

Numerical Taxonomy of Old World Phlebotominae (Diptera: Psychodidae).

2. Restatement of Classification upon Subgeneric Morphological Characters

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Numerical analyses (correspondence analysis, ascending hierarchical classification, and cladistics) were done with morphological characters of adult phlebotomine sand flies. The resulting classification largely confirms that of classical taxonomy for supra-specific groups from the Old World, though the positions of some groups are adjusted. The taxa Spelaeophlebotomus Theodor 1948, Idiophlebotomus Quate & Fairchild 1961, Australophlebotomus Theodor 1948 and Chinius Leng 1987 are notably distinct from other Old World groups, particularly from the genus Phlebotomus Rondani & Berté 1840. Spelaeomyia Theodor 1948 and, in particular, Parvidens Theodor & Mesghali 1964 are clearly separate from Sergentomyia França & Parrot 1920.

Key words: Old World sand flies - Psychodidae Phlebotominae - numerical taxonomy

Since the description of *Bibio papatasi* (Scopoli 1786) and the erection of the genus *Flebotomus* (Rondani 1840, Loew 1845), the taxonomy of phlebotomine sand flies has been based on monothetic principles, supported by morphological arguments. Successive classifications depended on a small number of subjectively chosen characters of adults, each credited *a priori* with discriminatory value and used to determine dichotomies. Thus erect or recumbent abdominal setae were used to identify two groups, *Phlebotomus* and *Sergentomyia*, first as subgenera, secondly as genera (Newstead 1911). Later, the structure of the male genitalia (França 1919, França & Parrot 1920, 1921), the alar index and other morphometric indices (França & Parrot 1921, Larrousse 1921) allowed the erection of subgenera. The importance of female characters such as the cibarial and pharyngeal armatures and spermathecae was introduced by Adler and Theodor (1926), and developed by Sinton (1927a, b, 1928) and Nitzulescu (1931). Classifications at the generic and subgeneric level have subsequently been based on a subjective selection of characters.

Although the use of these discriminant characters remains the basis of specific identification keys, there are still uncertainties in the systematic position and phylogenetic significance of many supra-specific taxa defined by these characters.

The polythetic concepts contrast with traditional monothetic analysis (Mayr 1969). All phenetic characters are given equal weight (Véron 1969), and are not given *a priori* discriminant value. Simultaneous consideration of all characters gives each phenon its identity and hierarchical position. Using automatic data processing methods, phenetic analysis shows relationships between groups as graphs of factor analysis, or as dendrograms.

Cladistic analysis indicates apomorphic characters and determines the most parsimonious evolutionary sequence. The final product of the analysis is a cladogram which enables hypotheses of phylogenetic relationships to be made and indicates the direction of evolutionary change in characters.

Numerical taxonomic studies on Arthropoda, whether phenetic or cladistic, have mainly been on Aranea, Coleoptera, Ephemeroptera, Hemiptera, Hymenoptera, Lepidoptera, Mecoptera, Paraneoptera and Plecoptera. Dipterists have been mainly interested in phenetic studies, which have been done on Culicidae (Rohlf 1963, 1977, Hendrickson & Sokal 1968, Steward 1968, Moss et al. 1979). While various groups, including Psychodidae (Jezek 1983), have been studied by qualitative traditional cladistic analysis, it seems that

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only the genus *Toxorhynchites* (Simon et al. 1982) and the family Keroplatidae (Matile 1990) have been studied by cladistic methods.

In this study, anatomical characters defining supra-specific groups of phlebotomine sand flies were analysed by phenetical and cladistical methods, as proposed by Lewis et al. (1977).

