The Phylogeny and Classification of Anopheles

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http://dx.doi.org/10.5772/54695

1. Introduction

Anopheles was introduced as a genus of mosquitoes in 1818 by Johann Wilhelm Meigen [1], a German entomologist famous for his revolutionary studies of Diptera. Little was done on the taxonomy of Anopheles until the discovery during the last two decades of the 19th century that mosquitoes transmit microfilariae and malarial protozoa, which initiated a drive to collect, name and classify these insects. In 1898, the Royal Society and the Rt. Hon. Joseph Chamberlain, Secretary of State for the Colonies of Britain, appointed a Committee to supervise the investigation of malaria. On 6 December 1898, Mr. Chamberlain directed the Colonies to collect and send mosquitoes to the British Museum (Natural History) (Figure 1), and in 1899 the Committee appointed Frederick V. Theobald to prepare a monograph on the mosquitoes of the world, which was published in five volumes between 1901 and 1910 [2-6]. As a consequence, many new generic names were introduced in an effort to classify numerous new mosquito species into seemingly natural groups. Theobald proposed 18 genera for species of Anopheles based on the distribution and shape of scales on the thorax and abdomen. Four of these proposed genera, Cellia, Kerteszia, Nyssorhynchus and Stethomyia, are currently recognized as subgenera of Anopheles and the other 14 are regarded as synonyms of one or other of subgenera Anopheles, Cellia or Nyssorhynchus. Theobald, however, was not the only person to propose generic names for species of Anopheles. During the first three decades of the 20th century, 37 genera (including the 18 recognized by Theobald) were established for species of Anopheles [7].

As additional new species were discovered, it became increasingly apparent that Theobald's system of classification was neither practical nor natural. Frederick Knab in North America, one of the early critics of Theobald's classification, stated that "the subject was made needlessly difficult by hasty work and by the sub-division of the old genus *Anopheles* into numerous ill-defined and fancifully differentiated genera. The intricacies of this 'system,' unwarranted from both a scientific and practical standpoint, even the trained entomologist could not tread with



safety, and to others it could be no less than hopeless or disastrous" [8]. Consequently, during the two decades following the completion of Theobald's monograph in 1910, significant changes were made toward a much more conservative system of classification, culminating in the reduction of 38 genus-group names (including Anopheles) to the recognition of the single genus Anopheles.

The current subgeneric classification of Anopheles is based primarily on the number and positions of specialized setae on the gonocoxites of the male genitalia (Figure 2), and this basis of classification has been accepted since it was introduced by Sir (Samuel) Rickard Christophers in 1915 [9]. Christophers proposed three generic subdivisions, which F.M. Edwards [10] and Francis Metcalf Root [11] formally recognized as subgenera Anopheles, Myzomyia (=Cellia) and Nyssorhynchus. Edwards adopted this system and added subgenus Stethomyia in his classical treatise on family Culicidae published in 1932 [12]. This system recognized Kerteszia as an informal group within subgenus Nyssorhynchus. Kerteszia was elevated to subgeneric status by W.H.W. Komp [13]. Subgenus Lophopodomyia was proposed by P.C.A. Antunes in 1937 [14] and subgenus Baimaia was introduced by Ralph E. Harbach and his colleagues in 2005 [15].

Genus Anopheles currently includes 465 formally named species that are disproportionately divided between seven subgenera: Anopheles (cosmopolitan, 182 species), Baimaia (Oriental, one species), Cellia (Old World, 220 species), Kerteszia (Neotropical, 12 species), Lophopodomyia (Neotropical, six species), Nyssorhynchus (Neotropical, 39 species) and Stethomyia (Neotropical, five species) [16]. Four of the subgenera, Anopheles, Cellia, Kerteszia and Nyssorhynchus, include the species that transmit human malarial parasites. Most vector species of Anopheles have been found to comprise complexes of sibling species.

2. Classification of genus *Anopheles*

The aim of classification is to group and categorize biological entities that share some unifying characteristics. Classification has been defined by Ernst Mayr & W.J. Bock [17] as "The arrangement of similar entities (objects) in a hierarchical series of nested classes, in which each more inclusive higher-level class is subdivided comprehensively into less inclusive classes at the next lower level." These classes (groups) are known as taxa (singular: taxon). The level of a taxon in a hierarchical classification is referred to as a taxonomic rank or category. Ideally, taxonomic categories should denote equivalent phylogenetic rank; however, in practice they are basically subjective groupings of subordinate taxa that are presumed to represent monophyletic groups of species that are assigned to taxonomic ranks based on shared morphological and biological characteristics that are not a measure of phylogenetic equivalence. For this reason, the taxonomic categories of genus Anopheles, including the formal rank of subgenus, should not be considered to represent equivalent phylogenetic ranks.

