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Review

Classification within the cosmopolitan genus *Culex* (Diptera: Culicidae): The foundation for molecular systematics and phylogenetic research

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ABSTRACT

The internal classification of the cosmopolitan and medically important genus *Culex* is thoroughly reviewed and updated to reflect the multitude of taxonomic changes and concepts which have been published since the classification was last compiled by Edwards in 1932. Both formal and informal taxa are included. The classification is intended to aid researchers and students who are interested in analyzing species relationships, making group comparisons and testing phylogenetic hypotheses. The genus includes 768 formally recognized species divided among 26 subgenera. Many of the subgenera are subdivided hierarchically into nested informal groups of morphologically similar species that are believed to represent monophyletic lineages based on morphological similarity. The informal groupings proposed by researchers include Sections, Series, Groups, Lines, Subgroups and Complexes, which are unlikely to be phylogenetically equivalent categories among the various subgenera.

Contents

1. Introduction

Mosquitoes, family Culicidae, are classified in two subfamilies, Anophelinae and Culicinae, and those of subfamily Culicinae are segregated into 11 tribes (Harbach and Kitching, 1998; Mitchell et al., 2002). Tribe Culicini is the second largest tribe with 795 species (about 25% of all known mosquito species) classified in four genera: *Culex* Linnaeus (cosmopolitan), *Deinocerites* Theobald (Neotropical), *Galindomyia* Stone and Barreto (Neotropical) and *Lutzia* Theobald (absent from the western Palaearctic and Nearctic Regions). Adult females of many species feed on humans and several species of subgenera *Culex* and *Melanoconion* Theobald are important vectors of encephalitis and other arboviruses. A few species of subgenus *Culex* are important vectors of filarial worms. *Culex* mosquitoes are of particular concern in view of the threat of emerging diseases in relation to global warming and environmental change.

Culex currently includes 768 formally recognized species. These species are divided between 26 subgenera, and the largest subgenera are further divided into hierarchical systems of informal taxonomic categories. Notwithstanding the phylogenetic studies of Mallampalli (1995), Miller et al. (1996), Navarro and Liria (2000), Juthayothin (2004), St John (2007), Vesgueiro et al. (2011) and Demari-Silva et al. (2011), the phylogeny of *Culex* remains unknown and its classification is problematic. The various formal and informal group taxa are based exclusively on morphological similarities that are interpreted by intuitive taxonomic methods to represent natural groupings of species. Three problems make it difficult to use the classification as a model on which to base systematic and phylogenetic studies and hypotheses. The classification lacks uniformity in the application of informal group names, the various species-group taxa have not been examined on a worldwide basis and the

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classification has not been updated and published in its entirety since Edwards (1932). This review is intended to overcome the third problem. The classification is presented here to assist students and researchers in assessing relationships, conducting comparative or revisionary studies and testing phylogenetic hypotheses involving groups of supposedly related and unrelated taxa. The classification is the foundation for integrated systematics studies which are needed to develop a testable phylogeny that indicates evolutionary relationships between taxa and provides a classification predictive of biological and ecological traits of scientific and economic importance. A sound classification of *Culex* mosquitoes is essential to identify evolutionary and co-evolutionary trends and specializations, to conduct zoogeographical analyses and make predictions about the biology of previously unknown or little-known species.

2. Explanation and procedures

In compiling the classification (Section 6), an effort was made to see all published references, regional studies and revisionary works that provide hierarchical arrangements of taxa. The current system of classification is based primarily on the schemes proposed by Edwards (1932, 1941), Lane and Whitman (1951), Belkin (1962), Forattini (1965), Bram (1967a,b), Berlin (1969), Sirivanakarn (1971, 1972, 1976, 1977a, 1983), Valencia (1973), Tanaka et al. (1979), Berlin and Belkin (1980), Harbach (1988) and Sallum and Forattini (1996). These authors treated nearly all of the infrasubgeneric groups and approximately 85% of the species that are currently recognized. The remaining groups and species were either described since the treatments of the above authors or represent earlier named taxa which have received little attention by taxonomists. The placement of these taxa in the classification was determined from statements made by the original authorities or inferred from information contained in the original or subsequent treatments.

Infrasubgeneric categories have no formal status under the *International Code of Zoological Nomenclature* (ICZN, 1999). They are convenience categories only, often based on superficial similarities that may not indicate natural relationships. The informal categories used by taxonomists to classify species of *Culex* into taxonomic hierarchies below subgenus level include Sections, Series, Groups, Lines, Subgroups and Complexes. The practice of constructing group names by placing the term denoting the level of classification after the specific name of the group, e.g. Pipiens Group, is followed here. Furthermore, since informal group names are not regulated by the *Code*, they are treated as vernacular names in the manner promulgated by Belkin (1962), explained by Peyton (1990) and employed for the informal classification of genus *Anopheles* Meigen by Harbach (1994, 2004). These names are printed in Roman type with the first letter capitalized even though the name of a nominal species precedes the term (capitalized) denoting the level of classification, e.g. Sitiens Group. Alternatively, in situations where this practice might be unacceptable, an italicized binomen should be used in combination with the term (not capitalized) denoting the level of classification, e.g. *Culex pipiens* group.

No subspecies are listed in the classification. Subspecies are phenetic concepts that have no real biological/phylogenetic meaning (F.C. Thompson, pers. com.). Most mosquito workers have either synonymized subspecific names with specific epithets or recognized them for distinct biological species. It should be noted that subspecies are not recognized in either the BioSystematic Database of World Diptera (http://www.sel.barc.usda.gov/Diptera/biosys.htm) or the Encyclopedia of Life (http://www.eol.org/).

Informal infrasubgeneric categories are basically subjective groupings of subordinate taxa that are defined by the included species. Which species are included in individual groups, and which morphological and biological characteristics of these species are used to define the groups, depends entirely upon the judgement and experience of the taxonomist. For this reason it is not possible to provide objective definitions or establish equivalent ranks for the various informal categories of classification now recognized within the genus. In reality, there is probably little or no quantifiable difference in the degree of morphological differentiation between some assemblages of species, especially Groups or Lines and Subgroups or Complexes. However, no attempt has been made herein to alter the names of categories or change species assignments established in the published literature.

The arrangement of taxa herein is strictly alphabetical and is not intended to show or imply evolutionary relationships. The groupings at each level of classification are believed to represent phylogenetically related assemblages of species based on morphological similarity. Some subgenera contain one or more seemingly unrelated species which are not assigned to infrasubgeneric groups. These species are identified as "Unplaced species" listed at the end of the informal groups recognized within the subgenus. The authorities who first introduced or most recently redefined the informal taxonomic groups are indicated by literature citations in the classification.

3. Taxonomic history

A tremendous amount of research has been done on *Culex* mosquitoes, but much of the taxonomic work has been directed primarily toward discriminating species and not on organising them into natural groups. The result is that the classification of *Culex* is based on the intuitive interpretation of morphological similarity and few attempts have been made to resolve phylogenetic relationships using modern techniques.

The genus has a cosmopolitan distribution and includes 768 species divided among 26 subgenera. The current system of subgeneric classification is based primarily on external adult characters, especially features of the male genitalia. The species of the larger subgenera are arranged in informal classifications that variously include Sections, Series, Groups, Lines, Subgroups and Complexes. The infrasubgeneric categories are often based on superficial similarities that may not reflect natural relationships. In general, the larger the group, the less likely it is to be a monophyletic assemblage of species. Furthermore, the informal categories in most cases probably do not represent phylogenetically equivalent (genealogically comparable) groups of species among the various subgenera.

Subgenus *Acalleomyia* – *Acalleomyia* was originally proposed as a distinct genus by Leicester (1908), with *obscurus* Leicester as its type and the only included species. Edwards (1913) transferred the species to genus *Micraedes* Coquillett where it remained until Edwards (1922a) recognized *Acalleomyia* as a subgenus of *Culex*.

Subgenus *Acallyntrum* – *Acallyntrum* was originally proposed as a subgenus of *Culex* by Stone and Penn (1948), with the new species *perkinsi* Stone and Penn as the type species. *Acallyntrum* currently includes eight species that comprise two species groups.

Subgenus *Aedinus* – *Aedinus* was originally proposed as a distinct genus in 1904 but its authorship was not resolved until Belkin (1968). It was classified as a subgenus of *Culex* by Edwards (1930). Stone et al. (1959) included subgenus *Aedinus* Lutz (in Bourroul, 1904) along with subgenera *Anoedioporpa* Dyar, *Micraedes* and *Tinolestes* Coquillett (as synonyms) in subgenus *Aedinus* Bourroul (*sic*) based on the short maxillary palpus of males. Belkin (1968) recognized that this character had evolved independently in several unrelated groups, and elevated *Aedinus* Lutz, as well as *Anoedioporpa*, *Micraedes* and *Tinolestes*, to subgeneric rank in *Culex*.

Subgenus *Afroculex* – *Afroculex* was originally proposed as a subgenus of *Culex* by Danilov (1989), with *Pseudohowardina lin-*

eata Theobald as its type and the only included species. Edwards (1914) transferred *Pseudohowardina lineata* to genus *Culex* and gave it the replacement name of *pulchrithorax* because *lineatus* was preoccupied by *Cx. lineatus* von Humboldt. The species was eventually placed in subgenus *Neoculex*, but its taxonomic position was open to question (Edwards, 1941). Its provisional placement in *Neoculex* continued until Sirivanakarn (1971) transferred it to subgenus *Maillotia* Theobald. Danilov (1989) realized that *Cx. lineatus* von Humboldt is actually a species of genus *Psorophora*, as recorded by Knight and Stone (1977), and reinstated *lineatus* as the valid name of the species and transferred it to the new subgenus *Afroculex* based on unique features of the adults and male genitalia. The immature stages remain unknown.