MATERIALS AND METHODS

Choice of taxa - For the numerical analysis, supra-specific taxa were chosen as the operational taxonomic units (OTU). Altogether, 21 taxa were considered. In addition to the long-recognised subgenera of *Phlebotomus* (Lewis 1982), the new taxa *Kasaulius* Lewis 1982, *Transphlebotomus* Artemiev & Neronov 1984 and *Chinius* Leng 1987 were included. *Neophlebotomus* França & Parrot 1920 (synonymous with *Rondanomyia*, according to Lewis 1978) and *Parrotomyia* Theodor 1958 were retained in the genus *Sergentomyia*, sensu França & Parrot 1920. Of *Capensomyia* Davidson 1979 and *Demeillonius* Davidson 1980, only the latter, considered by Artemiev and Neronov (1984) to be a separate genus, was retained.

Selection of characters - A preliminary list was drawn up of morphological characters from males and females classically used by specialists in the

identification and classification of sandflies. Many of these were first used by early authors when taxonomic or geographical knowledge of the group was limited. Easily visible structures predominate, notably the male genitalia and the cibarium, pharynx and spermathecae of females. Some characters of the head (mouthparts, palps and antennae), thorax including the wings, and abdomen are also included. Twenty characters were finally retained, relating to the antennae, palps, cibarium, thoracic and abdominal setae and the male and female genital structures.

Definition of character states - Coding requires clearly definable character states. After making a complete list of the possible forms of each structure, grouping was essential to reduce their variety. Wherever possible, grouping took account of known or suspected homologies. Table I shows the 55 states of the 20 characters described in the 21 OTU's, and identifies the state that we believe to be truly plesiomorphic.

Numerical analysis - Following the tabulation of character states for each OTU (Table II), analyses were carried out using an Olivetti M380 XP1 computer. For the phenetic analysis, programmes of the algorithm Analyse de Données of the software Biomeco 2.0 package (Biometrics Group of

TABLE I
Numerical taxonomy of Old World Phlebotominae. Twenty characters and their 55 states

A - Female antennal segments with two ascoids	none [0] / III - IX [1] / III - XIV [2]/III - XV [3] / III - XVI [4]
B - Male antenna with at least one ascoid on segment III ..	no [0] / yes (P) [1]
C - Male antennal segments with two ascoids	none [0] / III - VIII [1] / III - IX or X [2]/III - XIV [3] / III - XV [4] / IV - XIII[5]
D - Longest palpal segment	3 [3] / 5 [5]
E - Cibarial armature in female	absent [0] / present [1]
F - Cibarial teeth in a palisade	no [0] / yes [1]
G - Groups of mesanepisternal setae	none [0] / one [1] / two (P) [2]
H - Recumbent hairs on tergae II - VI	absent (P) [0] / present [1]
I - Basal lobe on coxite (*)	absent (P) [0] / present [1]
J - A tuft or row of hairs on coxite	absent (P) [0] / present [1]
K - Spines on style	two [2] / three [3] / four [4] / five [5] / six [6]
L - At least one non-deciduous seta on style	absent (P) [0] / present [1]
M - Parameres	simple (one-lobed) (P) [0] / complex [1]
N - Apex of simple parameres	rounded [1] / truncate or hooked [2] / spatulate[3]
O - Aedeagus	very short or rudimentary [1] / conical [2] / digitiform [3] / bifurcate, or with sclerotized appendages or extensions [4]
P - Intra-abdominal rods	absent (P) [0] / present [1]
Q - Wall of spermatheca	smooth [0] / ornamented [1]
R - Smooth spermathecae; definite capsule or demarcation from spermathecal duct	absent [0] / present [1]
S - Spermathecal ornamentation	segmented or annulated [1] / folded or striated [2]/with rows of spicules [3]
T - Spermathecal ducts:	uniform diameter (P) [0] / with a dilatation other than at the base [1]

(P): presumed plesiomorphic state; (*): terminology of male genitalia follows Abonnenc (1972).