CIRCULAR.

Downing Street,

6th December, 1898.

Sir.

In my Circular despatch of the 19th of August, last, I referred to an intended investigation of Malaria.

A Commission has now been appointed for the purpose and is about to proceed to Africa.

The Commissioners will report, from time to time, to a Committee appointed jointly by the Royal Society and myself, who will exercise a general supervision over the enquiry.

It has been suggested by this Committee, that, in view of the possible connection of Malaria with mosquitoes, it is desirable to obtain exact knowledge of the different species of mosquitoes and allied insects in the various tropical Colonies. I will therefore ask you, if there are facilities for the purpose, to be good enough to take the necessary steps at your early convenience to have collections made of the winged insects in the Colony which bite men or animals.

I enclose a printed copy of directions which have been drawn up by the British Museum for the guidance of those who may be employed on the work, and would add that several specimens of each kind of insect should be obtained and that they should be sent direct to the British Museum (Natural History), Cromwell Road, London, S.W., to be examined and classified. A first series of the specimens will be retained by the Museum, whilst the duplicates will be available for distribution as may be desired.

As the question of the scientific investigation of Malaria is one to which I attach great importance, I trust that every effort will be made to carry out as speedily and as thoroughly as possible the directions contained in this despatch.

I have the honour to be,

Sir.

Your most obedient, humble Servant.

J. CHAMBERLAIN.

The Officer Administering

the Government of

Figure 1. Letter issued from Downing Street on 6 December 1898 directing the British Colonies to collect and send mosquitoes to the British Museum (Natural History).

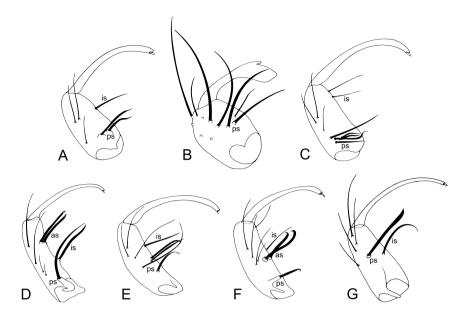


Figure 2. Subgenera of *Anopheles* – specialized setae on the gonocoxites of the male genitalia (after Harbach & Kitching [18]): A, *Anopheles*; B. *Baimaia*; C, *Cellia*; D, *Kerteszia*; E, *Lophopodomyia*; F, *Nyssorhynchus*; G, *Stethomyia*. as, accessory setae; is, inner seta; ps, parabasal seta(e).

Infrasubgeneric categories (taxonomic ranks below subgenus) have no formal status under the *International Code of Zoological Nomenclature* [19]. They are convenience categories only, often based on superficial similarities that may not indicate natural relationships. The informal categories used in the classification of *Anopheles* include Sections, Series, Groups, Subgroups and Complexes (see Appendix 1).

Unlike formal taxonomic categories, which precede the name of the taxonomic unit, for instance family Culicidae, genus *Anopheles* and species *gambiae*, the names of informal taxonomic categories follow the name of the taxonomic unit, for example the Pyretophorus Series, Hyrcanus Group or Gambiae Complex, which are written in Roman (i.e. non-italic) script with the first letter capitalized. It should be stressed that both formal and informal taxonomic entities are conceptual constructs invented by taxonomists for the purpose of creating some order in the diversity of species. For example, the species *gambiae* and the Hyrcanus Group, which are human-conceived taxonomic concepts, cannot be observed as entities or visualized under a microscope.

