

PREMIERE PARTIE

Morphologie et Systématique

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Synopsis of the genera  
of *Ceratopogonidae* (Diptera)

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*Summary.*

A synopsis is presented for the classification of the 78 genera and subgenera of Ceratopogonidae of the world. Taxonomic keys are given for the separation of the genera. A short history is given for the classification of the family. The biting midges of this family include important bloodsucking pests, vectors of several animal diseases, pollinators of several tropical crops, and parasites and predators of other insects.

*Résumé.*

**Tableau synoptique des genres de Ceratopogonidae (Diptera).**

Les auteurs présentent un tableau synoptique pour la classification des 78 genres et sous-genres de Ceratopogonides du monde. Des clefs de détermination sont données pour les genres. Un court historique est fait pour la classification de la famille. Les espèces agressives de cette famille sont importantes, comprenant des vecteurs de différentes maladies des animaux, des polinisateurs de différentes plantes tropicales, et des parasites et des prédateurs d'autres insectes.

For many years the biting midges were placed in the genus *Ceratopogon* in the family Chironomidae. The early authors, Meigen, Curtis, Walker, Winnertz, Loew, and Coquillett, followed this system, deviating only rarely to propose a new genus for some exceptionally odd form.

The ceratopogonids were usually regarded at most as a subfamily of the Chironomidae until 1917 when Malloch gave them family rank. In this he was strongly supported by Edwards in 1926, who pointed out two strong characters, the complete mouthparts and the forked media, which formed a clear line of division.

It was not until Kieffer began his work about the turn of the century that the division of the genus *Ceratopogon* really began. During the next 25 years Kieffer proposed more than 40 new genera out of a total of 139 genus group names proposed during the entire history of the family. Of the total, 78 names survive as valid genera or subgenera, of which 28 are attributed to Kieffer. Although much maligned, Kieffer's work has probably been of more importance than any other in the family.

Malloch in 1915 broke up Coquillett's and Loew's early treatment of the North American *Ceratopogon* into smaller genera, and with the help of Johannsen, established the basis for the classification of the North American species. In Europe Goetghebuer, Edwards, and Zilahi-Sebess set up a classification closely following Kieffer's although Edwards proposed valuable modifications of Kieffer's concepts.

Elsewhere important work on the generic level was done by Lutz and Lane in Brazil, Carter, Ingram, and Macfie, and De Meillon in Africa, Tokunaga in Japan and the Pacific, and Lee in Australia. From 1925 to 1949 Macfie served as the dominant authority who published a remarkable series of papers covering all parts of the world. Karl Mayer continued the important work begun by Thienemann and Lenz on the classification of the immature stages, while Saunders showed how necessary it is to consider the immatures in the Forcipomyiinae.

Edwards in 1926 divided the family into two groups, (1), those with short hairy body and wings, short costa, unmodified femora and claws, and large vertical membranous area of the pleura, the adults attacking vertebrates or insects larger than themselves and often with terrestrial larvae, and (2) those with slender, less hairy bodies, bare wings with long costa, modified femora and claws, narrow oblique membranous area on the pleura, the adults predaceous on small insects, and the aquatic larvae long and wormlike.

Kieffer (1925) divided the family into five groups for adult forms; *Forcipomyia*, *Dasyhelea*, *Culicoides*, *Palpomyia*, and *Bezzia* Groups; and three groups for larval forms: a « Genuinae » group including *Focipomyia* and *Atichopogon*, « Intermediae » for *Dasyhelea*, and « Vermiformes » including *Culicoides*, *Stilobezzia*, *Bezzia*, and *Palpomyia*. Mayer (1934) divided the family into six groups based on immature stages: *Forcipomyia*, *Dasyhelea*, *Culicoides*, *Stilobezzia*, *Palpomyia*, and *Leptocnops*. Macfie (1940) went even further and added the *Bezzia*, *Macropeza*, and *Ceratopogon* Groups to his adult classification for a total of nine groups. Johannsen

(1943) essentially followed Macfie, but split off *Atrichopogon* and put *Palpomyia* and *Bezzia* together.

In 1952 Wirth tried to reach a balance between the larval classification of Mayer (1934) and the adult groupings of Kieffer (1925), Macfie (1940), and Johannsen (1943). He ventured to endow their groups with nomenclaturally formalized subfamily and tribal names based on priority, most of which had already been proposed at one time or another. He used four subfamilies:

Leptoconopinae — *Leptoconops* Group;

Forcipomyiinae — *Forcipomyia* and *Atrichopogon* Groups;

Dasyheleinae — *Dasyhelea* Group;

Heleinae (now the Ceratopogoninae), with four tribes:

Culicoidini — *Culicoides* Group;

Heleini (Ceratopogonini) — *Ceratopogon* Group;

Stilobezziini — *Stilobezzia* Group;

Stenoxenini — *Macropeza*, *Palpomyia* and *Bezzia* Groups.

This system, naive as it was, took a step sorely needed and on the whole won acceptance, although minor points of criticism were voiced by Mayer (1952, 1957) concerning genera of the *Macropeza* Group, and by De Meillon and Hardy (1953) on the *Stilobezzia* Group. However for many years there had been written expressions of dissatisfaction with the primary breakdown of the Stenoxenine genera on wing venational characters, and to meet this problem, Wirth began the revisionary study that grew into the present work. He presented a first draft of this key at the Ceratopogonid Symposium held during the Detroit meetings of the Entomological Society of America in 1959. He distributed mimeographed copies of the draft to some workers at that time.

