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RELATIONSHIPS OF PHLEBOTOMINE SAND FLIES (DIPTERA)

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The status of phlebotomine sand flies in relationship to the family Psychodidae (Diptera) is reviewed. It is concluded that sand flies should be given familial recognition as Phlebotomidae, divided into the subfamilies Phlebotominae and Bruchomyiinae. A comparison is made between the evolution of Psychodidae and Phlebotomidae, and it is concluded that the two families represent contrasting evolutionary experiments at an early stage of the diversification of Diptera.

Key words: Psychodidae – sand flies – Phlebotominae – taxonomic relationships – nomenclature

Since the discovery that phlebotomine sand flies are of medical and veterinary importance, this group of small, primitive Diptera has been treated variously. The assemblage has sometimes been considered as a family, Phlebotomidae, but in most text books recommended to undergraduate and postgraduate students, sand flies are treated as a subfamily (Phlebotominae) of Psychodidae. This arrangement is difficult to convey to students with little experience of taxonomy. The most succinct definition for Psychodidae must include the phrase "with the exception of the subfamily Phlebotominae". Repeated use of this phrase invariably gives rise to a question: "Why are sand flies included in Psychodidae?".

The present paper is the result of an attempt to answer this question. It must be admitted that the original aim was to justify the inclusion of sand flies in Psychodidae. After reviewing the literature available, a contrary conclusion was reached. Segregation of sand flies from Psychodidae is warranted. As families, Psychodidae and Phlebotomidae can be considered as sister groups which, together, form a sister group of Ptychopteroidea of Hennig (1972).

Reasons for reaching this conclusion are based on the following review of literature. This is followed by a brief definition of the family Psychodidae and a more detailed definition of the family Phlebotomidae. The discussion is mainly concerned with the idea that Psychodidae and Phlebotomidae constitute two distinctly different evolutionary experiments.

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LITERATURE REVIEW

The most recent consideration of the status of phlebotomines was published by Lewis et al. (1977) who referred to several rare and old publications that are not often cited in recent literature. Although the title of the paper (*"Proposals for a stable classification of the Phlebotomine sandflies..."*) suggests that it deals with taxonomic problems, Lewis et al. (1977) stated that they were "mainly concerned with nomenclature". An acknowledged aim of Lewis et al. (1977) was to contest the contention of Abonnenc & Léger (1976) that Phlebotomidae, as a family name, has priority over Psychodidae. The opposing arguments of both Abonnenc & Léger (1976) and Lewis et al. (1977) are questionable. In dealing with past taxonomic proposals for sand flies, changes in orthography and syntax have to be taken into consideration.

The first recognizable description of a sand fly was published in 1691 but 150 years elapsed before Rondani & Berté (in Rondani, 1840) defined the genus *Flebotomus*. Rondani (1843) referred to the genus as *"Hebotomus"* but this seems to be a printer's misinterpretation of a manuscript rendering of *Flebotomus*. Other generic epithets were applied to sand flies (all listed by Barretto, 1947) but *Flebotomus* has priority. In 1954, the International Commis-

sion for Zoological Nomenclature suppressed *"Flebotomus"* as an invalid original spelling of *Phlebotomus,* on the grounds that *Flebotomus* is an incorrect transliteration and Latinization of words of Greek origin. The orthographical change also applies to suprageneric categories.

Rondani (1840) placed *Flebotomus* in the tribe Flebotomidae of the family Flebotominae. Allowing for changes in syntax, and also the orthographical change, sand flies were considered to be distinctive at family level when they were recognized to be distinctive at generic level. Abonnenc & Léger (1976) claimed that family status was given to sand flies in 1851 but, from the foregoing, this was recognized 10 years earlier.

With regard to the family name Psychodidae, Lewis et al. (1977) argued that it originates from 1834/1835 when the name "Psychodites" was used to define a 'natural order' to accomodate the genus *Psychoda.* According to Lewis et al. (1977) "Psychodites" can be amended, under the current International Code of Zoological Nomenclature, to Psychodidae. This argument is dubious. As a suprageneric category, Psychodites was rarely used and Hennig (1972) used *Psychodites* as the generic name from some fossil sand flies. If "Psychodites" is unacceptable as a precursor of Psychodidae, the epithet Psychodidae was first applied to an assemblage of Diptera in 1848, seven years after the introduction of Phlebotominae as a family name. Sand flies were incorporated into the family Psychodidae in 1864. In 1895, the family Psychodidae was divided into the subfamilies Psychodinae and Phlebotominae.