The internal classification of genus *Anopheles* (between genus and species levels) is based primarily on the schemes proposed by Edwards [12], John A. Reid & Kenneth L. Knight [20], Alexis Grjebine [21], M.T. Gillies & Botha de Meillon [22], Reid [23], Michael E. Faran [24] and Kenneth J. Linthicum [25]. These schemes were reviewed, amalgamated and updated in 1994 [26] and updated again in 2004 and 2012 [27,16 respectively]. The three largest subgenera, i.e. *Anopheles, Cellia* and *Nyssorhynchus*, are divided into hierarchical systems of informal taxo-

nomic categories (Appendix 1; examples shown in Figure 3). Subgenus Anopheles is divided into two Sections based on the shape of the pupal trumpet. The Laticorn Section was created for species with a wide funnel-shaped trumpet having the longest axis transverse to the stem, and the Angusticorn Section for species with a semi-tubular trumpet having the longest axis vertical more or less in line with the stem [20]. Subgenus Nyssorhynchus is divided into three Sections based on unique combinations of larval, pupal and adult characters [28]. Subgenus Cellia and the Sections of subgenera Anopheles and Nyssorhynchus are divided into Series, the larger Series are divided into species Groups, and some Groups are further divided into Subgroups and species Complexes. Most of the groupings at each level of classification are presumed to represent natural groups of species, thus implying phylogenetic relationships, but much additional basic taxonomic research is needed before the formal and informal taxa can be firmly established as monophyletic entities. The internal classification of the genus (subgenera and infrasubgeneric groups) is detailed in Appendix 1. An alphabetical list of all formally named, currently recognized species and their position in the classification is provided in Appendix 2. Similarly, all currently known sibling species complexes are listed in Appendix 3, and the unnamed and provisionally designated species of the complexes and their position in the classification are listed in Appendix 4.

3. Phylogeny of Anopheles

Anopheles is undoubtedly the most studied and best known genus of mosquitoes, largely because of their great impact on human health. As vectors of causative agents of malaria and filariasis, Anopheles mosquitoes have affected the lives of more humans than any other insects. As a matter of fact, Anopheles is one of few groups of eukaryote organisms that have had an impact on human evolution – the emergence of sickle cell anemia as a mode of resistance to malarial protozoa. As a result of more than a century of studies by medical entomologists, taxonomists and geneticists, 537 species of Anopheles are currently known and most have been formally named (87%) (Appendix 2), but until recently little work has been done to understand the evolution and phylogenetic relationships of these mosquitoes.



Figure 3. Hierarchical classification (from specific to general) of A. Anopheles freeborni, Freeborni Subgroup, Maculipennis Group, Anopheles Series, Angusticorn Section, Subgenus Anopheles; B. Anopheles minimus, Minimus Complex, Minimus Subgroup, Funestus Group, Myzomyia Series, Subgenus Cellia; C. Anopheles albimanus, Albimanus Series, Albimanus Section, Subgenus Nyssorhynchus.

The phylogenetic studies of anopheline mosquitoes conducted to date are summarized in Appendix 5. In view of the impact of malaria on human health, it is not surprising that most of these studies have dealt with species Groups, Subgroups and Complexes that include vectors of human malarial protozoa. It is obvious that the evolutionary relationships of malaria vectors and their closest allies have received more attention than other groups. However, none of these studies can be regarded as complete in terms of taxonomic coverage of any group, and the field of disease vector systematics presents many opportunities for further research. Phylogenetic patterns are used to interpret bionomic features such as differences in the nature of blood-feeding by adult females, feeding behavior and the occurrence of immature stages in aquatic habitats.

Mosquitoes probably evolved in the Jurassic [12,29,30] (146–200 Mya)¹, along with the early mammals, first birds and first flowering plants. Unfortunately, due to the paucity of mosquito fossils, there is no direct indication of the evolutionary history of anopheline mosquitoes. The second oldest fossil mosquito, *Paleoculicis minutus* [31] from the Late Cretaceous (66.0–100.5 Mya), has morphological features that indicate a closer affinity with culicine than anopheline mosquitoes, which suggests that this ancestral lineage is younger than the lineage that gave rise to subfamily Anophelinae. *Anopheles* (*Nyssorhynchus*?) *dominicanus* [32] and *An.* (?) *rottensis* [33] are the only fossil anopheline mosquitoes. The former is from the mid-Tertiary (about 15–45 Mya) and the latter is from the Late Oligocene of Germany (approximately 25 Mya). If the anopheline mosquitoes are indeed ancestral to all other Culicidae [18,34], it would appear from available fossil evidence that extant groups may have evolved in the Cenozoic Era (<66.0 Mya). From divergence times based on sequence data for nuclear protein-coding genes and fossil calibration points, it appears that major mosquito lineages date to the Early Cretaceous (100.5–145.0 Mya), and the ancestral lineage of anophelines may have appeared as early as the Jurassic (~145 Mya) [34].