A second draft of the key, with illustrations, was prepared by Ratanaworabhan as a doctoral thesis for the University of Florida under the direction of Blanton. The present draft is a part of a large comprehensive publication we are preparing of the genera of the world. This publication will include taxonomic keys, diagnoses, and illustrations of the valid genera and subgenera, a check list of all included species, and a complete taxonomic bibliography. Because of the size of this undertaking we anticipate a delay in publication of several years. We believe the immediate publication of the present provisional keys and synoptic arrangement of the genera and subgenera will fill a pressing need. Perhaps it will encourage current workers to test the keys and notify us of any errors, shortcomings, and suggestions for improvement in our definitive publication.

We have tried to make our keys as phylogenetic as possible but as a result the keys suffer somewhat from jumping from female sex to male, and to immature stages, for diagnostic characters. We think none of the characters used are new, but we have changed emphasis on many, particularly in the Ceratopogoninae. The

way the system works out, the immature stages are very heavily relied on for subfamily and tribal characters, and male and female secondary characters for generic and subgeneric differentiation. Throughout the key, the obvious and more easily used external characters of the female, which is the stage and sex most often dealt with in medical entomology and control work, are seized upon whenever possible.

The classification of the Forcipomyiinae is in better shape than that of any other group, thanks almost entirely to the fine work of the late Professor Saunders in Canada. Dr. Chan Kai Lok of Singapore has continued more recently in the tradition of Professor Saunders in describing several new subgenera, emphasizing all the time the importance of the immature stages in the classification of this subfamily. Dr. Paul Dessart working on cacao pollination in the Belgian Congo performed an admirable job in bringing the African species into the modern classification. Dr. H. Remm in Estonia has made similar advances in revising the Palaearctic species that are found in the Soviet Republics. Larvae, pupae, male genitalia, and habits offer excellent characters in the Forcipomyiinae, and the only drawback is the refusal of the female to cooperate in offering comparably good morphological characters.

The genera placed in the tribe Culicoidini appear to be as primitive and non-specialized as any in the family, and along with those in the subfamily Dasyheleinae and tribe Ceratopogonini may give us more clues to the ancestral lineage than other sections of the family. We believe it is no accident that the annectant genera *Paradasyhelea* and *Austroconops* from Australia, New Zealand, and Patagonia fall here.

We still have a long way to go in the classification of *Culicoides*, for although many subgenera have been proposed, most of these are valid only in one particular geographic region and must be revised or supplemented to bring the other species of the world into the system.

The tribe Ceratopogonini has been relatively neglected and needs a good revisionary study. In the tribe Stilobezziini, *Parabezzia* was a problem, and Wirth placed it erroneously in the tribe Stenoxenini in 1952. We have tried to make an acceptable classification of these two tribes, but we have been limited to the use of adult characters.

Beginning with couplet 8 of the key with the Ceratopogoninae, we use the female claws and fifth tarsomere for a primary breakdown of genera and have taken a cue from Mayer in supporting these with characters of the female abdomen and egg. Mayer (1952) pointed out the remarkable frilled egg cap of *Stenoxenus* and *Paryphoconus* and suggested that other genera, especially of the *Macropeza* Group, be studied for this character. After dissecting eggs out of gravid females of the various genera in our collection, we found that only *Stenoxenus* and *Paryphoconus* have the peculiar egg cap. In the key we give other characters to show how these two genera are abundantly distinct from the other *Macropeza* Group genera and that they seem to be closely related to the tribe Palpomyiini.

Tokunaga in his 1962 revision of the New Guinea Palpomyiinae adopted a conservative viewpoint with respect to these large predaceous midges, using the traditional characters of number of radial cells in the wing and the armature of the femora. However, a much better classification of genera can be secured by first separating those with the females having internal sclerotized gland rods and eversible glands on the abdomen. These genera, comprising the tribes Stenoxenini and Palpomyiini, are also characterized by the females having cordiform fourth tarsomeres, fifth tarsomere without true batonnets, and claws simple and equal. Wirth published this proposal in 1962, when he gave a key and a suggested arrangement for the remaining genera, which he placed in two tribes, the Heteromyiini and Sphaeromiini.

In the tribe Heteromyiini the female claws are unequal, at least on the hind pair of legs; the fifth tarsomere does not bear ventral batonnets and those on the fore legs are often inflated, while the fourth tarsomere is sometimes divided into spinose bifid lobes. Familiar genera of the tribe Heteromyiini are *Clinohelea* and *Neurohelea* and, in the tropics, such bizarre forms as *Heteromyia*, *Pellucidomyia*, and *Tetrabezzi*.

In the genera of the tribe Sphaeromiini is found the most striking development of the secondary sexual characters of the female tarsi. Common to all these genera is the development of the specialized, stout, blunt, black, ventral spines on the fifth tarsomere which Kieffer called « batonnets ». From genus to genus, these are arranged differently. Other convenient characters used for generic separation are whether the female claws are equal or unequal, whether the basal tooth is on the internal or external side of each claw, and whether the claw is straight or curved. The length of the costa is a better character than whether one or two radial cells are present, and the armature of the femur is only sometimes useful above the species level. On the other hand, certain genera characteristically have dull pollinose integument, especially on the thorax, while others are shining species. In the tribe Sphaeromiini the pupae of some genera have an unusual feature of ventral glandular discs on certain abdominal segments, which appear to be used to attach the pupa fast to emergent vegetation or objects above the water level preparatory to eclosion. This development probably is associated with the preferred larval habitat in larger streams with fluctuating water level or lakes with considerable wave action on the shores.