The status of phlebotomines was questioned by Adler & Theodor (1929): "In our opinion sandflies cannot be considered as belonging to one genus but should be raised to the rank of family, Phlebotomidae". The first part of this statement (generic status of sand flies) was accepted by Theodor (1948; 1958; 1965) when be conceded generic rank to *Phlebotomus* and *Sergentomyia* (Old World species) and *Brumptomyia, Lutzomyia, Warileya* and *Hertigia* (New World species). The 1948 proposals of Theodor were rejected, for different reasons, by Parrot (1951), Barretto (1955), Fairchild (1955) and Hennig (1972), but all of these authorities accepted phlebotomines as a subfamily of Psychodidae.

Rohdendorf (1964, 1974) reintroduced the idea that sand flies constitute a distinctive family. This view was accepted by Perfil'ev (1968) as "perfectly justified" but no explanation was given to explain how or why this conclusion was reached. Some western authors (Lewis 1971; 1973; 1974; Abonnenc & Léger, 1976) recognized the family Phlebotomidae.

In papers published from 1975 onwards, the late Dr D. J. Lewis reverted to the concept of sand flies as a subfamily of Psychodidae (Lewis, 1975a; 1975b; Lewis & Lane, 1976). Lewis et al. (1977) remarked that Rohdendorf gave no reasons for recognizing the family Phlebotomidae "apart from indicating the piercing trophi of sandflies and their larval life in relatively dry conditions, by which they differ from most Psychodidae". This statement sharply contrasts with that ("perfectly justified") of Perfil'ev (1968). Further on, Lewis et al. (1977) stated: "The question as to the rank to be given to *Phlebotomus* and its allies – Phlebotominae or Phlebotomidae – has been discussed by Hennig (1972) in his detailed analysis of the phylogenetics of the Psychodidae. His arguments for the recognition of but four subfamilies within... Psychodidae seem cogent as far as they go, but we prefer Duckhouse's (1973) treatment..."

Hennig (1972) recognized the subfamilies Bruchomyiinae, Phlebotominae, Trichomyiinae, Psychodinae within Psychodidae. In earlier considerations of the relationships within the family, emphasis was placed on wing structure and vein arrangement. Hennig (1972) discussed wing structure at length but, of the 40 characters used in his analysis, only seven are features of wings. The four subfamilies recognized by Hennig (1972) have only six characters in common: the presence of ascoids on flagellomeres, shared with the sister group, Ptychopteroidea; reduction of the base of the wing and in wing breadth; shortening of the posterior basal cell and the anal nerve; absence of a closed discal cell; reduction from three spermathecae. Apart from the presence of ascoids the family Psychodidae, as recognized by Hennig (1972), was defined by five synapomorphic characters. The cladogram of Hennig (1972) shows a clear separation between the Trichomyiinae/Psychodinae line on the one hand and the Bruchomyiinae/Phlebotominae line on the other, the latter designated as the group Phlebotomoinea. In the Trichomyiinae/Psychodinae line of Hennig (1972),

Psychodinae is so distinctive that it need not be considered further. Within the subfamily Trichomyiinae, Hennig (1972) included three extinct genera (*Eophlebotomus, Eatonisca, Posthon*) and three extant genera (*Horaiella, Sycorax, Trichomyia*). Duckhouse (1973a, b) differed from Hennig (1972) by separating *Horaiella* and *Sycorax* from Trichomyiinae and recognized Horaellinae and Sycoracinae as subfamilies. This was the arrangement accepted by Lewis et al. (1977).

Enderlein (1936) defined the subfamily Horaellinae to accomodate a curious Psychodid (*Horaiella*) described from India by Tonnoir (1933). Alexander (1953) accepted Horaellinae as a valid concept. The subfamily Sycoracinae was defined by Jung (1954) and redefined by Duckhouse (1972) and the assemblage was recognized as a subfamily of Psychodidae by Lewis et al. (1977) and Young (1979). Females of Horaellinae and Sycoracinae differ from those of Trichomyiinae by having mandibulate females and, thus, are comparable with females of Phlebotominae. Hennig (1972) emphasized that possession of complete mouth parts in the females of Horaellinae, Sycoracinae and Phlebotominae, and their known (or suspected) haematophagous habits, are plesiomorphic features and, based on an analysis of apomorphic characters, Horaellinae and Sycoracinae are only remotely related to Phlebotominae. The blood feeding habits of the females of the three groups has no relevance to an understanding of their relationships and evolution.