Anopheles is the nominotypical genus of subfamily Anophelinae. In addition to Anopheles (cosmopolitan), the subfamily includes two other genera: Bironella (Australasian) and Chagasia (Neotropical). Cladistic analyses of morphological data and DNA sequences of various ribosomal, mitochondrial and nuclear genes strongly support the placement of Chagasia in an ancestral relationship to all other anophelines [18,34–41].

In 2000, Sallum et al. [40] performed the first phylogenetic analysis of subfamily Anophelinae, based on morphological characters. The results indicated that genus *Anopheles* is paraphyletic because it included genus *Bironella*. Subgenera *Kerteszia*, *Nyssorhynchus*, *Cellia*, *Lophopodomyia* and *Stethomyia*, along with genus *Bironella*, were found to be monophyletic taxa dispersed among various Series and species Groups of subgenus *Anopheles*. The Christya Series of subgenus *Anopheles* was placed with *Kerteszia* + *Nyssorhynchus* and this clade was sister to *Cellia* + all other anophelines except *Chagasia*.

Two years later, Sallum et al. [41] conducted a molecular analysis of anopheline relationships based on ribosomal (18S, 28S) and mitochondrial (COI, COII) DNA sequences. The results of

¹ Geological ages of eras and periods follow the geological timescale determined by the International Commission on Stratigraphy (http://www.stratigraphy.org).

that study cannot be compared directly with the results of their earlier study [40] because significantly fewer taxa were included in the analyses. Nevertheless, the molecular data corroborated the paraphyly of genus *Anopheles* relative to *Bironella* and the sister-group relationship of *Kerteszia* and *Nyssorhynchus*, and supported the monophyly of the other subgenera and genus *Bironella*, which was reconstructed as the sister to *Lophopodomyia* rather than *Stethomyia*.

In 2005, Harbach & Kitching [36] revised and expanded the phylogenetic analysis of Sallum et al. [40], with special consideration of the specialized setae of the male gonocoxites (Figure 2) that diagnose the subgenera. Parsimony analysis of the data set under implied weighting supported the monophyly of subgenera *Cellia, Kerteszia* and *Nyssorhynchus*, and the sister relationship of *Kerteszia* + *Nyssorhynchus*. Subgenus *Anopheles* was recovered as a polyphyletic lineage basal to a monophyletic clade consisting of *Kerteszia* + *Nyssorhynchus* and *Cellia* in a sister-group relationship. *Bironella, Lophopodomyia* and *Stethomyia* were firmly nested within subgenus *Anopheles*, which would be paraphyletic even if these taxa were subsumed within it. Subgenus *Baimaia*, represented by *An. kyondawensis*, was supported as the sister of *Bironella* + all other *Anopheles*. *Bironella* and *Stethomyia*, contrary to the earlier study of Sallum et al. [40], were also supported as monophyletic clades separate from subgenus *Anopheles*. The preferred cladogram of Harbach & Kitching (Figures 4 and 5) is taken here to represent the best available estimate of anopheline phylogeny and evolutionary relationships because it is based on a greater number of taxonomic groups and homologous characters than all other hypotheses published to date.

A later analysis of subgenus Anopheles by Collucci & Sallum [42] included 38 species representing the same Series (6) and species Groups (15) of the subgenus that were included in the study of Sallum et al. [40]. The data were analyzed using successive approximations character weighting (SACW) and implied weighting (IW). Most of the relationships between members of the subgenus were either moderately or poorly supported. The Laticorn Section was recovered as a monophyletic clade in the IW analysis, suggesting that the laticorn development of the pupal trumpet is a derived condition for subgenus Anopheles. In the SACW analyses, members of the group comprised a paraphyletic lineage relative to the Cycloleppteron Series. The Angusticorn Section was recovered as a polyphyletic assemblage in both analyses. These results are contradicted by those of Sallum et al. [40] and Harbach & Kitching [36] who found that neither section is monophyletic. Below the section level of classification, only the Lophoscelomyia and Arribalzagia Series were recovered as monophyletic assemblages. The Myzorhynchus Series was paraphyletic relative to the Cycloleppteron, Christya and Arribalzagia Series, and the Anopheles Series was polyphyletic. Surprisingly, the two species of the Cycloleppteron Series included in the analyses were not grouped together, suggesting that the series is not monophyletic. In contrast, the Arribalzagia, Christya, Cycloleppteron, Lophoscelomyia and Myzorhynchus Series were recovered as monophyletic assemblages in the IW analysis of Harbach & Kitching (Figure 4). Furthermore, with the removal of subgenus Baimaia, the remaining species of the Anopheles Series included in their analysis also formed a monophyletic group. With the exception of the Pseudopunctipennis Group, all the species groups represented in the analysis of Collucci & Sallum (Aitkenii, Albotaeniatus, Culiciformis,