Subgenus *Allimanta* – *Allimanta* was originally proposed as a subgenus of *Culex* by Casal and Garcia (1968), with *tramazayguesi* Duret as its type and the only included species. *Culex tramazayguesi* was originally described as a species of subgenus *Culex*.

Subgenus *Anoedioporpa* – *Anoedioporpa* was originally proposed as a subgenus of *Culex* by Dyar (1923), with *conservator* Dyar and Knab as its type species. Most of the species currently included in the subgenus were previously assigned to other groups that have been recognized as subgenera of *Culex*, including *Isostomyia* Coquillett (Dyar, 1918a; Edwards, 1932), *Melanoconion* (Dyar, 1925, 1928) and *Tinolestes* (Lane, 1953). Stone et al. (1959) included *Anoedioporpa*, along with *Tinolestes* and *Micraedes*, in subgenus *Aedinus*, which at the time was attributed to Bourroul (1904). Belkin (1968) recognized *Anoedioporpa* as a distinct taxon and restored it to subgeneric rank in genus *Culex*. Berlin and Belkin (1980) divided the subgenus into two groups, the Conservator Group, which currently includes 11 species, and the monobasic Restrictor Group.

Subgenus *Barraudius* – *Barraudius* was originally proposed as a subgenus of *Culex* by Edwards (1921), with *pusillus* Macquart as its type species. *Barraudius* currently includes four species that are considered to comprise a homogeneous group without subdivision.

Subgenus *Belkinomyia* – *Belkinomyia* was originally proposed as a subgenus of *Culex* by Adames and Galindo (1973), with the new species *eldridgei* Adames and Galindo as its type and the only included species.

Subgenus *Carrollia* – *Carrollia* was originally proposed as a distinct genus by Lutz (1905), with *iridescens* Lutz as its type and the only originally included species. Dyar (1918a) appears to have been the first person to regard *Carrollia* as a subgenus of *Culex*, followed by Edwards (1932) and all later authors. The current internal division of the subgenus into two species groups, the Bihaicola and Iridescens Groups, the latter with two subgroups, the Urichii and Iridescens Subgroups, is attributable to Valencia (1973).

Subgenus *Culex* – The internal classification of subgenus *Culex* is in a chaotic condition. The subgenus has only been examined on a worldwide basis by Edwards (1932), who divided it into two groups: the Sitiens Group (Old World) and the Pipiens Group (cosmopolitan). Both groups are highly complex assemblages and include species that do not readily fit into either group. Four additional species groups have been recognized subsequently: the Guiarti Group (Edwards, 1941) for several Afrotropical species, the Atriceps Group (Belkin, 1962) for three South Pacific species, the Coronator Group (Forattini, 1965; Bram, 1967b) for a number of apparently related Neotropical species and the Duttoni Group (Harbach, 1988) for the unusual Afrotropical *Cx. duttoni* Theobald. Heinemann and Belkin (1977, and later publications) recognized two groups in the Neotropical Region, the Declarator and Inflictus Groups, but did not indicate which species they include. Strickman (1990) made reference to the Declarator Group, but he also did not mention which species comprise the group. The internal classification of the subgenus presented here is based principally on information extracted and integrated from the works of Edwards (1932, 1941), Belkin (1962), Forattini (1965), Bram (1967a,b), Sirivanakarn (1976), Tanaka et al. (1979) and Harbach (1988), but the inclusion of many species in groups and subgroups, especially New World species, is problematic.

Subgenus *Culiciomyia* – *Culiciomyia* was originally proposed as a distinct genus by Theobald (1907). Designation of the type species, *Culiciomyia inornata* Theobald (subjective synonym of *Culex fragilis* Ludlow), is attributed to Edwards (1912). *Culiciomyia* was reduced to subgeneric status in *Culex* by Edwards (1921). Edwards (1932) recognized two species groups in the subgenus: group A, the Fragilis Group, with species in the Oriental, Indomalayan and Australasian Regions, and group B, the Nebulosus Group, with species restricted to the Afrotropical Region. Three additional groups have since been recognized for species in the Oriental Region: the Dispectus Group (Bram, 1969), Tricuspis Group (Harrison, 1987) and the Shebbearei Group, which is the name given here, based on nomenclatural priority, for the unnamed "group or complex" of Sirivanakarn (1977b).

Subgenus *Eumelanomyia* – *Eumelanomyia* was originally proposed as a distinct genus by Theobald (1909), with *inconspicuosa* Theobald as its type and the only included species. *Eumelanomyia* was described as being similar to *Culiciomyia* but the true identity of the type species was not known until Edwards (1922b) re-examined the specimens and identified them as *Culex*. The name *inconspicuosa* was thus found to be preoccupied, and *Culex albiventris* was proposed for the species. Theobald (1910) recognized *Protomelanoconion* Theobald as a distinct genus based on a misidentified species of *Culex* which he named *Protomelanoconion fusca*. Edwards (1922b) also found this name to be preoccupied and proposed the replacement name *Culex horridus* for the species. In addition to these corrections, Edwards suggested that both *Eumelanomyia* and *Protomelanoconion* Theobald should be treated as subgenera of *Culex*. Eight years later, Edwards (1930) established *Mochthogenes* as a subgenus of *Culex* with *Aedes malayi* Leicester as the designed type species. No further changes were made to the taxonomy of these groups until Edwards (1932) examined the classification of *Culex* on a worldwide basis. As a result, Edwards retained *Mochthogenes* as a subgenus and included *Eumelanomyia*, *Protomelanoconion* and a number of other species within subgenus *Neoculex* Dyar, which he divided into three groups: Group A (*Neoculex* or *apicalis*-group), Group B (*Eumelanomyia* or *albiventris*-group) and Group C (*Protomelanoconion* or *uniformis*-group). In his later treatise on the Afrotropical Culicinae, Edwards (1941) recognized two additional groups, the *pulchrithorax* and *rima* groups, for species previously included in his *apicalis* group. No further changes were made to Edwards's classification until Sirivanakarn (1971) revised the classification of *Neoculex* to include nearly all species previously placed in subgenus *Mochthogenes* and a number of species previously included in subgenus *Neoculex*. Sirivanakarn synonymized *Protomelanoconion* and *Mochthogenes* with *Eumelanomyia* and recognized subgenus *Maillotia* in addition to subgenera *Eumelanomyia* and *Neoculex*. The current internal classification of subgenus *Eumelanomyia* was developed by Sirivanakarn (1971, 1972).

Subgenus *Kitzmilleria* – *Kitzmilleria* was originally proposed as a subgenus of *Culex* by Danilov (1989), with *moucheti* Evans as its type and the only included species. *Culex moucheti* was originally placed in the Pipiens Group of subgenus *Culex*, and was considered a member of the Decens Series (Edwards, 1932) until Danilov (1989) proposed subgenus *Kitzmilleria* based on its distinct adult, larval and pupal morphology.

Subgenus *Lasiosiphon* – *Lasiosiphon* was originally proposed as a subgenus of *Culex* by Kirkpatrick (1925), with *adairi* Kirkpatrick, 1926, a replacement name for *pluvialis* Kirkpatrick, 1925, as its type and the only included species.

Subgenus *Lophoceraomyia* – *Lophoceraomyia* was originally proposed as a distinct genus by Theobald (1905), with *uniformis* Theobald as its type and the only included species. It was reduced to

a subgenus of *Culex* by Edwards (1917). Edwards (1932) divided the subgenus (as subgenus *Lophoceratomyia*) into three groups: Group A (*minutissimus*-group), Group B (*Lophoceratomyia* or *fraudatrix*-group) and Group C (*Cyathomyia* or *mammilifer*-group). Edwards later (1934, in Barraud, 1934), amalgamated Groups A and B and subdivided Group C. Colless (1965), however, preferred to recognize only two major groups, with the second divided into two subgroups. Sirivanakarn (1977a) modified the classifications of Edwards (1932), Edwards (1934 [in Barraud, 1934]) and Colless (1965) to include three groups, the Fraudatrix, Mammilifer and Wilfredi Groups, based principally on structures of the antennae and genitalia of males. The division of these groups into subgroups and complexes by Sirivanakarn (1968, 1977a) forms the backbone of the current classification of the subgenus.

Subgenus *Maillotia* – *Maillotia* was originally proposed as a distinct genus by Theobald (1907), with *pilifera* Theobald (subjective synonym of *Culex hortensis* Ficalbi) as its type and the only included species. It was implicitly synonymized with *Culex* by Edwards (1911) and placed in synonymy with *Neoculex* by Edwards (1932), which was treated as a subgenus of *Culex*. Sirivanakarn (1971) removed *Maillotia* from synonymy to accommodate eight species divided between three groups, the Hortensis Group with three species, the monobasic Pulchrithorax Group for *pulchrithorax* Edwards and the Seyrigi Group with four species. The subgenus currently includes two species groups and an unplaced species. The Pulchrithorax Group was eliminated when Danilov removed *pulchrithorax* from *Maillotia* and proposed subgenus *Afroculex* to accommodate it.