TABLE II
Numerical taxonomy of Old World Phlebotominae. Character state matrix. Codes as in Table I

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
<i>Phlebotomus</i>	3	1	4	5	0	-	1	0	1	1	5	0	1	-	2	0	1	-	1	0
<i>Paraphlebotomus</i>	3	1	4	5	0	-	1	0	1	1	4	0	0	3	2	0	1	-	1	0
<i>Synphlebotomus</i>	3	1	2	5	0	-	1	0	1	1	5	0	0	3	2	0	1	-	1	0
<i>Larroussius</i>	3	1	1	5	0	-	1	0	0	1	5	0	0	1	3	0	1	-	1	0
<i>Transphlebotomus</i>	3	1	4	5	0	-	1	0	0	1	5	0	0	1	3	0	1	-	2	1
<i>Adlerius</i>	3	1	4	5	0	-	1	0	0	1	5	0	0	1	3	0	1	-	2	0
<i>Euphlebotomus</i>	3	1	2	5	1	0	1	0	0	1	5	0	1	-	2	1	1	-	1	0
<i>Kasaulius</i>	3	1	2	5	1	0	1	0	0	0	5	0	0	2	2	1	1	-	1	0
<i>Anaphlebotomus</i>	3	1	4	5	1	0	1	0	0	1	4	0	1	-	2	0	1	-	1	0
<i>Australophlebotomus</i>	2	1	3	5	1	0	1	0	0	0	3	0	0	2	1	0	1	-	2	0
<i>Spelaeophlebotomus</i>	3	1	2	3	0	-	0	0	0	0	4	1	0	1	2	1	0	0	-	0
<i>Idiophlebotomus</i>	4	0	5	3	1	0	0	0	0	0	3	1	0	1	4	1	0	1	-	0
<i>Sergentomyia</i>	3	1	0	5	1	1	0	1	0	0	4	1	0	1	2	0	0	0	-	0
<i>Parrotomyia</i>	3	1	0	5	1	1	0	1	0	0	4	1	0	2	2	0	0	1	-	0
<i>Neophlebotomus</i>	3	1	0	5	1	1	0	1	0	0	4	1	0	2	2	0	1	-	2	0
<i>Sintonius</i>	3	1	0	5	1	1	0	1	0	0	4	1	0	2	2	0	1	-	1	0
<i>Demeillonius</i>	3	0	0	5	1	1	0	1	0	0	6	1	0	1	2	0	1	-	1	0
<i>Spelaeomyia</i>	3	1	4	5	1	1	0	1	1	0	2	1	0	2	1	0	1	-	2	1
<i>Grassomyia</i>	0	0	0	5	1	1	2	1	0	0	4	1	0	1	2	0	1	-	3	0
<i>Parvidens</i>	3	1	4	5	1	0	2	0	0	1	5	0	1	-	2	0	0	1	-	0
<i>Chinius</i>	1	1	2	5	1	0	0	0	0	1	4	0	0	1	4	0	1	-	1	0

[-] no state applied to the coded taxon.

CEPE/CNRS, Montpellier) were used. The cladistic analysis used the MIX algorithm (Wagner parsimony), from the PHYLIP programme.

RESULTS

Phenetic analysis - Correspondence analysis and ascending hierarchical classification yielded similar results. The taxonomic positions of the OTU's are shown in Figs 1 and 2. Separation at the 50% level, which was taken to correspond to the generic level of classification, indicated at least six taxa at this level: *Phlebotomus*, *Sergentomyia*, *Australophlebotomus*, *Spelaeophlebotomus*, *Idiophlebotomus* and *Chinius*. The genus *Phlebotomus* appears to contain two clusters. The first contains two groups of closely related subgenera: *Phlebotomus*, *Paraphlebotomus* and *Synphlebotomus*; and *Adlerius*, *Transphlebotomus* and *Larroussius*. The second cluster contains *Euphlebotomus*, *Kasaulius* and *Anaphlebotomus*, with *Parvidens* loosely attached. Within the genus *Sergentomyia*, the taxon *Spelaeomyia* is clearly separate from the others. While conclusions cannot be secure without consideration of outgroups, the phenetic analysis clearly indicates that *Parvidens* is distinct from *Sergentomyia*. Abonnenc and Léger (1976) allied

Parvidens with New World sand flies, and the precise position of this group remains to be determined.