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Systematic Arrangement of the *Ceratopogonidae*

(3 870 species)

**Subfamily Leptoconopinae** Noé, 1907*Genus Leptoconops* Skuse 1889 (81 species).Subgenus *Brachyconops* Wirth and Atchley 1973.Subgenus *Holoconops* Kieffer 1918 (syn.: *Microconops* Kieffer 1921).Subgenus *Leptoconops* Skuse (syn.: *Tersesthes* Townsend 1893 ;    *Centrotypus* Grassi 1901 ; *Mycterotypus* Noé 1905 ; *Mycteromyia* Lutz 1912 ;  
    *Schizoconops* Kieffer 1918 ; *Protersesthes* Kieffer 1921).Subgenus *Megaconops* Wirth and Atchley 1973.Subgenus *Styloconops* Kieffer 1921 (syn.: *Acanthoconops* Carter 1921).**Subfamily Forcipomyiinae** Lenz 1934*Genus Atrichopogon* Kieffer 1906 (344 species).Subgenus *Atrichopogon* Kieffer (syn.: ? *Didymophleps* Weyenbergh 1883 (position uncertain) ; *Kempia* Kieffer 1913 ; *Gymnohelea* Kieffer 1921 ; *Lophomyidium* Cordero 1929).Subgenus *Dolichohelea* Edwards 1929.Subgenus *Melohelea* Wirth 1956.Subgenus *Psilokempia* Enderlein 1936.*Genus Forcipomyia* Meigen 1818 (613 species).Subgenus *Blantonia* Wirth and Dow 1971.Subgenus *Calofoforcipomyia* Saunders 1956.Subgenus *Euforcipomyia* Malloch 1915 (syn.: *Profoforcipomyia* Saunders 1956).Subgenus *Forcipomyia* Meigen (syn.: *Labidomyia* Stephens 1829 ; *Tetraphora* Philippi 1865 ; *Prohelea* Kieffer 1912).Subgenus *Lasiohelea* Kieffer 1921 (syn.: *Centrorhynchus* Lutz 1914, preocc. ; *Parapterobosca* Harant, Huttel and Huttel 1951 ; *Dacnoforcipomyia* Chan and Saunders 1965).Subgenus *Lepidohelea* Kieffer 1917.Subgenus *Metafoforcipomyia* Saunders 1956.Subgenus *Microhelea* Kieffer 1917 (syn.: *Phasmidohelea* Mayer 1937).Subgenus *Phytohelea* Remm 1971.Subgenus *Pterobosca* Macfie 1932.

- Subgenus Rhynchoforcipomyia Wirth and Dow 1972.
- Subgenus Schizoforcipomyia Chan and Leroux 1971.
- Subgenus Synthyridomyia Saunders 1956.
- Subgenus Thyridomyia Saunders 1925.
- Subgenus Trichohelea Goetghebuer 1919 (syn.: *Apelma* Kieffer 1919, preocc.; *Neoforcipomyia* Tokunaga 1959).
- Subgenus Warmkea Saunders 1956.

**Subfamily Dasyheleinae** Lenz 1934

*Genus Dasyhelea* Kieffer 1911 (398 species).

- Subgenus Dasyhelea Kieffer (syn.: *Cryptoscena* Enderlein 1936).
- Subgenus Dicroptoscena Enderlein 1936.
- Subgenus Prokempia Kieffer 1913.
- Subgenus Pseudoculicoides Malloch 1915.

**Subfamily Ceratopogoninae** Newman 1834

Tribe Culicoidini Kieffer 1911

*Genus Austroconops* Wirth and Lee 1959 (1 species).

*Genus Paradasyhelea* Macfie 1940 (5 species).

*Genus Culicoides* Latreille 1809 (924 species).

- Subgenus Anilomyia Vargas 1960.
- Subgenus Avaritia Fox 1955.
- Subgenus Beltranmyia Vargas 1953.
- Subgenus Culicoides Latreille.
- Subgenus Diphaeomyia Vargas 1960.
- Subgenus Drymodesmyia Vargas 1960.
- Subgenus Glaphiromyia Vargas 1960.
- Subgenus Haematomyidium Goeldi 1905.
- Subgenus Haemophoructus Macfie 1925.
- Subgenus Hoffmania Fox 1947.
- Subgenus Macfiella Fox 1955.
- Subgenus Mataemyia Vargas 1960.
- Subgenus Meijerehelea Wirth and Hubert 1961.
- Subgenus Monoculicoides Khalaf 1954.
- Subgenus Oeacta Poey 1851.
- Subgenus Pontoculicoides Remm 1968.
- Subgenus Selfia Khalaf 1954.
- Subgenus Trithecoides Wirth and Hubert 1959.

Subgenus *Wirthomyia* Vargas 1973.

(Generic synonyms: *Cotocripus* Brethes 1912; *Diplosella* Kieffer 1921; *Oxyhelea* Kieffer 1921; *Prosapelma* Kieffer 1925; *Psychophaena* Philippi 1865; *Synhelea* Kieffer 1925).

### **Tribe *Ceratopogonini* Newman 1834**

*Genus Alluaudomyia* Kieffer 1913 (115 species).

Subgenus *Alluaudomyia* Kieffer (syn.: *Neoceratopogon* Malloch 1915; *Prionognathus* Carter, Ingram and Macfie 1921; *Thysanognathus* Ingram and Macfie 1922; *Isoecacta* Garrett 1925).