Subgenus *Melanoconion* – *Melanoconion* was originally proposed as a distinct genus by Theobald (1903). The type species, *Culex atratus* Theobald, was subsequently designated by Dyar (1905). Dyar and Knab (1906) synonymized *Melanoconion* with *Culex* and proposed *Mochlostyrax* as a distinct genus with *caudelli* Dyar and Knab as its type species. Howard et al. (1915) considered both *Melanoconion* and *Mochlostyrax* as synonyms of *Culex*, and three years later Dyar (1918a) recognized them as separate subgenera of *Culex*. In the same paper, Dyar also proposed *Choeroporpa* as a subgenus of *Culex*, with *anips* Dyar as its type species. *Choeroporpa* included most of the species that Dyar had previously placed in *Culex* or *Mochlostyrax*. In a second paper published in the same year, Dyar (1918b) proposed *Helcoporpa* as another subgenus of *Culex*, with *menytes* Dyar as its type species. Five years later, Dyar (1923) instated *Gnophodeomyia* Theobald as a subgenus (previously questionably synonymized with *Culex* by Brunetti, 1914) and proposed *Anoedioporpa* as a replacement name for subgenus *Isostomyia*. Dyar (1928) made significant changes to the classification of New World *Culex*. He recognized *Melanoconion* and *Mochlostyrax* as subgenera and reduced the other nominal generic-level groups to informal sections: *Choeroporpa*, *Helcoporpa* and the newly proposed *Dinoporpa* became sections of *Mochlostyrax*, and *Tinolestes*, *Gnophodeomyia* and *Anoedioporpa* became sections of *Melanoconion*, which also included *americanus* (Neveu-Lemaire) and *antillummagnorum* Dyar of subgenus *Micraedes*. Edwards (1932), in his treatment of world Culicidae, reinterpreted the taxonomy of *Melanoconion* and *Mochlostyrax*. He considered *Melanoconion* as a subgenus with *Gnophodeomyia*, *Asebeomyia* Aiken, *Tinolestes*, *Choeroporpa*, *Helcoporpa* and *Dinoporpa* as its synonyms; restricted subgenus *Mochlostyrax* to include species included in the *Mochlostyrax* section of Dyar (1928); synonymized *Anoedioporpa* with subgenus *Isostomyia* (currently a valid genus in tribe Sabethini); and transferred *americanus* and *antillummagnorum* to subgenus *Micraedes*. During the same year Komp and Curry (1932) proposed *Upsiloporpa* as a new subgenus of *Culex*, with the new species *haynei* Komp and Curry as its type and only included species. Komp (1935) found *haynei* to be conspecific with *menytes*, thus *Upsiloporpa* became another synonym of *Melanoconion*. Except for the transfer of *ocellatus* Theobald from subgenus *Microculex* Theobald to subgenus *Melanoconion* by Lane and Whitman (1943), Edwards's classification remained unchanged until Rozeboom and Komp (1950) treated *Melanoconion* and *Mochlostyrax* as a single subgenus. Lane (1953) followed Rozeboom and Komp's classification but resurrected *Tinolestes* from synonymy with *Melanoconion* as a separate subgenus. A year later, Foote (1954) determined that *Mochlostyrax* was distinct based on larval morphology and considered it to be a subgenus separate from *Melanoconion*. Foote's separation of *Mochlostyrax* and *Melanoconion* prevailed until Belkin (1968), Belkin et al. (1970) and Sirivanakarn (1983) considered *Melanoconion* and *Mochlostyrax* to form a single subgenus.

Dyar (1928) recognized four sections in subgenus *Mochlostyrax*, the *Dinoporpa*, *Helcoporpa*, *Mochlostyrax* and *Choeroporpa* sections, and four sections in subgenus *Melanoconion*, the *Tinolestes*, *Gnophodeomyia*, *Melanoconion* and *Anoedioporpa* sections. Edwards (1932) recognized subgenus *Mochlostyrax*, without sections, and divided subgenus *Melanoconion* into three groups (Groups A, B and C) based on external features of adults. Rozeboom and Komp (1950) disagreed with Edwards's classification and largely adopted Dyar's (1928) scheme based chiefly on features of the male genitalia for their concept of subgenus *Melanoconion*, which included *Mochlostyrax* and excluded *Anoedioporpa*. Hence, Rozeboom and Komp divided the subgenus into seven sections, namely the *Choeroporpa*, *Dinoporpa*, *Gnophodeomyia*, *Helcoporpa*, *Melanoconion*, *Mochlostyrax* and *Tinolestes* sections. Nearly two decades later, Galindo (1969) established the Spissipes Group based on male genitalia and larval characters, and Duret (1969) recognized the Ocellatus Group based on distinctive features of adults and male genitalia. Both groups were retained and redefined in the revised scheme of classification proposed by Sirivanakarn (1983).

Sirivanakarn (1983) distinguished three sections within the subgenus, the Melanoconion, Ocellatus and Spissipes Sections, and divided the Melanoconion and Spissipes Sections into Groups and Subgroups based principally on structural differences of the male genitalia, characteristics of the scaling on the head and scutum of adults and features of the larvae. Pecor et al. (1992) removed the Ocellatus Section from the subgenus, and it remains without subgeneric placement within genus *Culex*. More recently, Sallum and Forattini (1996) refined the Spissipes Section to include eight Groups and three Subgroups.

Subgenus *Micraedes* – *Micraedes* was proposed as a distinct genus by Coquillett (1906), with the new species *bisulcatus* Coquillett as the type and only included species. Howard et al. (1915) synonymized *Micraedes* with *Culex* where it remained until Dyar (1918a) elevated it to subgeneric rank. Dyar (1928) synonymized *bisulcatus* with *Culex* (*Melanoconion*) *americanus* (Neveu-Lemaire), thus *Micraedes* became a synonym of *Melanoconion* where it remained until Edwards (1932) restored it to subgeneric rank. Lane (1953) synonymized it with subgenus *Tinolestes* and Stone et al. (1959) placed it in subgenus *Aedinus* Bourroul (*sic*) along with *Anoedioporpa* and *Tinolestes*. Berlin (1969), following Foote (1954) and Belkin (1968), once again treated *Micraedes* as a distinct subgenus of *Culex*.

Subgenus *Microculex* – *Microculex* was proposed as a distinct genus by Theobald (1907), with *argenteoumbrosus* Theobald, 1907 (subjective synonym of *Culex imitator* Theobald) as the type and only included species. Brunetti (1914) regarded *Microculex* to be a synonym of *Culex*, but it seems the synonymy was never recognized. It has been treated as a subgenus of *Culex* since Dyar (1918a). Lane and Whitman (1951) recognized four groups (series) of species known to occur in Brazil, but no attempt has been made to develop a classification for all species of the subgenus.

Subgenus *Neoculex* – *Neoculex* was originally proposed as a distinct genus by Dyar (1905), with *territans* Walker as its type

species. It was regarded as a synonym of *Culex* by Brunetti (1914) and treated as a subgenus of *Culex* by Dyar (1918a). In his comprehensive treatment of *Culex*, Edwards (1932) included *Maillotia*, *Eumelanomyia* and *Protomelanoconion* as synonyms of *Neoculex* and divided the subgenus into three groups: Group A (*Neoculex* or *apicalis*-group), Group B (*Eumelanomyia* or *albiventris*-group) and Group C (*Protomelanoconion* or *uniformis*-group). In his later work on the Afrotropical Culicinae, Edwards (1941) retained the *albiventris* and *uniformis* groups and split Group A into three groups, the *apicalis*, *pulchrithorax* and *rima* groups. King and Hoogstraal (1947) followed this scheme and recognized a sixth group, Group F, for *pedicellus* King and Hoogstraal and *crassistylus* Brug from New Guinea. As indicated by Mattingly and Marks (1955) and Belkin (1962), the groups recognized by Edwards (1932, 1941) and King and Hoogstraal (1947) give little idea of natural relationships because they are based on superficial characters that greatly overlap with characters exhibited by members of other subgenera of *Culex*. This is obvious from his treatment of *Mochthogenes* as a subgenus separated from the *Protomelanoconion* (i.e. *uniformis* group) of *Neoculex* based on the relative length of the male maxillary palpi. As pointed out by Bram (1969), these groups are so similar in the larval stage that they should be included in the same subgenus. With this as background, Sirivanakarn (1971) proposed a reclassification of *Neoculex* based principally on structural differences observed in the genitalia of males. Sirivanakarn removed *Eumelanomyia* and *Maillotia* from synonymy with *Neoculex*, established them as separate subgenera of *Culex* and synonymized *Mochthogenes* with *Eumelanomyia*. The restricted concept of *Neoculex* that resulted from these actions, including the recognition of three subordinate species groups, still stands today.

Subgenus *Nicaromyia* – *Nicaromyia* was originally proposed as a subgenus of *Culex* by González Broche and Rodríguez Rodríguez (2001), with *nicaroensis* Duret as its type and the only included species. *Culex nicaroensis* was originally described as a species of subgenus *Melanoconion*. Sallum and Forattini (1996) excluded it from *Melanoconion* and it remained without subgeneric placement until *Nicaromyia* was proposed to accommodate it.

Subgenus *Oculeomyia* – *Oculeomyia* was proposed as a distinct genus by Theobald (1907), with *sarawaki* Theobald (subjective synonym of *infula* Theobald) as the type and only included species. Brunetti (1914) considered *Oculeomyia* to be a genus of "uncertain validity". Edwards (1911) synonymized *sarawaki* with *agar* Giles, and subsequently (Edwards, 1913) with *bitaeniorhynchus* Giles, thus relegating *Oculeomyia* to synonymy with *Culex*. *Oculeomyia* remained in synonymy with *Culex*, specifically subgenus *Culex* as *bitaeniorhynchus* was classified as a member of the Bitaeniorhynchus Series/Subgroup of the Sitiens Group (Edwards, 1932, 1941; Belkin, 1962; Bram, 1967a; Sirivanakarn, 1976), until Tanaka (2004) resurrected it from synonymy and validated it as a subgenus to include *bitaeniorhynchus* and other species previously included in the Bitaeniorhynchus Subgroup.