Cladistic analysis - Fig. 3 shows the most parsimonious cladogram obtained. This is largely consistent with the phenetic dendrogram (Fig. 2). Taxa conventionally contained in the genera *Phlebotomus* and *Sergentomyia* split into two distinct clusters. The left-hand extremity contains *Sergentomyia*. *Spelaeomyia* is very distinct. Early off shoots from this branch give rise to *Spelaeophlebotomus* and *Idiophlebotomus*. The right-hand branch has an early fork giving *Chinius* and *Australophlebotomus* on the one hand, and *Parvidens* and *Anaphlebotomus* on the other. This is followed by *Euphlebotomus* and *Kasaulius*, then the six apparently most recent taxa: *Larroussius*, *Transphlebotomus*, *Adlerius*, *Synphlebotomus*, *Paraphlebotomus* and *Phlebotomus*. The subgenus *Phlebotomus*, surprisingly, has a terminal position on this most recent branch of the cladogram, despite the apparently plesiomorphic characters it shares with fossil forms. Indeed, considerations of specific morphological characters in the genus *Phlebotomus* has confirmed its place among the more primitive subgenera (Rispaill & Léger 1998).

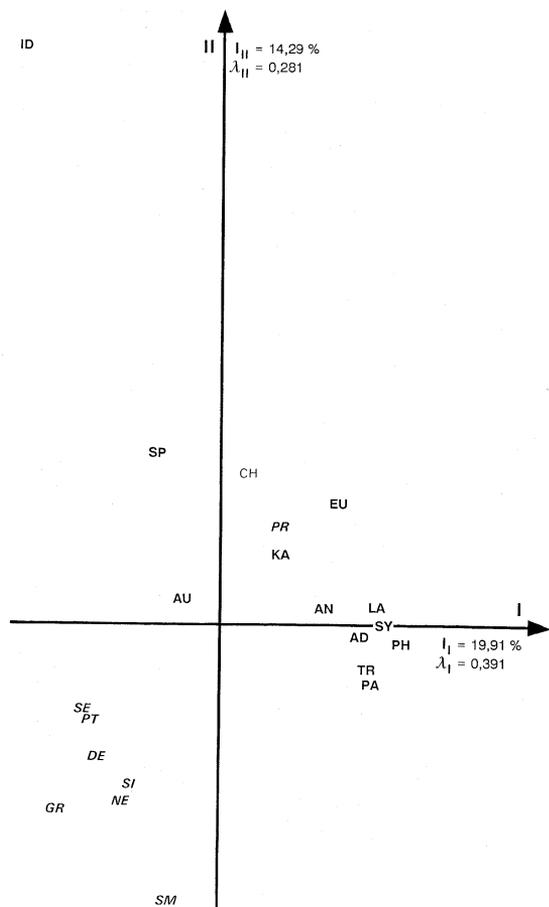


Fig. 1: Old World Phlebotominae. Correspondence analysis of supra-specific taxa. Plane formed by the first two axes. AD: *Adlerius* Nitzulescu 1931 AN: *Anaphlebotomus* Theodor 1948 AU: *Australophlebotomus* Theodor 1948 CH: *Chinius* Leng 1987 DE: *Demeillonius* Davidson 1980 EU: *Euphlebotomus* Theodor 1948 GR: *Grassomyia* Theodor 1958 ID: *Idiophlebotomus* Quate & Fairchild 1961 KA: *Kasaulius* Lewis 1982 LA: *Larrousius* Nitzulescu 1931 NE: *Neophlebotomus* França & Parrot 1920 PA: *Paraphlebotomus* Theodor 1948 PT: *Parrotomyia* Theodor 1958 PR: *Parvidens* Theodor & Mesghali 1964 PH: *Phlebotomus* Rondani & Berté 1840 SE: *Sergentomyia* França & Parrot 1920 SI: *Sintonius* Nitzulescu 1931 SM: *Spelaomyia* Theodor 1948 SP: *Spelaophlebotomus* Theodor 1948 SY: *Synphlebotomus* Theodor 1948 TR: *Transphlebotomus* Artemiev & Neronov 1984.