Subgenus *Paralluaudomyia* Clastrier 1960.

*Genus Baeohelea* Wirth and Blanton 1970 (3 species).

*Genus Brachypogon* Kieffer 1899 (17 species).

*Genus Camptopterohelea* Wirth and Hubert 1960 (1 species).

*Genus Ceratoculicoides* Wirth and Ratanaworabhan 1971 (4 species).

*Genus Ceratopogon* Meigen 1803 (18 species) (syn.: *Helea* Meigen 1800, rejected; *Psilohelea* Kieffer 1917).

*Genus Eohelea* Petrunkevitch 1956 (1 species) (fossil).

*Genus Fanthamia* De Meillon 1939 (3 species).

*Genus Isohelea* Kieffer 1917 (48 species) (syn.: *Nilohelea* Kieffer 1921; *Anakempia* Kieffer 1924; *Trishelea* Kieffer 1925).

*Genus Leptohelea* Wirth and Blanton 1970 (1 species).

*Genus Protoculicoides* Boesel 1937 (1 species) (fossil).

*Genus Rhynchohelea* Wirth and Blanton 1970 (1 species)

### **Tribe *Stilobezziini* Wirth 1952**

*Genus Afrohelea* Wirth 1965 (1 species).

*Genus Echinohelea* Macfie 1940 (18 species).

*Genus Fittkauhelea* Wirth and Blanton 1970 (1 species).

*Genus Luciamyia* De Meillon 1937 (1 species).

*Genus Monohelea* Kieffer 1917 (117 species).

Subgenus *Isthmohelea* Ingram and Macfie 1931.

Subgenus *Monohelea* Kieffer (syn.: *Allohelea* Kieffer 1917).

Subgenus *Schizohelea* Kieffer 1917.

*Genus Macrurohelea* Ingram and Macfie 1931 (5 species).

*Genus Parabezzia* Malloch 1915 (16 species) (syn.: *Diaphanabezzia* Ingram and Macfie 1931).

- Genus Parastilobezzia* Wirth and Blanton 1970 (1 species).  
*Genus Pseudostilobezzia* Wirth and Ratanaworabhan 1973 (1 species).  
*Genus Serromyia* Meigen 1818 (30 species) (syn.: *Prionomyia* Westwood 1840 ;  
*Ceratophus* Kieffer 1899 ; *Johannseniella* Williston 1907).  
*Genus Stilobezzia* Kieffer 1911 (248 species).
- Subgenus *Acanthohelea* Kieffer 1917.  
Subgenus *Eukraiohelea* Ingram and Macfie 1921.  
Subgenus *Neostilobezzia* Goetghebuer 1934.  
Subgenus *Stilobezzia* Kieffer (syn.: *Hartomyia* Malloch 1915).

### **Tribe Heteromyiini** Wirth 1962

- Genus Ceratobezzia* Kieffer 1917 (2 species).  
*Genus Clinohelea* Kieffer 1917 (34 species).  
*Genus Heteromyia* Say 1825 (12 species) (syn.: *Pachyleptus* Walker 1856).  
*Genus Metahelea* Edwards 1929 (2 species).  
*Genus Neurobezzia* Wirth and Ratanaworabhan 1973 (1 species).  
*Genus Neurohelea* Kieffer 1925 (5 species).  
*Genus Pellucidomyia* Macfie 1939 (7 species) (syn.: *Macfiehelea* Lane 1946).  
*Genus Tetrabezzia* Kieffer 1917 (4 species).

### **Tribe Sphaeromiini** Newman 1834

- Genus Calyptopogon* Kieffer 1910 (3 species).  
*Genus Dibezzia* Kieffer 1911 (3 species).  
*Genus Homohelea* Kieffer 1917 (12 species) (syn.: *Schizodactylus* Ingram and  
Macfie 1921 : *Ankistrodactylus* Ingram and Macfie 1922).  
*Genus Jenkinshalea* Macfie 1913 (8 species) (syn.: *Jenkinsia* Kieffer 1913,  
preocc.).  
*Genus Johannsenomyia* Malloch 1915 (25 species) (syn.: *Dicrohelea* Kieffer  
1917).  
*Genus Lanehelea* Wirth and Blanton 1972 (2 species).  
*Genus Mackerrasomyia* Debenham 1970 (2 species).  
*Genus Macropeza* Meigen 1818 (17 species) (syn.: *Macroptilum* Becker 1903 ;  
*Haasiella* Kieffer 1913).  
*Genus Mallochohelea* Wirth 1962 (44 species).  
*Genus Mixohelea* Kieffer 1917 (16 species).  
*Genus Neobezzia* Wirth and Ratanaworabhan 1972 (7 species).  
*Genus Neosphaeromias* Das Gupta and Wirth 1971 (4 species).  
*Genus Nilobezzia* Kieffer 1921 (64 species) (syn.: *Crespinia* Kieffer 1924 ;  
*Parrotia* Kieffer 1924 ; *Sphaerobezzia* Zilahi-Sebess 1940).

*Genus Probezzia* Kieffer 1906 (21 species) (syn. : *Dicrobezzia* Kieffer 1919).

*Genus Sphaeromias* Curtis 1829 (37 species) (syn. : *Xylocrypta* Kieffer 1899).

*Genus Xenohela* Kieffer 1917 (10 species).

*Genus A* — Debenham, in press (2 species).

*Genus B* — Debenham, in press (2 species).

*Genus C* — Debenham, in press (5 species).