Hyrcanus, Plumbeus, Umbrosus Groups) were recovered as monophyletic assemblages with moderate to strong support [the Pseudopunctipennis Group was also found to be polyphyletic in the study of Harbach & Kitching (Figure 4)]. The Hyrcanus Group was paired with *An. coustani*, which corroborates previous hypotheses of a close relationship between the Hyrcanus and Coustani Groups [20,36,40,43]. Unfortunately, the analyses of Collucci & Sallum are biased by the selection of outgroup taxa whose interrelationships with the ingroup taxa were unresolved in previous studies. Thus, the results of their study cast doubt on their assertion that subgenus *Anopheles* is monophyletic. Based on the relationships recovered by Harbach & Kitching, subgenus *Anopheles* would be monophyletic if subgenus *Lophopodomyia* were to be reduced to the status of a species Group of the Anopheles Series (Figure 4). The Anopheles Series is a morphologically diverse assemblage of species and informal taxonomic groups, a number of which at one time or another were deemed to merit recognition as subgenera [20]. Sallum et al. [40] also found the Anopheles Series to be polyphyletic, but with its members interspersed in a complexity of inter-group relationships rather than arrayed in a pectinate sequence (Figure 4).

All phylogenetic studies conducted to date have demonstrated the monophyly of subgenera *Cellia* [36,38–41], *Kerteszia* [36,38–41,44] and *Nyssorhynchus* [36,38–41], and the sister pairing of *Kerteszia* and *Nyssorhynchus* [36,40,41]. The sister relationship of *Cellia* and the two New World subgenera is not inconsistent with the molecular analyses of Sallum et al. [41] if *Lophopodomyia* + *Bironella* is excluded from the clade that contains *Kerteszia* + *Nyssorhynchus*, but it differs markedly from the results of their earlier study based on morphology and a larger number of taxa [40], which placed *Kerteszia* + *Nyssorhynchus*, along with *An. implexus* (Christya Series), in a sister-group relationship with *Cellia* + a clade comprised of *Bironella*, *Lophopodomyia*, *Kerteszia* and *Nyssorhynchus*. *Anopheles implexus* (Christya Series) is sister to the terminal clade formed by *Kerteszia*, *Nyssorhynchus* and *Cellia* in Figure 4.

4. Distribution and phylogeography of Anopheles

Interpreting the current distributions of anophelines in an evolutionary context is problematic. The supercontinent of Pangaea existed in the Late Paleozoic and Early Mesozoic Eras from about 300–200 Mya and gradually separated 200–145 Mya into the two supercontinents of Laurasia and Gondwana [45]. As noted above, evidence from DNA sequence data and fossil calibration points [34] indicates that ancestral anophelines diverged from ancestral culicines about 217 Mya (230–192 Mya), before the complete splitting of Pangaea. If this was the case, then the separation of *Anopheles* and *Bironella* about 54 Mya (75.8–37.1 Mya, end of the Cretaceous to near the end of the Eocene Epoch of the Cenozoic) [34] must have occurred after the separation of Gondwana into multiple continents, i.e. Africa, South America, India, Antarctica and Australia, in the Cretaceous. Atlantica (the land mass that comprised present-day South America and Africa) separated from eastern Gondwana (the land mass that comprised Antarctica, India and Australia) 150–140 Mya. South America started to separate from Africa in a south-to-north direction during the Middle Cretaceous (about 125–115 Mya) [46]. At the same time, Madagascar and India began to separate from Antarctica, and separated

from each other 100–90 Mya during the Cenomanian and Turonian Stages of the Late Cretaceous. India continued to move northward and collided with Eurasia about 35 Mya. Laurasia split to give rise to North America/Greenland and Eurasia about 60–55 Mya. Africa began to move northeastward toward Europe and South America moved northward to separate from Antarctica. North and South America were joined by the Isthmus of Panama during the Pliocene, approximately 3.7–3.0 Mya.