Certain characters, hitherto considered to be of specific interest only may in fact have systematic relevance. For example, the subgenera *Grassomyia* and *Parvidens* share with New World groups the presumably plesiomorphic character of “two groups of mesanepisternal setae”; the taxa on the right-hand branch of the cladogram retain only the antero-inferior group of setae, while the groups on the left-hand branch have lost both groups. The proposed phylogeny is consistent, therefore, with

the ancestral state of both groups of setae. Furthermore, the cladogram suggests evolutionary sequences for characters for which the direction of evolution was not previously proposed. For example, the presence of a well developed cibarial armature in most of the groups argues in favour of the plesiomorphic nature of this state. With the exception of *Spelaophlebotomus*, all the groups lacking, or with a rudimentary armature, lie on the terminal portion of the right-hand branch, the members of which show various synapomorphies. “Cibarium unarmed” thus appears to be an apomorphic state.

DISCUSSION

Theodor (1948), in a detailed study of the known forms of phlebotomine sand flies proposed their division into four genera, two of them from Old World. The genus *Phlebotomus* contained the subgenera *Phlebotomus*, *Paraphlebotomus*, *Synphlebotomus*, *Larrousius*, *Adlerius*, *Euphlebotomus*, *Anaphlebotomus*, *Australophlebotomus* and *Spelaophlebotomus*. The genus *Sergentomyia* was divided into the subgenera *Sergentomyia*, *Sintonius* and *Spelaomyia*.

New discoveries in later years led to the erection of the new subgenera, *Idiophlebotomus* in *Phlebotomus* (Quate & Fairchild 1961), and *Parrotomyia*, *Rondanomyia*, *Grassomyia* (Theodor 1958) and *Parvidens* (Theodor & Mesghali 1964) in *Sergentomyia*. *Parvidens* contained three species of uncertain position previously included in *Euphlebotomus*. Abonnenc and Minter (1965) proposed generic status for *Spelaophlebotomus*. Hennig (1972), while deploring the inadequacy of many descriptions, considered the Phlebotominae as a monophyletic group composed of three monophyletic sub-groups: the genus *Phlebotomus*, the genus *Sergentomyia* (he did not conclusively include *Parvidens*), and the whole of the two genera *Brumptomyia* and *Lutzomyia*. Abonnenc (1972) supported Fairchild's classification (1955), but recognised only the genera *Phlebotomus*, *Warileya* and *Hertigia* and added *Spelaophlebotomus* and *Idiophlebotomus*. Rejecting the excessive division of such a small, homogeneous group of insects, he proposed the division of *Phlebotomus* into eight subgenera, based largely on chetotaxy. *Phlebotomus*, *Sergentomyia*, *Parvidens*, *Spelaomyia* and *Grassomyia* were the Old World members. Lewis (1973, 1974) recognised Phlebotomidae as a family with six genera, two in the Old World and four in the New. The genus *Phlebotomus* was divided into 11 subgenera, and *Sergentomyia* into six. Reverting to subfamily status for the entire group, Lewis et al. (1977) attempted to instill a degree of stability, keeping only five genera, each contain-