#### **Tribe Palpomyiini** Enderlein 1936

*Genus Bezzia* Kieffer 1899 (247 species) (syn. : *Pseudobezzia* Malloch 1915 ; *Allobezzia* Kieffer 1917 ; *Lasiobezzia* Kieffer 1925 ; *Homobezzia* Macfie 1932).

*Genus Pachyhelea* Wirth 1959 (1 species).

*Genus Palpomyia* Meigen 1818 (248 species) (syn. : *Apogon* Rondani 1856 ; *Alasion* Rondani 1857 ; *Diplohelea* Kieffer 1925).

*Genus Phaenobezzia* Haeselbarth 1965 (14 species).

#### **Tribe Stenoxenini** Coquillett 1899

*Genus Paryphoconus* Enderlein 1912 (26 species).

*Genus Stenoxenus* Coquillett 1899 (18 species).

### Key to the Genera of *Ceratopogonidae*

1. Crossvein r-m present ; antenna of female usually 15-segmented ; larva with head capsule present, mouthparts well developed ..... 2
- Crossvein r-m absent ; antenna of female with 12-14 segments ; wing without macrotrichia ; larva without sclerotized head capsule, mouthparts reduced, body with neither prolegs nor anal bristles ; pupa free from larval skin ; pupal respiratory organ short and barrel-shaped distally, apicolateral processes simple (*Leptoconopinae*) ..... *Leptoconops* Skuse
2. Empodium small or vestigial ; claws gently curved ; larval skin free from pupa .. 4
- Empodium well developed, at least in female ; claws markedly curved ; wing usually with numerous macrotrichia ; larva with both anterior and posterior prolegs, body usually with short spines or long processes ; larval skin usually attached to posterior segments of pupa ; respiratory organs of pupa short and knoblike ; egg short and cylindrical with tapered ends (*Forcipomyiinae*) ..... 3

3. Microtrichia of wing large and conspicuous; macrotrichia when present scattered, sub-rect, not scalelike; fringe on posterior border of wing simple, a single row of alternating short and very short, simple straight hairs; costa reaching well beyond middle of wing; second radial cell longer than first and usually open ... *Atrichopogon* Kieffer
- Microtrichia minute; macrotrichia more abundant, covering greater part of wing, sloping, often scalelike; fringe more complex, not a single row of hairs; costa short or long; first radial cell narrow, often obliterated ..... *Forcipomyia* Meigen
4. Antennal segments sculptured; last segment of antenna usually not longer than preceding one; first radial cell of wing nearly or completely obliterated; second obliterated or square-ended, usually ending at or before middle of wing; female claws small and equal; eyes very short pubescent; larvae clambering, anterior prolegs absent, posterior prolegs retractile with hooks; pupal apicolateral processes bearing caudal bristle; egg horseshoe-shaped (*Dasyheleinae*) ..... *Dasyhelea* Kieffer
- Antennal segments not sculptured, last segment longer than preceding one; one or both radial cells of wing well developed, the second not markedly square-ended, ending past middle of wing (except in *Paradasyhelea*); eyes usually bare; larvae vermiform, swimming with spirochete motion, anterior and posterior prolegs absent; apicolateral processes of pupa without caudal bristle; egg long and cigar-shaped (*Ceratopogoninae*) ..... 5
5. Media petiolate, forking distal to level of r-m crossvein (in *Echinohelea*, with spinose legs, media forks just at the crossvein); M2 sometimes obsolescent basally ..... 6
- Media sessile, forking at or proximad of level of crossvein; M2 nearly always complete ..... 8
6. Claws of both sexes small, equal and simple; macrotrichia usually abundant; two more or less equal radial cells usually present; humeral pits prominent; empodium small or rudimentary (*Culicoidini*) ..... 11
- Claws of female usually large, equal or unequal, those of male smaller and equal; macrotrichia absent or scanty; one or two radial cells, the second usually larger than the first; r-m crossvein more or less perpendicular to R4 + 5; humeral pits small or absent; empodium absent ..... 7
7. Second radial cell small, not or little longer than the first, one or both radial cells may be obliterated (in *Alluaudomyia* first radial cell obliterated, second long, wing usually with small black spots); eyes usually pubescent; wing with or without macrotrichia, often milky white (*Ceratopogonini*) ..... 13
- Second radial cell long, much longer than first, which may be obliterated; eyes usually bare; macrotrichia usually absent; wing hyaline or with dark pattern, not milky (*Stilobezziini*) ..... 24
8. Fifth tarsomere armed ventrally with stout, black, blunt spines (batonnets); female abdomen without internal sclerotized gland rods; eighth segment of female often with ventral pair of hair tufts near gonopore (*Sphaeromiini*) ..... 42
- Fifth tarsomere unarmed or provided only with slender, sharp-tipped spines, if armed, female abdomen with internal sclerotized gland rods; eighth segment of female without ventral pair of hair tufts near gonopore ..... 9

9. Claws of female usually unequal, at least on hind leg, or a single claw with basal tooth; female abdomen without internal sclerotized gland rods (*Heteromyiini*) ..... 35
- Claws of female equal on all legs; female abdomen with internal sclerotized gland rods ..... 10
10. Body not unusually slender or dorsoventrally flattened; one or two radial cells, if cells narrow, costa not extending nearly to wing tip; r-m crossvein longer, the cell between R and M well formed and not very narrow; eyes narrowly to moderately separated; eighth abdominal segment of female not modified; legs usually not extremely long or hairy; femora often armed; claws usually moderately long; eggs not modified (*Palpomyiini*) ..... 60
- Body unusually slender and dorsoventrally flattened; one very narrow radial cell usually extending to wing tip; r-m crossvein often very short, the cell between R and M very narrow or even obliterated; eyes broadly separated; eighth abdominal segment of female narrowed distally with genital sclerotization; legs long and slender, with fine hairs, femora unarmed; claws very short; egg with peculiar frilled subapical collar (*Stenoxenini*) ..... 63