The group Phlebotomoinea of Hennig (1972) is monophyletic and a sister group to his Trichomyiinae/Psychodinae line. Together, Phlebotomoinea/Trichomyiinae/Horaellinae/Sycoracinae/Psychodinae constitute a sister group to Ptychopteroidea. Acceptance of these relationships is the basis for a classification scheme that involves few nomenclatorial changes and does not hinder information retrieval.

Family PSYCHODIDAE

Small Diptera, rarely exceeding 5 mm in length, densely covered with fine hairs, and with short, relatively robust legs. Head sometimes with an eye bridge. Antenna usually with 14 flagellomeres, but sometimes fewer. Some or all flagellomeres with one, or paired, or multiple ascoids. Palp with three or four palpomeres. Proboscis short or very short, even in females with mandibulate mouth parts, and less than the head height. Females of two subfamilies with a pair of distally toothed mandibles. When at rest, wings either held horizontally or folded over the abdomen. Radial vein with four or five terminal branches. When with four terminal branches, R_{2+3} extending to the wing margin. Larvae adapted to predominantly wet habitats, including running water but some larvae found in drier habitats and with wood-boring habits.

Subfamily HORAIELLINAE: one genus (*Horaiella*)

Subfamily SYCORACINAE: three genera (*Sycorax, Parasycorax, Aposycorax*).

Subfamily TRICHOMYIINAE: one genus (*Trichomyia*) divided into several subgenera and species-groups.

Subfamily PSYCHODINAE: many genera, some known only from fossils.

Family PHLEBOTOMIDAE

Small Diptera, usually 2-3 mm in length, densely invested with fine hairs but some parts of the body with intermingling scales, and with relatively long, slender legs. Head never with an eye bridge, eyes well separated in both sexes. Antenna usually with 14 flagellomeres but one genus with about 30 flagellomeres and another with 100+. Some flagellomeres with one, or paired, or multiple ascoids, either digitiform or discoidal. Palp with five palpomeres but palpomeres 1 and 2 almost completely fused. Proboscis of females non-mandibulate in one subfamily and shorter than head height. Females of the other subfamily with distally toothed mandibles and the proboscis at least equal to the head height or longer. When at rest, the wings held divergently and in a semi-erect position. Radial vein with five terminal branches, both R_2 and R_3 extending to the wing margin. Larvae adapted to damp but not moist or aquatic habitats.

Subfamily BRUCHOMYIINAE: Three genera (*Bruchomyia, Eutonnoiria, Nemopalpus*).

Subfamily PHLEBOTOMINAE: six genera (*Chinius, Phlebotomus, Sergentomyia* – Old World; *Brumptomyia, Lutzomyia, Warileya* – New World).

IDENTIFICATION OF ADULTS BELONGING TO THE FAMILIES PSYCHODIDAE AND PHLEBOTOMIDAE

The following key has been prepared as a simple means for distinguishing between Psychodidae (and its subfamilies) and Phlebotomidae (and its subfamilies and the genera of the subfamily Bruchomyiinae).

1. – Palp with three or four palpomeres (PSYCHODIDAE) 2
   – Palp with five palpomeres ..... (PHELEBOTOMIDAE) 5

2. – Radial vein with five terminal branches ..... PSYCHODINAE
   – Radial vein with four terminal branches, R_{2+3} extending to the wing margin ... 3

3. – Cubital vein long, extending well beyond cross-vein *m-cu*. Females with non-mandibulate mouth-parts TRICHOMYIINAE
   – Cubital vein short, extending to or only slightly beyond *m-cu,* or very short and almost vestigeal 4

4. – $R_{2+3} + R_4$ branching distal to the separation of R_5 from R_s. M_3 and M_4 dividing about the level of crossvein *m-cu* .... SYCORACINAE
   – R_{2+3} branching proximal to the separation of R_4 and R_5. M_3 and M_4 dividing well distal to a very faint basal *m-cu* crossvein ..... HORAIELLINAE