Subgenus *Phenacomyia* – *Phenacomyia* was originally proposed as a subgenus of *Culex* by Harbach and Peyton (1992), with *corniger* Theobald as its type species. Prior to the recognition of *Phenacomyia*, *Cx. corniger* and its two related species, *Cx. lactator* Dyar and Knab and *Cx. airozai* Lane, were included in subgenus *Culex*.

Subgenus *Phytotelmatomyia* – *Phytotelmatomyia* was originally proposed as a subgenus of *Culex* by Rossi and Harbach (2008), with *renatoi* Lane and Ramalho as its type species. Prior to the recognition of *Phytotelmatomyia*, *Cx. renatoi* and its related species were included in subgenus *Culex*.

Subgenus *Sirivanakarnius* – *Sirivanakarnius* was originally proposed as a subgenus of *Culex* by Tanaka (2004), with *boninensis* Bohart as its type and the only included species. *Culex boninensis* was regarded as a member of the Sitiens Group of subgenus *Culex* until Tanaka (2004) established subgenus *Sirivanakarnius* based on distinct characters of the adults and male genitalia.

Subgenus *Tinolestes* – *Tinolestes* was proposed as a distinct genus by Coquillett (1906), with the new species *latisquama* Coquillett as its type and only included species. Howard et al. (1915) synonymized *Tinolestes* with *Culex*, and Dyar (1918a) resurrected it to subgeneric rank. Dyar (1928) placed *latisquama* in subgenus *Melanoconion*, and as a consequence *Tinolestes* became a synonym of *Melanoconion*. Lane (1953) restored *Tinolestes* to subgeneric rank and synonymized subgenera *Micraedes*, *Isostomyia* and *Anoedioporpa* with it. Stone et al. (1959) included *Tinolestes*, along with *Micraedes* and *Anoedioporpa*, in subgenus *Aedinus* Bourroul (*sic*) based on the short palpus in males, but Belkin (1968) noted that this character occurs independently in several obviously unrelated groups and reinstated *Tinolestes* as a monobasic subgenus of *Culex*. Two species, *breviculus* Senevet and Abonnenc and *cauchensis* Floch and Abonnenc were transferred from subgenus *Melanoconion* to subgenus *Tinolestes* by Sirivanakarn (1983).

Subgenus uncertain – Five species of the Ocellatus Group of Sirivanakarn (1983), i.e. *flochi* Duret, *inornata* (Theobald), *nigrimacula* Lane and Whitman, *ocellatus* Theobald and *punctiscapularis* Floch and Abonnenc, were removed from subgenus *Melanoconion* by Pecor et al. (1992), and are retained in genus *Culex* without subgeneric placement.

Mattingly and Marks (1955) noted that *Pseudoskusea cairnsensis* Taylor was a species of *Culex*, probably of subgenus *Lophoceraomyia*, but its subgeneric placement must await a revision of the Australian species of that subgenus.

According to Belkin (1970), the identity of *Gnophodeomyia inornata* Theobald "may never be determined with certainty as the type series consists of females only".

4. Discussion

Considerable mosquito evolution occurred in the late Cretaceous and Tertiary (Edwards, 1932; Bertone et al., 2008; Reidenbach et al., 2009). As a result, most of the currently recognized generic-level taxa are restricted to either the Old World or the New World. In the case of *Culex*, only subgenera *Culex* and *Neoculex* occur naturally in both hemispheres (*Neoculex* is predominantly an Old World subgenus but several species occur in the Nearctic Region). The immature stages of *Culex* occupy a spectrum of aquatic environments (Belkin, 1962; Laird, 1988). They occur primarily in temporary or permanent bodies of ground water, but many species occupy rock holes, crab holes and phytotelmata. Some utilize artificial containers as well as the normal ground-water habitats. The immature stages of subgenera *Belkinomyia*, *Nicaromyia* and *Tinolestes* are found exclusively in crab holes. Species of subgenus *Culex*, as well as those of subgenera *Culiciomyia*, *Eumelanomyia*, *Kitzmilleria*, *Lophoceraomyia* and *Phenacomyia*, typically occur in ground-water habitats, but a number of the species also inhabit rock holes, crab holes, tree holes, bamboo and the leaf axils of plants. Species of subgenera *Acalleomyia*, *Acallyntrum*, *Anoedioporpa*, *Carrollia*, *Micraedes* and *Microculex* are found exclusively in phytotelmata (leaf axils, flower bracts, tree holes, bamboo internodes, pitcher plants, bromeliads and aroids, fruit shells and husks, fallen leaves and spathes). The taxa that breed exclusively in phytotelm habitats are most likely not older than their angiosperm host plants. The oldest angiosperm fossils are from the Early Cretaceous (130–136 Mya) (Friis et al., 2006); thus, lineages associated with angiosperms are no older than this. However, the oldest fossil *Culex* (five species) are from the Tertiary (Poinar et al., 2000; Poinar, 2005), with ages between 16.0 and 55.8 Mya (Harbach, 2011).

Information on the biology and medical importance of *Culex* mosquitoes can be found in numerous publications, including

Hopkins (1952), Delfinado (1966), Horsfall (1972), Laird (1988), Lee et al. (1988, 1989a,b), Clements (1992, 1999) and Rattanarithikul et al. (2005a,b) in addition to the revisionary and regional studies cited in Section 3. The majority of *Culex* larvae feed on suspended particulate matter and microorganisms that they extract from the water with filamentous mouth brushes. Some larvae resort to scavenging or cannibalism when food is scarce. The females of most species feed on humans, other mammals and birds. Some species appear to feed primarily on birds, and some are known to feed on frogs and lizards. Several species, primarily of subgenus *Culex*, are more or less closely associated with humans. The eggs of most *Culex* species are laid in rafts on the water surface, but species that inhabit axils of plants are likely to lay their eggs individually, possibly in individual gelatinous coverings like species of subgenus *Microculex*.

A number of species of genus *Culex* are of medical importance. Subgenus *Culex* contains most of the medically important and pest species of the genus. *Culex fuscocephala* Theobald, *Cx. gelidus* Theobald, *Cx. tritaeniorhynchus* Giles and *Cx. vishnui* Theobald transmit Japanese encephalitis virus in the Oriental Region and *Cx. nigripalpus* Theobald, *Cx. pipiens* Linnaeus, *Cx. restuans* Theobald and *Cx. tarsalis* Coquillett are recognized vectors of encephalitis viruses in North America. Murray Valley encephalitis and Ross River viruses in Australia are spread by *Cx. annulirostris* Skuse. Three closely related species (*Cx. neavei* Theobald, *Cx. perexiguus* Theobald and *Cx. univittatus* Theobald) transmit West Nile fever virus in Africa. Rift Valley fever virus is transmitted by *Cx. pipiens* in Egypt and *Cx. theileri* Theobald in southern Africa. A few species of the subgenus, especially *Cx. quinquefasciatus* Say, are important vectors of filariasis in the tropics, and *Cx. pipiens* and *Cx. antennatus* (Becker) are important vectors of filarial worms in Egypt. Several species of subgenus *Melanoconion* are important vectors of encephalitis viruses and other arboviruses in South and Central America.

Despite the significant amount of taxonomic work that has been done on *Culex* mosquitoes, little progress has been made toward achieving a natural classification based on phylogenetic relationships. A number of published and unpublished phylogenetic studies based on limited taxon sampling and restricted morphological and molecular data support the monophyly of all of the generic-level groups except subgenera *Culex* and *Neoculex* (Mallampalli, 1995; Miller et al., 1996; Navarro and Liria, 2000; Juthayothin, 2004; St John, 2007; Vesgueiro et al., 2011; Demari-Silva et al., 2011). However, the genealogical relationships of subgenera have not been resolved and it is not possible to construct a natural classification of the genus. The current classification is based almost entirely on external adult characters, especially features of the male genitalia. Larval and pupal characters have been largely neglected, but are likely to be of value in arriving at a natural classification (Belkin, 1962). DNA sequence data are proving indispensable for resolving the phylogenetic relationships of numerous groups of organisms, but so far sequences are publicly available for only 75 named species representing 11 subgenera of *Culex*, including 39 from subgenus *Culex* and 16 from subgenus *Melanoconion*, surprisingly few considering the medical importance of these groups (www.ncbi.nlm.nih.gov, accessed 1 June 2011).

Clearly the monophyly, phylogeny and classification of taxa included in *Culex*, and their relationships with other genera of tribe Culicini, are in need of resolution. The current taxonomy is complicated by the fact that 11 nominal generic-level names are considered to be synonyms of *Culex*, 19 are synonyms of other subgenera, i.e. *Aedinus* (1), *Carrollia* (1), *Culiciomyia* (5), *Eumelanomyia* (2), *Lophoceraomyia* (2) and *Melanoconion* (8), and 14 taxa currently regarded as subgenera of *Culex* were originally recognized as genera, including *Acalleomyia*, *Aedinus*, *Carrollia*, *Culex*, *Culiciomyia*, *Eumelanomyia*, *Lophoceraomyia*, *Maillotia*, *Melanoconion*, *Micraedes*, *Microculex*, *Neoculex*, *Oculeomyia* and *Tinolestes*.