#### *Tribe Culicoidini*

11. Palpus four-segmented, only one segment distal to one bearing sensory organ; wing without macrotrichia; two broad radial cells; costa extending to 0.83 of wing length; antenna without minute sensory pits ringed with fine setae *Austroconops* Wirth and Lee
- Palpus three- to five-segmented, always two segments distal to one bearing sensory organ; wing usually with some macrotrichia; radial cells present or absent, the first never broad; costa extending to 0.45-0.78 of wing length; antenna with sensory pits ringed with fine setae present on some segments ..... 12
12. Palpus five-segmented; wing usually with two radial cells present; costa extending at least halfway to wing tip ..... *Culicoides* Latreille
- Palpus three- or four-segmented, the primitive first and second segments fused or absent; wing with both radial cells completely obliterated; costa short, extending less than halfway to wing tip ..... *Paradasyhelea* Macfie

#### *Tribe Ceratopogonini*

- 13 (7). Palpus two- or three-segmented, only one segment distal to one bearing sensory organ; proboscis short ..... 14
- Palpus five-segmented as usual, two segments distal to one bearing sensory organ; proboscis of normal length ..... 16
14. Female with only a single moderately long claw on each leg; wing greatly modified, with transverse folds and patches of coarse microtrichia ..... *Camptopterohelea* Wirth and Hubert
- Female with small paired claws; wing without transverse folds and patches of coarse microtrichia ..... 15

15. Costa extending to less than midlength of wing; radial cells obsolete; vein M2 present ..... *Baeohelea* Wirth and Blanton  
 — Costa extending to more than 0.7 of wing length; a single large radial cell present; vein M2 absent ..... *Leptohelea* Wirth and Blanton
16. Wing with two complete radial cells ..... 17  
 — Wing with at least one radial cell obsolete ..... 19
17. Costa extending to well past middle of wing, radial cells elongate ..... 18  
 — Costa extending to about middle of wing; radial cells short with adjacent veins thickened; (one or two large spermathecae present; male parameres usually broadly fused proximally) ..... *Isohelea* Kieffer
18. Recent species; eyes hairy; (usually three large spermathecae present; male parameres separate) ..... *Ceratopogon* Meigen  
 — Fossil species in Cretaceous amber; eyes bare ..... *Protoculicoides* Boesel
19. Female antenna 14-segmented, very short, with segments moniliform; proboscis stout and truncate; palpus stout, third segment greatly broadened; radial cells absent; vein M1 obsolete distally, M2 absent ..... *Rhynchohelea* Wirth and Blanton  
 — Female antenna 15-segmented, elongate with slender segments; proboscis of normal breadth; palpus slender; radial cells and media various ..... 20
20. Female claws unequal on hind legs ..... 21  
 — Female claws equal on all legs ..... 22
21. Eyes contiguous or narrowly separated; wing with first radial cell obsolete, second radial cell well developed; wing pattern usually of small, isolated black spots or streaks; female claws large on all legs; male antenna with plume .... *Alluaudomyia* Kieffer  
 — Eyes broadly separated; wing with first radial cell complete, second radial cell obsolete; wing pattern various; female claws small on fore and mid legs; male antenna without plume, last five segments elongated as in female ..... *Fanthamia* De Meillon
22. Female claws large on all legs ..... 23  
 — Female claws small, at least on hind legs; (first radial cell obsolete, second present but small; eyes broadly separated; male genitalia with well developed apicolateral processes) ..... *Ceratoculicoides* Wirth and Ratanaworabhan
23. Costa short, usually extending to about 0.6 of wing length; radial cells obsolete; eyes contiguous; recent species; (male genitalia with apicolateral processes absent) .....  
 ..... *Brachypogon* Kieffer  
 — Costa long, extending to wing tip, one large radial cell present; eyes narrowly separated; wing with conspicuous area of transverse ridges in anterodistal portion of cell R5; fossil species, Oligocene ..... *Eohelea* Petrunkevitch

#### *Tribe Stilobezziini*

- 24 (7). Femora armed with one or more stout ventral spines, at least on one pair of legs 25  
 — Femora not armed with stout ventral spines ..... 27