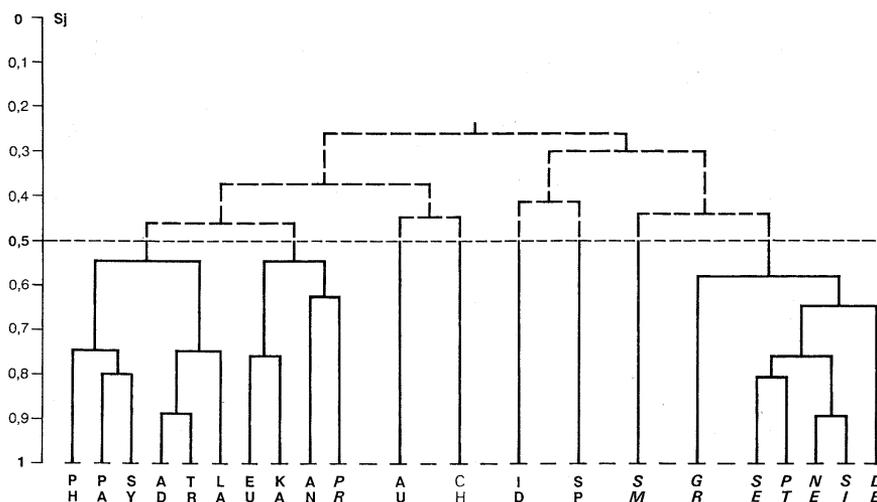


Fig. 2: Old World Phlebotominae. Ascending hierarchical classification. Dendrogram constructed using Jaccard's similarity index and clustering by median linkage. Symbols are the same as in Fig. 1.

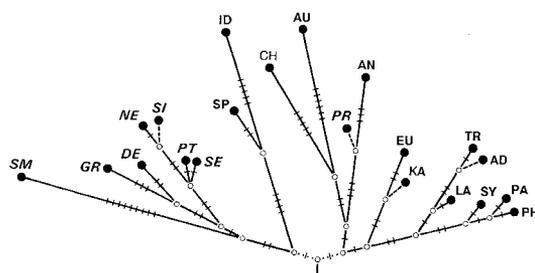


Fig.3: Old World Phlebotominae. Most parsimonious cladogram (78 steps). Symbols are the same as in Fig. 1. Bars indicate the number of steps.

ing many taxa. The Old World genera were *Phlebotomus* and *Sergentomyia*, while *Lutzomyia*, *Warileya* and *Brumptomyia* were restricted to the New World. Retaining this 1977 "stable" proposal of five genera, Lewis (1982) declined to recognise generic status for *Spelaeophlebotomus* and *Idiophlebotomus*. The genus *Phlebotomus* thus had 11 subgenera, including *Kasaulius* which was described at the time. Artemiev and Neronov (1984) included 14 genera in the subfamily Phlebotominae as follows: *Australophlebotomus*, *Brumptomyia*, *Demeillonius*, *Grassomyia*, *Hertigia*, *Idiophlebotomus*, *Lutzomyia*, *Parvidens*, *Phlebotomus*, *Psychodopygus*, *Sergentomyia*, *Spelaeomyia*, *Spelaeophlebotomus* and *Warileya*. Including fossil forms, Artemiev (1991) finally divided this subfamily into 24 genera.

Numerical analysis, applied to anatomical char-

acters of supra-specific groups of phlebotomine sand flies of the Old World, by and large, coincides with traditional taxonomic opinion, but contributes to the levels of some divisions, and to some specific positions. Thus, this study generally confirms Theodor's classification (1948). It supports the hypothesis of generic rank assigned to the taxa *Australophlebotomus*, *Idiophlebotomus*, *Spelaeomyia* and *Spelaeophlebotomus* by Abonnenc and Minter (1965), Abonnenc (1972) and Artemiev and Neronov (1984). Also, in another way, it supports Hennig's doubts (1972) about the precise taxonomic position of the taxon *Parvidens*, particularly as belonging to the genus *Sergentomyia*. Lastly, it keeps the taxon *Demeillonius* within the genus *Sergentomyia*, although this group and *Chinius* were intuitively placed on the same level.

Quantitative characters, although important for identification, were rarely used in this numerical analysis. On the other hand, characters which have little use in specific identification are sometimes of considerable systematic value. Future studies will benefit from a clearer identification of plesiomorphic characters states; the identification of the sister group would help in this analysis.

A new classification of the Old World phlebotomine sand flies is however proposed (Table III). It is inevitable that this classification will be modified as new information becomes available, especially when larval, pupal and imaginal characters of both Old and New World groups are taken into account, or even extended to encompass all Psychodidae.