5. – Proboscis of females equal to or longer than the longitudinal axis of the head. Digitiform ascoids arising from the proximal half of flagellomeres except on flagellomere I. Females with paired mandibles and maxillae capable of piercing vertebrate skin. Ninth abdominal tergite of males bearing lateral lobes. Females with paired spermathecae .... PHLEBOTOMINAE
   – Proboscis of females shorter than the longitudinal axis of the head. Flagellomeres with multiple and short, digitiform ascoids, or with circular/ovoid ascoids usually situated in the distal half. Females with rudimentary mandibles or non-mandibulate. Maxillae membranous with a ciliate border, incapable of piercing vertebrate skin. Ninth abdominal tergite of males without lateral lobes. Females with one spermatheca ..... (BRUCHOMYIINAE) 6

6. – Antenna with 14 flagellomeres; vein Cu_1 short ..... *Nemopalpus*
   – Antenna with more than 14 flagellomeres; vein Cu_1 long 7

7. – Antenna with about 30 flagellomeres; ascoids discoidal. Basistyle of male with a distal tuft of setae. Neotropical .... *Bruchomyia*
   – Antenna with about 110 flagellomeres; ascoids digitiform and forked. Basistyle of male without a distal tuft. Afrotropical ..... *Eutonnoiria*

DISCUSSION

In earlier works (for example, Lewis, 1973; Abonnenc & Léger, 1976) that conferred family status on sand flies, Bruchomyiinae was not included in the family. However, Lewis et al. (1977), citing Duckhouse (1973a), stated that "if the Phlebotominae were treated as a family, the Bruchomyiinae should be united with them, and the small groups Sycoracinae and Horaellinae should also be given family rank..."

The close relationship between Phlebotominae and Bruchomyiinae was recognized by Fairchild (1955) who divided Phlebotominae into the tribes Phlebotomini and Bruchomyiini. This close relationship was again shown by the studies of Hennig (1972), whose methods of analysis were different from those of Fairchild (1955).

Within his concept to Phlebotomini, Fairchild (1955) advocated the retention of the generic name *Phlebotomus* in a broad sense. He argued that "the name *Phlebotomus* is now firmly established in the medical as well as entomological literature as the name for the bloodsucking pyschodid sandflies. Any attempt to rename or separate off a considerable part of these insects would lead to much confusion, and...would be unjustifiable on practical grounds".

The arrangement now proposed obviates the nomenclatorial difficulties predicted by Fairchild (1955). The Phlebotomids with blood feeding females are all placed in the subfamily Phlebotominae. The phrase 'phlebotomine sand flies' (= 'flebotomíneos' in Portuguese) remains valid vernacularly in at least two languages. Both formal and informal nomenclatorial changes have, therefore, been avoided.

Segregation of Phlebotominae and Bruchomyiinae from Psychodidae possibly provides insights about the evolution of primitive Diptera. Hennig (1972) emphasized that possession of mandibulate mouth parts is a pleisomorphic character. In both Psychodidae and Phlebotomidae, mandibulate females have the ability to pierce vertebrate skin to obtain blood meals, the only source of the nutrients needed for oogenesis. Within the two families, blood feeding habits must be accepted as a primitive feature. The larval forms of most Psychodidae are aquatic or semi-aquatic and this is probably a primitive feature of the family, but larvae of at least some members of the subfamily Trichomyiinae have adapted to drier habitats and some are wood borers. The immature stages of Phlebotomidae occur in moist, but not wet, habitats. This, like the wood-boring habits of larval Trichomyiinae, seems to be an apomorphic feature. Few haematophagous Psychodids are known to be invertebrate hosts of organisms parasitic in vertebrates*.

In contrast, haematophagous Phlebotomids are the invertebrate hosts of a variety of organisms (viruses, bacteria, Protozoa) that are pathogenic when inoculated into susceptible vertebrate hosts. The medical, veterinary and economic importance of phlebotomines is the result of the persistence of a pleisomorphic feature: mandibulated mouth parts and the ability to blood feed on vertebrates.

The different combinations of pleisomorphic and apomorphic features within Psychodidae and Phlebotomidae is reflected in the contrasting evolutionary histories of the two families.