25. All femora armed with numerous spines, at least in male sex, these not confined ventrally; two well-developed radial cells; reddish yellow pruinose species; male antenna not plumose, last five segments elongated as in female ..... *Echinohelea* Macfie  
 — Only hind and/or fore femur armed with ventral spines; one or two radial cells; male antenna plumose; color various ..... 26
26. Fore femur slender and unarmed, hind femur greatly swollen and arcuate, and armed with numerous ventral spines; two well-developed radial cells; shining black species ..... *Serromyia* Meigen  
 — Fore femur with 1-2 ventral spines; first radia cell obliterated; pruinose yellowish or brownish species ..... *Stilobezzia* subgenus *Eukraiohelea* Ingram and Macfie
27. One radial cell present ..... 28  
 — Two radial cells present ..... 30
28. Costa of female short, ending at 0.8 of wing length, not extending past tip of R4 + 5; palpus five-segmented, third segment with sensory pit; claws small with basal tooth ..... *Afrohelea* Wirth  
 — Costa of female long, extending past end of R4 + 5 and ending nearly at wing tip; palpus four-segmented, third segment without pit; claws large, simple ..... 29
29. Eyes broadly separated, pubescent; male coxa without long spinelike hairs; male ninth tergum with strong sclerotized lobes on ventral face *Fittkauhelea* Wirth and Blanton  
 — Eyes moderately separated, bare; male coxa with long spinelike hairs; male ninth tergum without strong sclerotized lobes on ventral face ..... *Parabezzia* Malloch
30. Claws of female all equal or but slightly unequal; fifth tarsomere unarmed .... 31  
 — Claws of female very unequal, or a single long claw with or without a smaller basal barb, at least on one pair of legs; fifth tarsomere often with ventral spines .... 32
31. Female costa extending to wing tip, which is bilobed; cell R5 broad distally, vein R4 + 5 joining costa and vein M1 at wing tip; posterior end of female abdomen not modified ..... *Luciamyia* De Meillon  
 — Female wing with costa shorter, not reaching tip of wing, which is normal; posterior end of female abdomen elongated and modified, tenth segment bent forward ventrally ..... *Macrurohelea* Ingram and Macfie
32. Claws of female unequal on all legs or a single long claw with small basal tooth 33  
 — Claws of female unequal on only one pair of legs (fore or hind); equal on other two pairs ..... 34
33. Female wing with second radial cell extremely long, costa produced past end of cell to wing tip; palpus short, apparently four-segmented; female claws single with minute basal barb ..... *Parastilobezzia* Wirth & Blanton  
 — Female wing with second radial cell extending to 0.55-0.85 of wing length; costa not produced beyond cell; palpus long, five-segmented; female claws large and unequal on all legs ..... *Stilobezzia* Kieffer

34. Claws of female equal on four anterior legs, hind claw with one long talon and with or without another short one; tarsi with some strong ventral spines; wing usually with conspicuous color pattern; eyes bare ..... *Monohelea* Kieffer  
 — Claws of female equal on four posterior legs, long and unequal on fore leg; tarsi without strong ventral spines; wing without color pattern; eyes hairy .....  
 ..... *Pseudostilobezzia* Wirth and Ratanaworabhan

### Tribe *Heteromyiini*

- 35 (9). Costa greatly prolonged beyond tip of vein R4 + 5 ..... 36  
 — Costa not prolonged beyond tip of vein R4 + 5 ..... 37
36. Two radial cells; claws equal on all legs; fifth tarsomere of fore leg somewhat inflated ..... *Neurohelea* Kieffer  
 — One radial cell; claws equal on fore and mid legs, unequal on hind leg; fifth tarsomere of fore leg not inflated ..... *Neurobezzia* Wirth and Ratanaworabhan
37. Fourth tarsomere cylindrical or cordiform, but not divided into spinose bifid lobes (fifth tarsomere of fore legs inflated, fusiform; claws equal on fore and mid legs, very unequal on hind legs) ..... 38  
 — Fourth tarsomere ending in two bifid lobes armed with spines, at least on one pair of legs ..... 39
38. Fore femur greatly swollen and armed ventrally, the tibia arcuate; fourth tarsomere cordiform; one or two radial cells; wing fasciate; body more or less shining ..... *Heteromyia* Say  
 — Fore femur slender, unarmed; fourth tarsomere not cordiform; one radial cell; wing milky; body densely pollinose ..... *Pellucidomyia* Macfie
39. Claws equal on fore leg, unequal on mid and hind legs; fifth tarsomere of fore leg greatly swollen; fourth tarsomere with bifid spinose lobes on mid and hind legs, cordiform on fore leg ..... 40  
 — Claws unequal on all legs; fifth tarsomere of fore leg not greatly swollen; fourth tarsomere with bifid spinose lobes on fore and mid legs or on all legs ..... 41
40. One radial cell; mesonotal spine strongly developed ..... *Ceratobezzia* Kieffer  
 — Two radial cells; mesonotal spine poorly developed ..... *Clinohelea* Kieffer
41. Fourth tarsomere with bifid spinose lobes on fore and mid legs, long and cylindrical on hind leg; one radial cell ..... *Tetrabezzi* Kieffer  
 — Fourth tarsomere with bifid spinose lobes on all legs; two radial cells .....  
 ..... *Metahelea* Edwards

### Tribe *Sphaeromyiini* (key for females)

- 42 (8). Tarsal claws unequal, at least on hind legs, or a single long claw with basal barb (abdomen petiolate; eighth segment of abdomen with ventral pair of hair tufts; costa extending to approximately 0.8 of wing length; usually two radial cells) ..... 43  
 — Tarsal claws equal on all legs ..... 47