TABLE III
Classification of the Old World Phlebotominae

Previous classification ^a	New proposed classification
Genus I <i>Phlebotomus</i> Rondani & Berté 1840	Genus I <i>Phlebotomus</i> Rondani & Berté 1840
. Subgenus 1 <i>Adlerius</i> Nitzulescu 1931	. Subgenus 1 <i>Adlerius</i> Nitzulescu 1931
. Subgenus 2 <i>Anaphlebotomus</i> Theodor 1948	. Subgenus 2 <i>Anaphlebotomus</i> Theodor 1948
. Subgenus 3 <i>Australophlebotomus</i> Theodor 1948	. Subgenus 3 <i>Euphlebotomus</i> Theodor 1948
. Subgenus 4 <i>Euphlebotomus</i> Theodor 1948	
. Subgenus 5 <i>Idiophlebotomus</i> Quate & Fairchild 1961	. Subgenus 4 <i>Kasaulius</i> Lewis 1982
. Subgenus 6 <i>Kasaulius</i> Lewis 1982	. Subgenus 5 <i>Larroussius</i> Nitzulescu 1931
. Subgenus 7 <i>Larroussius</i> Nitzulescu 1931	. Subgenus 6 <i>Paraphlebotomus</i> Theodor 1948
. Subgenus 8 <i>Paraphlebotomus</i> Theodor 1948	. Subgenus 7 <i>Phlebotomus</i> Rondani & Berté 1840
. Subgenus 9 <i>Phlebotomus</i> Rondani & Berté 1840	
. Subgenus 10 <i>Spelaeophlebotomus</i> Theodor 1948	. Subgenus 8 <i>Synphlebotomus</i> Theodor 1948
. Subgenus 11 <i>Synphlebotomus</i> Theodor 1948	. Subgenus 9 <i>Transphlebotomus</i> Artemiev & Neronov 1984
. Subgenus 12 <i>Transphlebotomus</i> Artemiev & Neronov 1984	
	Genus II <i>Australophlebotomus</i> Theodor 1948
	Genus III <i>Idiophlebotomus</i> Quate & Fairchild 1961
	Genus IV <i>Spelaeophlebotomus</i> Theodor 1948
Genus II <i>Sergentomyia</i> França & Parrot 1920	Genus V <i>Sergentomyia</i> França & Parrot 1920
. Subgenus 1 <i>Demeillonius</i> Davidson 1980	. Subgenus 1 <i>Demeillonius</i> Davidson 1980
. Subgenus 2 <i>Grassomyia</i> Theodor 1958	. Subgenus 2 <i>Grassomyia</i> Theodor 1958
. Subgenus 3 <i>Neophlebotomus</i> França & Parrot 1920	. Subgenus 3 <i>Neophlebotomus</i> França & Parrot 1920
. Subgenus 4 <i>Parrotomyia</i> Theodor 1958	. Subgenus 4 <i>Parrotomyia</i> Theodor 1958
. Subgenus 5 <i>Parvidens</i> Theodor & Mesghali 1964	
. Subgenus 6 <i>Sergentomyia</i> França & Parrot 1920	. Subgenus 5 <i>Sergentomyia</i> França & Parrot 1920
. Subgenus 7 <i>Sintonius</i> Nitzulescu 1931	. Subgenus 6 <i>Sintonius</i> Nitzulescu 1931
. Subgenus 8 <i>Spelaeomyia</i> Theodor 1948	
	Genus VI <i>Spelaeomyia</i> Theodor 1948
Genus III <i>Chinius</i> Leng 1987	Genus VII <i>Chinius</i> Leng 1987
	Incertae sedis <i>Parvidens</i> Theodor & Mesghali 1964

a: after Theodor 1948, 1958, Quate & Fairchild 1961, Theodor & Mesghali 1964, Davidson 1980, Lewis 1982 and Leng 1987.

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