5. Conclusions

The classification presented in Section 6 serves as the foundation for studies aimed at achieving a natural classification for genus *Culex*. A natural classification will have considerable practical value in making predictions about the genetics, ecology, control and disease relations of the species. Although the current literature and the system of classification can be used to conduct phylogenetic studies and analyse relationships between existing taxa, the results of such studies can only be regarded as preliminary. Much additional integrated systematics research is needed before the formal and informal taxa can be firmly established as monophyletic groups. However, it should be noted that specimens of many poorly known, uncommon and as yet undiscovered species will need to be obtained before comprehensive studies that will yield meaningful results can be undertaken.

There is no doubt that the application of explicit methods of phylogenetic analysis will reveal weaknesses in the current phenetic classification of genus *Culex*. The principal problem is not in recognizing monophyletic groups, but in deciding which taxonomic ranks (categories) should be assigned to such taxa once their phylogenetic relationships have been established. The ranking of natural groups based on arbitrary or subjective criteria, as in the past, is unacceptable if the classification is to be based on evolutionary relationships. In cases where a taxon is found to be paraphyletic or polyphyletic, it will be necessary to reclassify the group to ensure that taxonomic ranking reflects monophyly. On that basis, current data suggest that many of the subgenera and Species Groups of genus *Culex* may need to be raised to generic level. It is noteworthy that more than half of the subgenera of genus *Culex* were originally described as genera.

6. Classification of genus *Culex*

Numbers of species and regional distribution are provided for each generic-level taxon. As noted in Section 2, the authorities who first proposed and/or are credited with the current concept of the infrasubgeneric groups are indicated in parentheses following the informal group names.

Genus *Culex* (768 species: Cosmopolitan)
Subgenus *Acalleomyia* (monobasic: Indo-Malayan Subregion of Oriental Region)
- *obscurus* (Leicester)

Subgenus *Acallyntrum* (8 species: tropical areas of Australasian Region)
Bicki Group (Belkin, 1962)
- *bicki* Stone and Penn
- *binigrolineatus* Knight and Rozeboom
- *miyagii* Mogi and Toma

Perkinsi Group (Belkin, 1962)
- *axillicola* Steffan
- *belkini* Stone and Penn
- *bougainvillensis* Steffan
- *pallidiceps* (Theobald)
- *perkinsi* Stone and Penn

Subgenus *Aedinus* (4 species: Neotropical Region)
- *accelerans* Root
- *amazonensis* (Lutz)
- *clastrieri* Casal and Garcia
- *guyanensis* Clastrier

Subgenus *Afroculex* (monobasic: South Africa)
- *lineatus* (Theobald)

Subgenus *Allimanta* (monobasic: Argentina)
- *tramazayguesi* Duret

Subgenus *Anoedioporpa* (12 species: Neotropical Region)
Conservator Group (Berlin and Belkin, 1980)
- *bamborum* Rozeboom and Komp
- *belemensis* Duret and Damasceno
- *browni* Komp
- *canaanensis* Lane and Whitman
- *chaguanco* Casal, García and Fernández

conservator Dyar and Knab
corrigani Dyar and Knab
damascenoi Duret
luteopleurus (Theobald)
originator Gordon and Evans
quasioriginator Duret
Restrictor Group (Berlin and Belkin, 1980)
restrictor Dyar and Knab
Subgenus *Barraudius* (4 species: Palaearctic, Afrotropical Regions)
inatomii Kamimura and Wada
modestus Ficalbi
pusillus Macquart
richeti Brunhes and Venhard
Subgenus *Belkinomyia* (monobasic: Pacific coast of Colombia)
eldridgei Adames and Galindo
Subgenus *Carrollia* (18 species: Neotropical Region)
Bihaicola Group (Valencia, 1973)
bihaicola Dyar and Nuñez Tovar
guerreroi Cova García, Sutil and Pulido
infoliatus Bonne-Wepster and Bonne
metempsytus Dyar
rausseoi Cova Garcia, Sutil Oramas and Pulido F.
Iridescens Group (Valencia, 1973)
Urichii Subgroup (Valencia, 1973)
anduzei Cerqueira and Lane
urichii (Coquillett)
Iridescens Subgroup (Valencia, 1973)
antunesi Lane and Whitman
babahoyensis Levi Castillo
bonnei Dyar
cerqueirai Valencia
insigniforceps Clastrier and Claustre
iridescens (Lutz)
kompi Valencia
secundus Bonne-Wepster and Bonne
soperi Antunes and Lane
wannonii Cova Garcia and Sutil O.
wilsoni Lane and Whitman
Subgenus *Culex* (198 species: Cosmopolitan)
Atriceps Group (Belkin, 1962)
atriceps Edwards
kesseli Belkin
marquesensis Stone and Rosen
Coronator Group (Forattini, 1965, as coronator complex)
camposi Dyar
coronator Dyar and Knab
covagarciai Forattini
ousqua Dyar
usquatissimus Dyar
usquatus Dyar
yojoae Strickman
Duttoni Group (Harbach, 1988)
duttoni Theobald
Guiarti Group (Edwards, 1941)
grahamii Theobald
guiarti Blanchard
ingrami Edwards
pajoti Ramos and Ribeiro
schwetzi Edwards
verutus Harbach
weschei Edwards
Pipiens Group (Edwards, 1932, in part)
abnormalis Lane
andersoni Edwards
argenteopunctatus (Ventrillon)
astridianus de Meillon
bickleyi Forattini
bukavuensis Wolfs
calurus Edwards
carleti Brunhes and Ravaonjanahary
chorleyi Edwards
comorensis Brunhes
demeilloni Doucet
guayasi Leví-Castillo
hancocki Edwards
hopkinsi Edwards
levicastilloi Lane
mirificus Edwards
musarum Edwards
nakuruensis Mattingly
nilgiricus Edwards
ninagongoensis Edwards
ornatothoracis Theobald
perfidiosus Edwards
perfuscus Edwards
philipi Edwards
prosecutor Séguy
pruina Theobald
pseudopruina van Someren
quasiguiarti Theobald
riojanus Duret
scottii Theobald
seldeslachtsi Wolfs
shoae Hamon and Ovazza
striatipes Edwards
telesilla de Meillon and Lavoipierre
terzii Edwards
toroensis Edwards and Gibbins
trifoliatus Edwards
umbripes Edwards
vansomereni Edwards
ventrilloni Edwards
watti Edwards
zombaensis Theobald
Restuans Complex (Bram, 1967b, as *restuans-laticlasper-acharistus* complex)
acharistus Root
brethesi Dyar
laticlasper Galindo and Blanton
restuans Theobald
Salinarius Complex (Bram, 1967b)
alani Forattini
archegus Dyar
dolosus (Lynch Arribálzaga)
salinarius Coquillett
spinosus Lutz
Apicinus Subgroup (Edwards, 1932, as *salinarius-apicinus* series)
ameliae Casal
apicinus Philippi
aquarius Strickman
articularis Philippi
bonneae Dyar and Knab
brami Forattini, Rabello and Lopes
carcinoxenus de Oliveira Castro
chidesteri Dyar
curvibrachius Angulo
diplophyllum Dyar
dohenyi Hogue
delys Howard, Dyar and Knab
eduardoi Casal and García
erythrothorax Dyar
foliaceus Lane
inflictus Theobald
lahillei Bachmann and Casal
mollis Dyar and Knab
nigripalpus Theobald
plicatus Olivares
scimitar Branch and Seabrook
sphinx Howard, Dyar and Knab
tatoi Casal and García
Decens Subgroup (Harbach, 1988)
antennatus (Becker)
decens Theobald
invidiosus Theobald
litwakae Harbach
Gelidus Subgroup (Sirivanakarn, 1976)
bihamatus Edwards
gelidus Theobald
vicinus (Taylor)
Pipiens Subgroup (Sirivanakarn, 1976)
globocoxitus Dobrotworsky
huangae Meng
Pipiens Complex (Smith and Fonseca, 2004)
australicus Dobrotworsky and Drummond
pipiens Linnaeus
quinquefasciatus Say
Simpsoni Subgroup (Harbach, 1988)
simpsoni Theobald
sinaiticus Kirkpatrick
Tarsalis Subgroup (Edwards, 1932, as *tarsalis* series)

bahamensis Dyar and Knab
bidens Dyar
brevispinosus Bonne-Wepster and Bonne
chitae Duret
cuyanus Duret
declarator Dyar and Knab
duplicator Dyar and Knab
garciai Broche
habilitator Dyar and Knab
interfor Dyar
interrogator Dyar and Knab
janitor Theobald
lygrus Root
maracayensis Evans
maxi Dyar
paramaxi Duret
pinarocampa Dyar and Knab
pseudostigmatosoma Strickman
saltanensis Dyar
secutor Theobald
stenolepis Dyar and Knab
stigmatosoma Dyar
surinamensis Dyar
tarsalis Coquillett
thriambus Dyar

Theileri Subgroup (Sirivanakarn, 1976)
laticinctus Edwards
mattinglyi Knight
tenagius van Someren
theileri Theobald

Trifilatus Subgroup (Mattingly and Rageau, 1958)
asteliae Belkin
banksensis Maffi and Tenorio
guizhouensis Chen and Zhao
hutchinsoni Barraud
iyengari Mattingly and Rageau
miraculosus Bonne-Wepster
pacificus Edwards
pervigilans von Bergroth
rotoruae Belkin
tamsi Edwards
torrentium Martini
trifilatus Edwards
vagans Wiedemann

Univittatus Subgroup (Sirivanakarn, 1976)
fuscocephala Theobald
neavei Theobald
perexiguus Theobald
univittatus Theobald