43. Tarsal claws unequal on four posterior legs, equal on fore legs; femora unarmed (fifth tarsomere of male hind leg with 2-3 pairs of batonnets) ..... 44  
 — Tarsal claws unequal on all legs ..... 45
44. Costa extending to wing tip, CR 0.99; fifth tarsomere with four pairs of batonnets on basal half ..... Genus B, Debenham, in press  
 — Costa not extending to wing tip, CR 0.8-0.9; fifth tarsomere with numerous batonnets not restricted to basal half of segment ..... *Johannsenomyia* Malloch
45. Tarsal claws single with slender basal barb ..... 46  
 — Tarsal claws paired, each with blunt, external, basal tooth; three or more pairs of batonnets along length of fifth tarsomere; femora unarmed (type-species) or armed ..  
 ..... *Dibezzia* Kieffer
46. Mesonotum shining black; fifth tarsomere with 2-3 pairs of ventral batonnets on basal portion only; fourth tarsomere cordiform ..... *Mixohelea* Kieffer  
 — Mesonotum densely whitish to grayish pollinose; fifth tarsomere with four or more pairs of ventral batonnets along entire length; fourth tarsomere cylindrical .....  
 ..... *Xenohelea* Kieffer
- 47 (42). Claws with internal basal barb and external basal tooth; fifth tarsomere with ten pairs of short, stout batonnets; fore femur greatly swollen with 15-20 stout ventral spines ..... *Neosphaeromias* Das Gupta and Wirth  
 — Claws with internal basal barb or external basal tooth, but not both in combination 48
48. Claws with slender internal basal barb, gently curved distally ..... 49  
 — Claws with blunt external basal tooth, at least on one pair of legs, usually straight or flattened distally ..... 53
49. Costa extending nearly to wing tip ..... 50  
 — Costa extending to about 0.75-0.85 of wing length ..... 52
50. Fifth tarsomere with 1-2 basal pairs of batonnets ..... *Homohelea* Kieffer  
 — Fifth tarsomere with three or more pairs of batonnets along length of segment .. 51
51. Claws with slender internal basal tooth; all claws distinctly shorter than fifth tarsomere ..... *Sphaeromias* Curtis  
 — Claws simple, without internal basal tooth; all claws as long as or longer than fifth tarsomere ..... Genus C, Debenham, in press
52. Fore femur greatly swollen, with numerous short, stout, ventral spines; costal ratio 0.75 ..... *Mackerrasomyia* Debenham  
 — Fore femur slender, unarmed ventrally or armed with only one ventral spine; costal ratio 0.82-0.85; (fifth tarsomere slender and armed ventrally with four or more pairs of strong batonnets; claws long; femora swollen distally) *Lanehelea* Wirth and Blanton
- 53 (48). Costa short, extending to less than 0.8 of wing length ..... 54  
 — Costa long, extending nearly to wing tip; CR over 0.84 ..... 55

54. Body slender; mesonotum shining yellow to black with little or no pollen; femora armed or unarmed; two radial cells (male genitalia with well developed basistyle and articulated dististyle) ..... *Mallochohelea* Wirth  
 — Body stout; mesonotum dull, usually with dense whitish to grayish pollen; femora ventrally and tibiae dorsally armed with numerous fine sharp spines; one or two radial cells (male genitalia with short, stout basistyle and immovable, budlike dististyle) ....  
 ..... *Nilobezzia* Kieffer
55. Wing with large, angular, anal lobe ..... 56  
 — Wing with anal lobe not angularly developed ..... 57
56. Eyes broadly separated; palpus five-segmented; fourth tarsomere cordiform; wing unusually broad; r-m crossvein long ..... *Jenkinshalea* Macfie  
 — Eyes broadly contiguous; palpus four-segmented; fourth tarsomere cylindrical; wing not unusually broad, r-m crossvein short ..... Genus A, Debenham, in press
57. Thorax sharply pointed in front, produced markedly over head; fifth tarsomere swollen on fore leg; radial cell extremely narrow ..... *Calyptopogon* Kieffer  
 — Thorax bluntly rounded or bluntly conical in front, not produced markedly over head; fifth tarsomere not swollen; radial cell not extremely narrow ..... 58
58. Claws short and curved, sharp-pointed, each with inconspicuous external basal tooth; mesonotum without strong erect bristles ..... *Macropeza* Meigen  
 — Claws longer, straighter, and somewhat flattened distally, each with strong external basal tooth ..... 59
59. External tooth of claw short and blunt; mesonotum with strong erect bristles; clypeus broad and convex; eighth sternum with prominent hair tufts; femora not swollen at apex (male parameres separate distally) ..... *Probezia* Kieffer  
 — External tooth of claw long and slender; mesonotum without strong erect bristles; clypeus narrow and flattened; eighth sternum with only a few long bristly hairs; femora usually conspicuously swollen at apex (male parameres fused distally) .....  
 ..... *Neobezzia* Wirth and Ratanaworabhan

### Tribe *Palpomyiini*

- 60 (10). Two radial cells ..... 61  
 — One radial cell ..... 62
61. Hind femur greatly swollen; femora unarmed ..... *Pachyhelea* Wirth  
 — Hind femur not greatly swollen, if moderately swollen at least one pair of femora armed with ventral spines; fore femur often swollen ..... *Palpomyia* Meigen
62. Femora usually armed, at least on fore legs; costa short, costal ratio 0.67-0.75; fifth tarsomere without stout ventral spines; male dististyle well developed, articulated ....  
 ..... *Bezzia* Kieffer  
 — Femora unarmed; costa longer, costal ratio 0.87; female fifth tarsomere with stout ventral spines with sharp, bent tips; male dististyle short and not articulated, or absent  
 ..... *Phaenobezzia* Haeselbarth

**Tribe Stenoxenini**

- 63 (10). Thorax broadly rounded anteriorly, without median spine; female wing with vein M2 strikingly elbowed at base; palpus four-segmented; two spermathecae present; male parameres fused apically ..... *Stenoxenus* Coquillett
- Thorax narrowed in front, more or less conical with erect anteromedian spine; female with vein M1 not elbowed at base; palpus five-segmented; one spermatheca present; male parameres separate apically ..... *Paryphoconus* Enderlein

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