera and groups are given. Further division of some of the larger groups into series is suggested, particularly in the case of some of the New World groups. It is emphasized that the divisions, especially into groups and series, are highly tentative and will need much revision as further information becomes available. A list of the New World species, placed in subgenera, groups and series is given, together with a discussion of the characters of the various subdivisions.

REFERENCES CITED

- Addis, C. J. 1945. *Phlebotomus (Dampfomyia) anthroporus*, n. sp. and *Phlebotomus diabolicus* Hall from Texas. Jour. Parasit. 31 (2): 119-127, figs. 1-18.
- Alexander, C. P. 1929. A revision of the American two-winged flies of the sub-family Bruchomyiinae. Proc. U. S. Nat. Mus., 75, Art. 7: pp. 1-9, 2 figs.
1953. Undescribed species of Nematoceros Diptera. Part II. Bull. Brooklyn Ent. Soc. 48 (2): 41-49.
- Biagi, F., Francisco, and Ana Maria de B. de Biagi. 1953. Algunos flebotomos del área endémica de Leishmaniasis tegumentaria americana del E. de Campeche, Mex. Medicina (Mexico) 23 (679): 315-19.
- Costa Lima, A. 1932. Sobre os flebotomos americanos. Mem. Inst. Osw. Cruz, 26 (1): 15-69, Plates I-XXXI.
- Crampton, G. C. 1925. A phylogenetic study of the thoracic sclerites of the non-tipuloid nematoceros Diptera. Ann. Ent. Soc. Amer., 18: 47-74, 5 plates.
- Dampf, A. 1947. Notas sobre Flebotomidos Americanos. II. La posición taxonómica de *Phlebotomus imperatrix* Alexander 1944. Rev. Ent. 18 (3): 305-15. 9 figs.
- Edwards, F. W. 1926. The phylogeny of nematoceros Diptera: a critical review of some recent suggestions. Verhandl. III, Intern. Ent.-Kongress, Zurich, 1925, 2: 111-30, 2 figs.
1932. Diptera, Fam. Culicidae, in Wytzman's Genera Insectorum, Fasc. 194.
- Enderlein, G. 1937. Klassifikation der Psychodiden. Deutsche Ent. Zeits., 1936 (3-4): 81-112 (June 1937).
- Fairchild, G. B. 1949. A new fly related to *Phlebotomus* from Panama. Proc. Ent. Soc. Washington, 51 (2): 81-84, 5 figs.
1951. Some nomenclatorial notes on Psychodidae. Bull. Brooklyn Ent. Soc., 46 (1): 10-18.

1952. Notes on *Bruchomyia* and *Nemopalpus* (Dipt. Psychodidae) Ann. Ent. Soc. Amer., 45 (2): 259-328, 56 figs.
- and Hertig, M. 1950. Notes on the *Phlebotomus* of Panama. VII The Subgenus *Shannonomyia* Pratt. Ann. Ent. Soc. Amer., 44 (3): 399-421, Plates I-VII.
- Hendel, Fr. 1936. Diptera, in Kükenthal und Krumbach, Handbuch der Zoologie, 4 (2): 1729-1998, figs. 1855-2173. (Quoted in Dampf, 1947).
- Hertig, M. 1948. A New Genus of bloodsucking psychodids from Peru. Ann. Ent. Soc. Amer., 41 (1): 8-16, 12 figs.
- Jung, H. F. 1954. Einige neue mitteleuropäische Psychodiden. Zool. Anz. 152 (1-2): 16-31, figs. 1-7.
- Mangabeira, O. 1942. 7a. Contribuição ao estudo dos Flebotomos. Descrição dos machos de 24 novas espécies. Mem. Inst. Osw. Cruz, 37 (2): 111-218, 148 figs.
- and Galindo, Pedro. 1944. The Genus *Flebotomus* in California. Amer. J. Hygiene, 40 (2): 182-98, Plates I-III.
- Meunier, F. 1905. Monographie des Psychodidae de l'ambre de la Baltique. Ann. Hist.-Nat. Mus. Nat. Hungarici, 3: 235-55. 2 Plates.
- Parrot, L. 1951. Notes sur les Phlebotomes. LXI. A propos de classification. Arch. Inst. Pasteur d'Algérie, 29 (1): 28-45.
- del Rosario, F. 1936. The American species of *Psychoda*. Philippine J. Sci., 59 (1): 85-148, 6 Plates, 1 text fig.
- Satchell, G. H. 1950. The New Zealand Psychodidae. Trans. Roy. Ent. Soc. London, 101 (5): 147-178, 23 figs.
1953. The Australian Psychodidae. Part 1. Australian J. Zool. 1 (3): 357-418.
1953. On the early stages of *Bruchomyia argentina* Alexander. Proc. Roy. Ent. Soc. London, Ser. A., (1-3): 1-12, figs. 1-14.
- Theodor, O. 1948. Classification of the Old World species of the subfamily Phlebotominae (Dipt. Psychodidae). Bull. Ent. Res. 39 (1): 85-115, figs. 1-15, Plates I-II.
- Tonnoir, A. L. 1929. Diptera of Patagonia and South Chile, Part II, fascicle I. Psychodidae, pp. 1-32, Plates I-IV. British Museum (Natural History) London, 1929.
1933. Descriptions of remarkable Indian Psychodidae. Records Indian Mus., 35: 53-75, 7 figs., Pl. II.
1935. The Australian species of the Genus *Phlebotomus*. Bull. Ent. Res., 26 (2): 137-47.
- Vargas, L. and A. Diaz Najera. 1953. *Trichomyia fairchildi* n. sp. y *Eubonetia* n. gen. (Diptera Psychodidae). Rev. Inst. Salub. Enf. Trop., Mexico 13 (2): 153-58, 3 Plates.