Sitiens Group (Edwards, 1932, in part)
castelli Hamon
crinicauda Edwards
omani Belkin
roseni Belkin
sechani Brunhes and Boussès
thalassius Theobald
toviiensis Klein, Rivière and Séchan
whittingtoni Belkin

Barraudi Subgroup (Sirivanakarn, 1976)
barraudi Edwards
edwardsi Barraud

Mimeticus Subgroup (Mimeticus Series of Edwards, 1932)
diengensis Brug
fasyi Baisas
jacksoni Edwards
mimeticus Noè
mimuloides Barraud
mimulus Edwards
murrelli Lien
orientalis Edwards
propinquus Colless
solitarius Bonne-Wepster
tianpingensis Chen
tsengi Lien

Sitiens Subgroup (Bram, 1967a; Sitiens Series of Edwards, 1932, in part)
alis Theobald
annulirostris Skuse
litoralis Bohart
palpalis Taylor
sitiens Wiedemann
whitmorei (Giles)

Vishnui Subgroup (Bram, 1967a)
alienus Colless
annulus Theobald
incognitus Baisas
perplexus Leicester
philippinensis Sirivanakarn
pseudovishnui Colless
tritaeniorhynchus Giles
vishnui Theobald
whitei Barraud

Unplaced species
annuliventris (Blanchard)
beta Séguy
brumpti Gailiard
fernandezi Casal, García and Cavalieri
gameti Bailly-Choumara
mauesensis Lane
quitensis Levi-Castillo
pseudojanthinosoma Senevet and Abonnenc
scheuberi Carpintero and Leguizamón

Subgenus *Culiciomyia* (55 species: Afrotropical, Oriental, Australasian Regions)

Dispectus Group (Bram, 1969)
cheni Kong, Wang and Lu
dispectus Bram
hainanensis Chen

Fragilis Group (Edwards, 1932) (Oriental and Australasian species)
bahri (Edwards)
barrinus Bram
ceramensis Sirivanakarn and Kurihara
fragilis Ludlow
fuscicinctus King and Hoogstraal
lampangensis Sirivanakarn
maplei Knight and Hurlbut
nailoni King and Hoogstraal
nigropunctatus Edwards
pallidothorax Theobald
papuensis (Taylor)
pullus Theobald
ramakrishnii Wattal and Kalra
ramalingami Sirivanakarn
ryukyensis Bohart
scanloni Bram
spathifurca (Edwards)
spiculothorax Bram
termi Thurman
thurmanorum Bram
viridiventer Giles
yaoi Tung

Nebulosus Group (Edwards, 1932) (Afrotropical species)
cambournaci Hamon and Candara
cinerellus Edwards
cinereus Theobald
eouzani Geoffroy
furlongi van Someren
gilliesi Hamon and van Someren
grenieri Eouzan
harleyi Peters
liberiensis Peters
macfiei Edwards
milloti Doucet
mongiro van Someren
muspratti Hamon and Lambrecht
nebulosus Theobald
pandani Brunhes
ruthae Peters
semibrunneus Edwards
subaequalis Edwards

Shebbearei Group (unnamed "group or complex" of Sirivanakarn, 1977b)
bailyi Barraud
harrisoni Sirivanakarn
javanensis Bonne-Wepster
kyotoensis Yamaguti and LaCasse
megaonychus Yang, Li and Chen
rajah Tsukamoto
sasai Kano, Nitahara and Awaya
shebbearei Barraud
spiculostylus Chen

Tricuspis Group (Harrison, 1987)

azurini Toma, Miyagi and Cabrera
delfinadoae Sirivanakarn
tricuspis Edwards

Subgenus *Eumelanomyia* (77 species: Afrotropical, Oriental, extensions into Australasian Region)
Eumelanomyia Group (Sirivanakarn, 1971)
acrostichalis Edwards
albiventris Edwards
adersianus Edwards
garioui Bailly-Choumara and Rickenbach
kanyamwerima van Someren
kilara van Someren
tauffliebi Geoffroy and Hervé
vinckei Hamon, Holstein and Rivola
Mochthogenes Group (Sirivanakarn, 1971)
mohani Sirivanakarn
Bokorensis Subgroup (Sirivanakarn, 1972)
bokorensis Klein and Sirivanakarn
Femineus Subgroup (Sirivanakarn, 1971)
femineus Edwards
Foliatus Subgroup (Sirivanakarn, 1972)
foliatus Brug
latifoliatus Delfinado
Hinglungensis Subgroup (Sirivanakarn, 1971)
baisasi Sirivanakarn
castrensis Edwards
cataractarum Edwards
hinglungensis Chu
manusensis Sirivanakarn
Inconspicuosus Subgroup (Sirivanakarn, 1971)
castor de Meillon and Lavoipierre
fimbriforceps Edwards
germaini Geoffroy
hamoni Brunhes, Adam and Bailly-Choumara
helenae Brunhes, Adam and Bailly-Choumara
inconspicuosus (Theobald)
mijanae Brunhes, Adam and Bailly-Choumara
orstom Brunhes, Adam and Bailly-Choumara
quintetti Brunhes, Adam and Bailly-Choumara
simpliciforceps Edwards
Iphis Subgroup (Sirivanakarn, 1972)
iphis Barraud
Khazani Subgroup (Sirivanakarn, 1972)
khazani Edwards
Malayi Subgroup (Sirivanakarn, 1971)
laureli Baisas
malayi (Leicester)
yeageri Baisas
Okinawae Subgroup (Sirivanakarn, 1972)
miaolingensis Chen
okinawae Bohart
Otachati Subgroup (Sirivanakarn, 1971)
otachati Klein and Sirivanakarn
richardgarciai Jeffery, Oothuman and Rudnick
Pluvialis Subgroup (Sirivanakarn, 1972)
campilunati Carter and Wijesundara
pluvialis Barraud
selai Klein and Sirivanakarn
Tenuipalpis Subgroup (Sirivanakarn, 1972)
hackeri Edwards
hayashii Yamada
kiriensis Klein and Sirivanakarn
macrostylus Sirivanakarn and Ramalingam
megafolius Chen and Dong
oresbius Harbach and Rattanarithikul
richei Klein
tenuipalpis Barraud
Uncinatus Subgroup (Sirivanakarn, 1971)
uncinatus Delfinado
Protomelanoconion Group (Sirivanakarn, 1971)
brevipalpis (Giles)
horridus Edwards
phangngae Sirivanakarn
stellatus van Someren
Rubinotus-rima Group (Sirivanakarn, 1971)
brenquesi Brunhes and Ravaonjanahary
jefferyi Sirivanakarn
Rima Subgroup (Sirivanakarn, 1971)
adami (Hamon and Mouchet)
albertianus Edwards
amaniensis van Someren and Hamon
calabarensis Edwards
chauveti Brunhes and Rambelo
galliardi Edwards
insignis (Carter)
laplantei Hamon, Adam and Mouchet
mundulus Grünberg
rima Theobald
subrima Edwards
sunyaniensis Edwards
vattieri Geoffroy
wansoni Wolfs
wigglesworthi Edwards
Rubinotus Subgroup (Sirivanakarn, 1971)
andreanus Edwards
kingianus Edwards
malayensis Sirivanakarn
pseudoandreanus Bailly-Choumara
rubinotus Theobald
simplicicornis Edwards

Subgenus *Kitzmilleria* (monobasic: Equatorial Africa)
moucheti Evans

Subgenus *Lasiosiphon* (monobasic: northern Africa, southwestern Asia)
adairi Kirkpatrick

Subgenus *Lophoceraomyia* (126 species: Oriental and Australasian Regions)
Fraudatrix Group (Edwards, 1934, in Barraud, 1934)
cubiculi Marks
gossi Bohart
kusaiensis Bohart
orbostiensis Dobrotworsky
Fraudatrix Subgroup (Sirivanakarn, 1977a)
Alphus Complex (Sirivanakarn, 1977a)
alphus Colless
Bergi Complex (Belkin, 1962)
bergi Belkin
laffooni Belkin
oweni Belkin
winkleri Belkin
Buxtoni Complex (Belkin, 1962)
buxtoni Edwards
lairdi Belkin
Christiani Complex (Sirivanakarn, 1968)
christiani Colless
gressitti Sirivanakarn
minjensis Sirivanakarn
pseudornatus Colless
Cinctellus Complex (Sirivanakarn, 1977a)
cinctellus Edwards
fulleri (Ludlow)
Cottlei Complex (Sirivanakarn, 1968)
cottlei Sirivanakarn
Fraudatrix Complex (Sirivanakarn, 1968)
atracus Colless
collessi Sirivanakarn
fraudatrix (Theobald)
insequens Marks
insularis Sirivanakarn
kaviengensis Sirivanakarn
rajaneeae Sirivanakarn
schilfgaardei Sirivanakarn
submarginalis Sirivanakarn
Hilli Complex (Sirivanakarn, 1968)
carolinensis Bohart and Ingram
hilli Edwards
lakei Sirivanakarn
Hurlbuti Complex (Belkin, 1962)
hurlbuti Belkin
perryi Belkin
Inculus Complex (Sirivanakarn, 1977a)
inculus Colless
Marksae Complex (Sirivanakarn, 1968)
kowiroensis Sirivanakarn
leei King and Hoogstraal
marksae King and Hoogstraal
muruae Sirivanakarn
versabilis Sirivanakarn
wamanguae Sirivanakarn
Ornatus Complex (Sirivanakarn, 1968)
gagnei Evenhuis and Gon
Petersi Complex (Sirivanakarn, 1968)