In Psychodidae, the subfamilies Sycoracinae and Horaiellinae, with mandibulate females and haematophagous habits, can be considered as declining groups, probably on the verge of extinction and the products of unsuccessful evolutionary experiments. Horaiellinae occur only in the Oriental Region and, there, they have a limited geographical range. Sycoracinae (with three genera) is more diversified and is known from material collected in all zoogeographical regions except Nearctica and middle Palearctica. The distributional records of extant sycoracines suggests that they are relicts of a once widely distributed group.

The two subfamilies of Psychodidae with non-mandibulate females also display evolutionary contrasts. Trichomyiinae seem to have undergone greatest diversification in the southern hemisphere. This could be interpreted as evidence of a transantarctic origin, comparable to that proposed by Brundin (1967) for certain Chironomids. The evidence that pleisomorphic species occur in Australasia and the southern cone of America supports the idea of a transantarctic connection. The trichomyiines of Australasia and southern Neotropica, however, could be relicts of an earlier rich fauna that has receeded from the tropical and subtropical belts. The idea that Trichomyiinae now consistute a relict fauna conforms with the concepts of Darlington (1965). The most successful subfamily of Psychodidae is Psychodinae, with about 20 genera accepted as valid and having an almost cosmopolitan distribution. The diversity and wide geographical range of psychodines is most probably due to exploitation of available larval habitats.

The evolutionary history of Phlebotomids seems to have followed quite different lines. All members of the subfamily Bruchomyiinae are rare insects. The genera *Bruchomyia* and *Eutonnoiria* are confined, respectively, to the Neotropical and Afrotropical Regions. *Nemopalpus* is the most diversified element of the subfamily and enjoys a wider geographical range but, taking into account the known fossil members of the genus, the extant species of *Nemopalpus* most probably are relicts of a previously widely distributed group. In contrast to Trichomyiinae and Psychodinae of Psychodidae, the Phlebotomids with apomorphic mouth parts in females must be recognized as result of an unsuccessful evolutionary experiment.

Phlebotominae are the successful evolutionary line of Phlebotomids because they have been conservative in two respects. Sand flies are conversative by retention, in females, of complete insectan mouthparts, adapted for piercing and sucking. In contrast to the diversity of larval habitats in Psychodidae, the immature forms of Phlebotomidae have an ecological uniformity that is reflected in the morphological similarities of immature phlebotomines and bruchomyiines.

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* *Sycorax silacea* is one of the known insect hosts of *Icosiella glecta*, a filarial parasite of the edible frog (Desportes, 1942). This information is unlikely to diminish the appetite of a gourmet presented with a relishing dish of frogs' legs!

The geographical distribution of phlebotomines provides evidence of their evolutionary success. Sand flies have been recorded as far north as 48-49°N in the Old World and at 50°39'N in the New World. In both the eastern and western hemispheres, the southern limit is about 40°S. Within these geographical limits, phlebotomines manifest interesting and contrasting ecological differences. Based on the generic divisions of the subfamily recognized by Lewis et al. (1977), *Phlebotomus,* which includes all known vectors of Old World leishmaniases, is predominantly a genus with a northern hemisphere distribution. The other Old World genus recognized by Lewis et al. (1977), *Sergentomyia,* with females mostly blood feeding on cold blooded vertebrates, occurs mainly in tropical and subtropical areas of the southern hemisphere, but with northern extensions. In the Old World, leishmaniases are of primarily public health importance in subtropical and warm temperate areas of the northern hemisphere and most usually, in arid or semi-arid climates. In the New World, where species of *Lutzomyia* are responsible for the transmission of *Leishmania* to susceptible vertebrate hosts, leishmaniases are of greatest public health importance in South America, though disease foci occur through Central America to southern USA. In the New World, cutaneous leishmaniasis is associated with forested areas (or originally forested areas that have been greatly changed by human activity) whereas visceral leishmaniasis predominantly occurs in arid or semi-arid regions.

The leishmaniases are the most important group of diseases transmitted by phlebotomines. Because Old and New World sand flies have been separated for about 120 million years, the contrasting epidemiological patterns of leishmaniases in the western and eastern hemispheres needs to be viewed against the evolutionary backgrounds of the parasites, their vertebrate hosts, and Phlebotomidae.

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