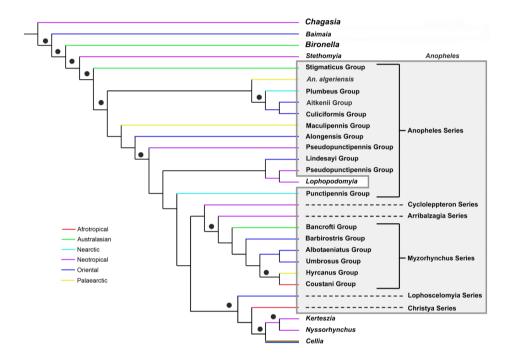


Figure 4. Phylogeny of subfamily Anophelinae, modified from Harbach & Kitching [36], indicating relationships within subgenus *Anopheles*. Filled circles indicate Bremer support values greater than 0.8.

Belkin [47] hypothesized that anophelines initially differentiated in the American Mediterranean Region. In concert with this postulate, Harbach & Kitching [36] suggested a possible New World origin of subfamily Anophelinae based on the basal placement of *Chagasia* relative to *Anopheles + Bironella* in their phylogeny of mosquito genera. Based on a phylogeny of 16 anopheline species inferred from sequences of two protein-coding nuclear genes and the Neotropical distribution of *Chagasia* and four of the seven subgenera of *Anopheles*, Krzywinski et al. [39] agreed with the hypothesis that South America was the center of origin of Anophelinae. However, as will be seen below, more recent studies suggest a different scenario for the evolution of the extant groups of the subfamily. This scenario closely reflects Christophers [48] insightful observations:

Subgenus *Anopheles* appears to be the oldest of the predominant subgenera, not only on [morphological grounds], but by reason of its worldwide distribution and the greater diversity and distinctness of its forms; almost every species of the subgenus appears to be as distinctive as are the species groups of subgenus *Myzomyia* [=Cellia], if not more so.

Nyssorhynchus appears to be a Neotropical development from some pre-Anopheles form, whilst the group Arribalzagia appears to be a highly specialized development of subgenus Anopheles.

Myzomyia shows every evidence of being a new and actively disseminating branch, as is suggested by its complete absence from the New World. Had it been once disseminated throughout North America it is unlikely that it would have been eliminated from the whole continent so completely as to leave not a single species in this area, though there is no actual proof that this did not occur. The apparent affinity between the group Neomyzomyia and subgenus Nyssorhynchus suggests an intermediate ancestor, though not necessarily one in the south, i. e., such affinity does not prove or suggest a land-connection between Australia and South America, as the common ancestor may have been derived from the north and later eliminated. [next paragraph omitted]

The date of isolation of South America, judging by the history of mammals, would be from the middle of the Eocene, when connections between North and South America were severed, until the end of the Pliocene (*Zittel*). The anopheline fauna, therefore, arose from elements which pre-dated this period, and there were already subgenus *Anopheles*-like forms, as well as some earlier type from which *Nyssorhynchus* arose.

At some unknown period a similar special development took place, resulting in an early form (*Neomyzomyia*) of subgenus *Myzomyia*. This form appears to have once been distributed throughout the Oriental, Ethiopian [i.e. Afrotropical], and Australian Regions, and to have later undergone some regression, eventually remaining in greatest strength in the Australian Region.

Edwards, in reviewing the fossil remains of mosquitoes, notes that probably all the main divisions of the family [Culicidae] existed in Mid-Tertiary much as they do today, and with almost identical characters, and considers that, though no fossil *Anopheles* have been found, there can be no doubt from its morphology that this is also an old genus, probably older than any culicine form.

Based on the relationships shown in Figure 4, distributions of the principal group taxa (Appendix 6) and the geological dates listed above, it would appear that the ancestral lineage of Anopheles existed before the breakup of Pangaea and subsequently diversified into the modern subgenera and species after the separation of the continents. This would explain the cosmopolitan distribution and greater diversity of subgenus Anopheles, but not the earlier divergence of genus Chagasia and subgenus Stethomyia, which are confined to the Neotropical Region, the Oriental subgenus Baimaia and the Australasian genus Bironella (Figure 4). Chagasia possess several features that characterize species of subfamily Culicinae, including the strongly arched mesonotum, trilobed scutellum (Figure 6) and setae on the postpronotum. Based on these shared features, Chagasia has been considered an ancient group showing affinities with non-anophelines and phylogenetic analyses of morphological data and DNA sequences of various ribosomal, mitochondrial and nuclear genes strongly support its placement in an ancestral relationship to all other anophelines [33,35-41]. From the foregoing, however, it is inferred here that Chagasia, with only seven species, is a relic of a once more widely distributed taxon that is now confined to residual areas of South and Central America. It is also possible, although less likely, that Chagasia, as suggested by the late John N. Belkin for other mosquitoes [47], may have originated through hybridization between early anopheline and culicine forms.