- *crowei* Sirivanakarn
- *petersi* Colless
- *shanahani* Sirivanakarn
- *steffani* Sirivanakarn
- Pseudorubithoracis Complex (Sirivanakarn, 1968)
  - *castaneus* Sirivanakarn
  - *pseudorubithoracis* Sirivanakarn
  - *sedlacekae* Sirivanakarn
- Quadripalpis Complex (Sirivanakarn, 1977a)
  - *aculeatus* Colless
  - *aestivus* Sirivanakarn
  - *paraculeatus* Sirivanakarn
  - *quadripalpis* (Edwards)
  - *reidi* Colless
- Rubithoracis Complex (Sirivanakarn, 1977a)
  - *gibbulus* Delfinado
  - *niger* (Leicester)
  - *rubithoracis* (Leicester)
  - *sangenluoensis* Wang
- Seniori Complex (Sirivanakarn, 1977a)
  - *seniori* Barraud
- Solomonis Complex (Belkin, 1962)
  - *becki* Belkin
  - *durhami* Sirivanakarn
  - *solomonis* Edwards
  - *walukasi* Belkin
- Variatus Complex (Sirivanakarn, 1977a)
  - *cubitatus* Colless
  - *gracicornis* Sirivanakarn
  - *josephinae* Baisas
  - *macdonaldi* Colless
  - *pairoji* Sirivanakarn
  - *variatus* (Leicester)
  - *whartoni* Colless
- Minutissimus Subgroup (Sirivanakarn, 1977a)
  - *alorensis* Sirivanakarn
  - *cylindricus* Theobald
  - *infantulus* Edwards
  - *minutissimus* (Theobald)
- Mammilifer Group (Edwards, 1932)
  - *szemaoensis* Wang and Feng
- Bolii Subgroup (Sirivanakarn, 1968)
  - *bolii* Sirivanakarn
- Brevipalpus Subgroup (Colless, 1965)
- Brevipalpus Complex (Sirivanakarn, 1977a)
  - *acutipalus* Colless
  - *brevipalpus* (Theobald)
  - *eminentia* (Leicester)
  - *lucaris* Colless
- Curtipalpis Complex (Sirivanakarn, 1977a)
  - *curtipalpis* (Edwards)
- Hewitti Complex (Sirivanakarn, 1977a)
  - *hewitti* (Edwards)
- Jenseni Complex (Sirivanakarn, 1977a)
  - *jenseni* (de Meijere)
- Navalis Complex (Sirivanakarn, 1977a)
  - *coerulescens* Edwards
  - *navalis* Edwards
- Digoelensis Subgroup
  - *digoelensis* Brug
  - *singuawaensis* Sirivanakarn
- Mammilifer Subgroup (Colless, 1965)
  - *kuhnsi* King and Hoogstraal
- Flavicornis Complex (Sirivanakarn, 1977a)
  - *flavicornis* Barraud
  - *lasiopalpis* Sirivanakarn
  - *raghavanii* Rahman, Chowdhury and Kalra
- Singhbhumensis Complex (Natarajan and Rajavel, 2009)
  - *singhbhumensis* Natarajan and Rajavel
- Mammilifer Line (Sirivanakarn, 1977a)
- Mammilifer Complex (Sirivanakarn, 1977a)
  - *demissus* Colless
  - *mammilifer* (Leicester)
  - *wardi* Sirivanakarn
- Impostor Complex (Sirivanakarn, 1977a)
  - *impostor* Sirivanakarn
- Traubi Complex (Sirivanakarn, 1977a)
  - *lavatae* Stone and Bohart
  - *traubi* Colless
  - *uniformis* (Theobald)
- Minor Line (Sirivanakarn, 1977a)
- Ganapathi Complex (Sirivanakarn, 1977a)
  - *ganapathi* Colless
  - *spiculosus* Bram and Rattanarithikul
- Minor Complex (Sirivanakarn, 1977a)
  - *bandoengensis* Brug
  - *bengalensis* Barraud
  - *bicornutus* (Theobald)
  - *crassicomus* Colless
  - *incomptus* Bram and Rattanarithikul
  - *kuhnsi* King and Hoogstraal
  - *minor* (Leicester)
  - *tuberis* Bohart
- Peytoni Complex (Sirivanakarn, 1977a)
  - *eukrines* Bram and Rattanarithikul
  - *peytoni* Bram and Rattanarithikul
- Pholeter Complex (Sirivanakarn, 1977a)
  - *pholeter* Bram and Rattanarithikul
- Wilfredi Group (Sirivanakarn, 1977a)
  - *hirtipalpis* Sirivanakarn
  - *pilifemoralis* Wang and Feng
  - *wilfredi* Colless

Subgenus *Maillotia* (9 species: Africa, southwestern Asia)

- Hortensis Group (Sirivanakarn, 1971a)
  - *arbieeni* Salem
  - *hortensis* Ficalbi
  - *quettensis* Mattingly
- Seyrigi Group (Sirivanakarn, 1971a)
  - *avianus* de Meillon
  - *peringueyi* Edwards
  - *salisburiensis* Theobald
  - *seyrigi* Edwards
  - *subsalisburiensis* Hervé and Geoffroy

Unplaced species

- *deserticola* Kirkpatrick

Subgenus *Melanoconion* (160 species: southern Nearctic, Neotropical Regions)

Melanoconion Section (Sirivanakarn, 1983)

- *anoplicitus* Forattini and Sallum
- *guedesi* da Silva Mattos and Xavier
- *herrerai* Sutil Oramas, Pulido, F. and Amarista, M.
- Atratus Group (Sirivanakarn, 1983)
  - *atratus* Theobald
  - *caribeanus* Galindo and Blanton
  - *commevynensis* Bonne-Wepster and Bonne
  - *dunni* Dyar
  - *ensiformis* Bonne-Wepster and Bonne
  - *trigeminatus* Clastrier
  - *zeteki* Dyar
- Bastagarius Group (Sirivanakarn, 1983)
  - *diamphidius* Peyton and Harbach
- Bastagarius Subgroup (Sirivanakarn, 1983)
  - *alinkios* Sallum and Hutchings
  - *bastagarius* Dyar and Knab
  - *brachiatus* Hutchings and Sallum
  - *comatus* Senevet and Abonnenc
  - *coppenamensis* Bonne-Wepster and Bonne
  - *creole* Anduze
  - *intonsus* Galindo and Blanton
  - *phyllados* Hutchings and Sallum
  - *tournieri* Senevet and Abonnenc
- Iolambdis Subgroup (Sirivanakarn, 1983)
  - *bifoliolatus* Duret and Barreto
  - *confundior* Komp and Rozeboom
  - *corentynensis* Dyar
  - *dolichophyllus* Clastrier
  - *dureti* Casal and Garcia
  - *iolambdis* Dyar
  - *limacifer* Komp
  - *quasihibridus* Galindo and Blanton
- Distinguendus Group (Sirivanakarn, 1983)
- Distinguendus Subgroup (Sirivanakarn, 1983)
  - *alcocki* Bonne-Wepster and Bonne
  - *comminutor* Dyar
  - *distinguendus* Dyar
  - *maxinocca* Dyar
  - *niccerienis* Bonne-Wepster and Bonne
  - *patientiae* Floch and Fauran
  - *productus* Senevet and Abonnenc
- Galindoi Subgroup (Sirivanakarn, 1983)