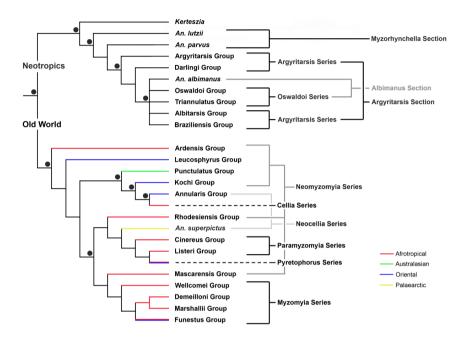


Figure 5. Phylogeny of subgenera *Cellia, Kerteszia* and *Nyssorhynchus*, modified from Harbach & Kitching [36], indicating relationships within subgenera *Cellia* and *Nyssorhynchus*. Filled circles indicate Bremer support values greater than 0.8.

Similarly, *Bironella* (as suggested by Christophers [48]), *Baimaia* and *Stethomyia*, with few species and restricted distributions, are also the remnants of once much more widely distributed forms. The isolation of ancestral members of subgenus *Anopheles* in South America also explains the uniqueness of the extant Neotropical fauna of the subgenus, especially the well-differentiated Arribalzagia Series. In accordance with this hypothesis, the following groups are also probably residual elements of once more widely distributed ancestral forms of subgenus *Anopheles*: the Afrotropical Christya Series (two species), the Australasian Atratipes (two species) and Stigmaticus (six species) Groups, the Oriental Alongensis (two species) and Culiciformis (three species) Groups, the Oriental Lophoscelomyia Series (five species) and the Neotropical Cycloleppteron Series (two species). It is noteworthy that the extant members of the relict groups are not vectors of human malarial parasites.

As noted previously, subgenus *Anopheles* has an almost world-wide distribution. Species are found at elevations from coastal areas to mountainous terrain in temperate, subtropical and tropical areas, but are absent from the majority of the Pacific Islands, including the large ones of New Zealand, Fiji and New Caledonia. The sole species of subgenus *Baimaia* has been found only in forested hilly and mountainous areas between 14° and 17° north on either side of the

Thai-Myanmar border and at a location near the Thai-Laos border in Thailand, and is probably also a relict taxon that has retained generalized ancestral features of the male genitalia [36]. Most species of subgenus Cellia have distributions in the Afrotropical, Australasian and Oriental Regions, but some species occur in southern areas of the Palaearctic. Species of Cellia are conspicuously absent from the majority of the islands of the Pacific, including New Zealand, Fiji and New Caledonia. Species of subgenus Kerteszia are found in the Neotropical Region, from Veracruz State in Mexico through Central America and Atlantic South America, along the Andes and along the coast, to the States of Misiones in Argentina and Rio Grande do Sul in Brazil, and also occur south along the Pacific Coast of South America to the State of El Oro, Ecuador. The subgenus is absent from all islands of the West Indies except Trinidad, and from most of the vast expanse of the Amazon basin in South America [49]. Species of subgenus Lophopodomyia are known to occur in areas of Panama and northern South America (Brazil, Colombia, Ecuador, French Guiana and Venezuela). Species of subgenus Nyssorhynchus are restricted to the Neotropical Region, except for An. albimanus, which extends into the Nearctic Region (northern Mexico and along the Rio Grande River in Texas). Finally, species of subgenus Stethomyia principally occur in southern Central America (Costa Rica and Panama) and northern South America (Brazil, Colombia, French Guiana, Guyana, Suriname and Venezuela), but one or two species are known to occur on the islands of Trinidad and Tobago and as far south as Peru and Bolivia.

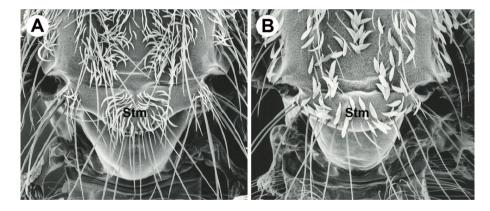


Figure 6. Two forms of the mosquito scutellum (Stm): A, trilobed scutellum of *Chagasia* and species of subfamily Culicinae; B, evenly rounded scutellum of *Anopheles*, with few exceptions. Original images from Harbach & Kitching [18].