- *galindoi* Komp and Rozeboom
- Putumayensis Subgroup (Sirivanakarn, 1983)
  - *bahiensis* Duret
  - *phlabistus* Dyar
  - *putumayensis* Matheson
- Rorotaensis Subgroup (Sirivanakarn, 1983)
  - *rorotaensis* Floch and Abonnenc
- Conspirator Group (Sirivanakarn, 1983)
  - *aliciae* Duret
  - *conspirator* Dyar and Knab
  - *dyius* Root
  - *elevator* Dyar and Knab
  - *jocasta* Komp and Rozeboom
  - *lucifugus* Komp
  - *madininensis* Senevet
  - *martinezi* Casal and García
  - *olimpioi* Xavier, da Silva and da Silva Mattos
  - *terebor* Dyar
- Educator Group (Sirivanakarn, 1983)
  - *cristovaoi* Duret
  - *educator* Dyar and Knab
  - *eknomios* Forattini and Sallum
  - *inadmirabilis* Dyar
  - *rachoui* Duret
  - *theobaldi* (Lutz)
  - *vaxus* Dyar
- Erraticus Group (Sirivanakarn, 1983)
  - Clarki Subgroup (Sirivanakarn, 1983)
    - *clarki* Evans
  - Erraticus Subgroup (Sirivanakarn, 1983)
    - *aureonotatus* Duret and Barreto
    - *erraticus* (Dyar and Knab)
    - *invocator* Pazos
  - Psatharus Subgroup (Sirivanakarn, 1983)
    - *psatharus* Dyar
- Evansae Group (Sirivanakarn, 1983)
  - *batesi* Rozeboom and Komp
  - *changuinolae* Galindo and Blanton
  - *evansae* Root
  - *johnnyi* Duret
- Inhibitator Group (Sirivanakarn, 1983)
  - *spathulatus* Forattini and Sallum
  - Egcymon Subgroup (Sirivanakarn, 1983)
    - *caudatus* Clastrier
    - *egcymon* Dyar
    - *elephas* Komp
    - *isabelae* Duret
    - *serratimarge* Root
  - Inhibitator Subgroup (Sirivanakarn, 1983)
    - *abonnenci* Clastrier
    - *albinensis* Bonne-Wepster and Bonne
    - *amitis* Komp
    - *bejaranoi* Duret
    - *carcinophilus* Dyar and Knab
    - *contei* Duret
    - *ernanii* Duret
    - *ernsti* Anduze
    - *flabellifer* Komp
    - *inhibitator* Dyar and Knab
    - *kummi* Komp and Rozeboom
    - *mesodenticulatus* Galindo and Mendez
    - *oedipus* Root
    - *orfilai* Duret
    - *pavlovskyi* Casal and García
    - *phlogistus* Dyar
    - *plectoporpe* Root
    - *rabelloi* Forattini and Sallum
    - *symbletos* Sallum and Hutchings
    - *vidali* Floch and Fauran
    - *wepsterae* Komp and Rozeboom
  - Mulrennani Subgroup (Sirivanakarn, 1983)
    - *mulrennani* Basham
- Intrincatus Group (Sirivanakarn, 1983)
  - Andricus Subgroup (Sirivanakarn, 1983)
    - *andricus* Root
  - Eastor Subgroup (Sirivanakarn, 1983)
    - *eastor* Dyar
  - Idottus Subgroup (Sirivanakarn, 1983)
    - *fairchildi* Galindo and Blanton
    - *ferreri* Duret
    - *idottus* Dyar
    - *ronderosi* de Linero
    - *sardinerae* Fox
  - Intrincatus Subgroup (Sirivanakarn, 1983)
    - *bequaerti* Dyar and Shannon
    - *equinoxialis* Floch and Abonnenc
    - *glyptosalpinx* Harbach, Peyton and Harrison
    - *intrincatus* Brèthes
    - *johnsoni* Galindo and Mendez
    - *milwardi* Xavier and da Silva Mattos
    - *misionensis* Duret
    - *mutator* Dyar and Knab
    - *pifanoi* Anduze
    - *quadrifoliatus* Komp
    - *rabanicola* Floch and Abonnenc
    - *silvai* Duret
    - *sursumptor* Dyar
    - *trilobulatus* Duret and Barreto
    - *trisetosus* Fauran
    - *ybarmis* Dyar
  - Penai Subgroup (Sirivanakarn, 1983)
    - *penai* Sirivanakarn
  - Tecmarsis Subgroup (Sirivanakarn, 1983)
    - *tecmarsis* Dyar
- Peccator Group (Sirivanakarn, 1983)
  - *abominator* Dyar and Knab
  - *anips* Dyar
  - *peccator* Dyar and Knab
- Pilosus Group (Sirivanakarn, 1983)
  - Caudelli Subgroup (Sirivanakarn, 1983)
    - *alogistus* Dyar
    - *arboricola* Galindo and Mendez
    - *caudelli* (Dyar and Knab)
    - *foliafer* Komp and Rozeboom
    - *galvaoi* Duret
    - *garcesi* Duret
    - *lacertosus* Komp and Rozeboom
    - *palaciosi* Duret
    - *vexillifer* Komp
  - Pilosus Subgroup (Sirivanakarn, 1983)
    - *innovator* Evans
    - *pilosus* (Dyar and Knab)
    - *rooti* Rozeboom
    - *unicornis* Root
- Saramaccensis Group (Sirivanakarn, 1983)
  - *saramaccensis* Bonne-Wepster and Bonne
- Trifidus Group (Sirivanakarn, 1983)
  - *trifidus* Dyar

Spissipes Section (Sirivanakarn, 1983)

- Crybda Group (Sallum and Forattini, 1996)
  - Paracrybda Subgroup (Sirivanakarn, 1983)
    - *delpontei* Duret
    - *paracrybda* Komp
  - Pedroi Subgroup (Sirivanakarn, 1983)
    - *adamesi* Sirivanakarn and Galindo
    - *crybda* Dyar
    - *epanastasis* Dyar
    - *pedroi* Sirivanakarn and Belkin
    - *ribeirensis* Forattini and Sallum
  - Pereyrai Subgroup (Sirivanakarn, 1983)
    - *pereyrai* Duret
- Faurani Group (Sirivanakarn, 1983)
  - *faurani* Duret
- Jubifer Group (Sirivanakarn, 1983)
  - *jubifer* Komp and Brown
  - *simulator* Dyar and Knab
- Lopesi Group (Sirivanakarn, 1983)
  - *lopesi* Sirivanakarn and Jakob
- Ocossa Group (Sirivanakarn, 1983)
  - *ocossa* Dyar and Knab
  - *panocossa* Dyar
- Spissipes Group (Sirivanakarn, 1983)
  - *spissipes* (Theobald)
- Taeniopus Group (Sallum and Forattini, 1996)
  - *akritos* Forattini and Sallum
  - *cedecei* Stone and Hair
  - *ikelos* Forattini and Sallum
  - *taeniopus* Dyar and Knab
- Vomerifer Group (Sallum and Forattini, 1996)
  - *gnomatos* Sallum, Hutchings, Leila and Ferreira

portesi Senevet and Abonnenc
sacchettae Sirivanakarn and Jakob
vomerifer Komp
Subgenus *Micraedes* (8 species: American Mediterranean Region)
Bisulcatus Group (Berlin, 1969)
antillummagnorum Dyar
arawak Berlin
biscaynensis Zavortink and O'Meara
bisulcatus (Coquillett)
Schicki Group (Berlin, 1969)
jalisco Berlin
schicki Berlin
sandrae Berlin
Erethyzonfer Group (Berlin, 1969)
erethyzonfer Galindo and Blanton
Subgenus *Microculex* (33 species: Neotropical Region)
Consolator Series (Lane and Whitman, 1951)
consolator Dyar and Knab
hedys Root
reducens Lane and Whitman
worontzowi Pessoa and Galvão
Imitator Series (Lane and Whitman, 1951)
carioca Lane and Whitman
dubitans Lane and Whitman
imitator Theobald
Inimitabilis Series (Lane and Whitman, 1951)
aphylactus Root
inimitabilis Dyar and Knab
microphyllus Root
neglectus Lutz
Pleuristriatus Series (Lane and Whitman, 1951)
albipes Lutz
aureus Lane and Whitman
azymus Dyar and Knab
davisi Kumm
gairus Root
intermedius Lane and Whitman
lanei de Oliveira Coutinho and Forattini
pleuristriatus Theobald
xenophobus Ronderos
Unplaced species
chryselatus Dyar and Knab
daumastocampa Dyar and Knab
elongatus Rozeboom and Komp
gaudeator Dyar and Knab
jenningsi Dyar and Knab
kukenan Anduze
pulidoi Cova García and Sutil Oramas
reginae Floch and Fauran
rejector Dyar and Knab
shopei Forattini and Toda
siphanulatus Lourenço-de-Oliveira and da Silva
stonei Lane and Whitman
sutili Cova García and Pulido F.
Subgenus *Neoculex* (26 species: Old World, Nearctic Region;)
Crassistylus Group (Sirivanakarn, 1971)
crassistylus Brug
leonardi Belkin
pedicellus King and Hoogstraal
Pseudomelanoconia Group (Sirivanakarn, 1971)
chaetoventralis (Theobald)
cheesmanae Mattingly and Marks
douglasi Dobrotworsky
dumbletoni Belkin
fergusoni (Taylor)
gaufini Belkin
latus Dobrotworsky
millironi Belkin
postspiraculosus Lee
pseudomelanoconia Theobald
Territans Group (Sirivanakarn, 1971)
apicalis Adams
arizonensis Bohart
boharti Brookman and Reeves
derivator Dyar and Knab
europaeus da Cunha Ramos, Ribeiro and Harrison
impudicus Ficalbi
judaicus Edwards
martinii Medschid
reevesi Wirth
rubensis Sasa and Takahashi
territans Walker
Unplaced species
gamma Séguy
johni Cova García, Pulido F. and Escalante de Ugueto
Subgenus *Nicaromyia* (monobasic: Cuba)
nicaroensis Duret
Subgenus *Oculeomyia* (19 species: Afrotropical, Australasian, Oriental, eastern Palaearctic Regions)
Bitaeniorhynchus Complex (Sirivanakarn, 1976)
bitaeniorhynchus Giles
infula Theobald
longicornis Sirivanakarn
luzonensis Sirivanakarn
pseudosinensis Colless
selangorensis Sirivanakarn
Geminus Complex (Sirivanakarn, 1976)
geminus Colless
kinabaluensis Sirivanakarn
Sinensis Complex (Sirivanakarn, 1976)
cornutus Edwards
epidesmus (Theobald)
sinensis Theobald
Unplaced species
albinervis Edwards
annulioris Theobald
aurantapex Edwards
giganteus Ventrillon
poicilipes (Theobald)
samoaensis (Theobald)
squamosus (Taylor)
starckeae Stone and Knight
Subgenus *Phenacomyia* (3 species: Neotropical Region)
airozai Lane
corniger Theobald
lactator Dyar and Knab
Subgenus *Phytotelmatomyia* (4 species: Neotropical Region)
castroi Casal and Garcia
hepperi Casal and García
machadoi Mattos, Guedes and Xanier
renatoi Lane and Ramalho
Subgenus *Sirivanakarnius* (monobasic: Bonin Islands)
boninensis Bohart
Subgenus *Tinolestes* (3 species: Central America, Florida)
breviculus Senevet and Abonnenc
cauchensis Floch and Abonnenc
latisquama (Coquillett)
Subgenus uncertain
cairnsensis (Taylor)
flochi Duret
inornata (Theobald)
nigrimacula Lane and Whitman
ocellatus Theobald
punctiscapularis Floch and Abonnenc
romeroi Surcouf and Gonzalez-Rincones

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