Subgenera Kerteszia, Lophopodomyia, Nyssorhynchus and Stethomyia, and the Arribalzagia and Cycloleppteron Series of subgenus Anopheles are special to the Neotropical Region, where they probably originated following the separation of South America and Africa. The derived position of subgenera Cellia and Kerteszia + Nyssorhynchus relative to subgenus Anopheles (Figure 4) supports the hypothesis that the stem lineage of these subgenera originated in Gondwana and diverged following the separation of Atlantica to give rise to Cellia in Africa and Kerteszia and Nyssorhynchus in South America. It is interesting to note that Lophopodo-

myia and the Pseudopunctipennis Group are sister taxa in Figure 4, which is plausible in view of the hypothesized evolution of these groups from Neotropical ancestors. The Pseudopunctipennis Group is nearly restricted to the Neotropics, except for An. franciscanus and a minor extension of An. pseudopunctipennis into the Nearctic Region, which undoubtedly occurred relatively recently, after the land bridge formed to connect North and South America 3.7-3.0 Mya. Except for these two species, all Anopheles species in the Nearctic Region are members of the Anopheles Series of subgenus Anopheles. Half of the species of the Holarctic Maculipennis Group (24 species) occur in the Nearctic Region and the other half occur in the Palaearctic. This indicates that the Maculipennis Group must have evolved in the Northern Hemisphere prior to the separation of North America and Eurasia during the Paleocene and Eocene Epochs (60-55 Mya). The Plumbeus Group includes species in the Nearctic (2), Neotropical (4) and Palaearctic (3) Regions. Its position in the cladogram shown in Figure 4 is based on An. judithae, a Nearctic species. This group may be what paleontologists call a "stem group" [50], a paraphyletic or polyphyletic assemblage of species that share features of extinct taxa. The spotted distribution of these "living fossil" species suggests that their extinct relatives, ancestral forms of the Anopheles Series, existed before the separation of Pangaea. This bodes well with Christophers & Barraud's 1931 hypothesis [51] that the eggs of species of the Plumbeus Group are primitive compared to other species of subgenus Anopheles.

Species in subgenus Cellia are confined to the Eastern Hemisphere, with members in the Afrotropical, Australasian, Oriental and Palaearctic regions (Figure 5, Appendix 6). The Afrotropical Region is characterized by a large number of species of subgenus Cellia and relatively few species of subgenus Anopheles. The Myzomyia Series is especially dominant, but species of the Neocellia, Neomyzomyia and Pyretophorus Series also occur in the region. The Myzomyia, Neocellia and Pyretophorus Series are represented in the Afrotropical and Oriental Regions, but no species, species groups or subgroups of these series (with the exception of the Minimus Subgroup) are common to both regions (see Appendix 6). The Myzomyia Series is a dominant group in Africa, where An. funestus is a principal malaria vector [52,53]. Related species of the Funestus Group, including An. minimus and other members of the Minimus Subgroup, are major vectors of malarial parasites in southern Asia [52,54]. Evidence from phylogenetic analyses of mitochondrial DNA (ITS2 and D3 sequences) indicates that the Funestus Group originated in the Afrotropical Region [55]. The Neocellia Series also includes several important malaria vectors in southern Asia, notably An. stephensi and members of the Maculatus Group [52,54]. The Pyretophorus Series includes the formidable malaria vectors of the Gambiae Complex in Africa and important vectors of the Sundaicus and Subpictus Complexes in Southeast Asia [53,54]. The morphology-based phylogeny of Anthony et al. [56] indicates that the Pyretophorus Series originated in Africa and suggests that the capacity to vector malarial parasites is an ancestral condition subsequently lost independently in several lineages.

The anopheline fauna of the Australasian Region also shows evidence of isolation, but not to the degree indicated by the Neotropical fauna. The isolation appears to be more recent, corresponding to the separation of Australia from Antarctica between 37.0-33.5 Mya. The region includes a preponderance of species of the Neomyzomyia Series of subgenus Cellia, which may signal a relatively recent arrival from the Oriental Region, with some diversification. Members of the Neomyzomyia Series are the only Anopheles in the South Pacific [47]. Species groups of the series are confined to the Afrotropical (Ardensis, Mascarensis, Pauliani, Ranci, Rhodesiensis and Smithii Groups), Australasian (Punctulatus Group, Lungae Complex and unassigned species) or Oriental Region (Kochi, Leucosphyrus and Tessellatus Groups) (Appendix 6). The Neomyzomyia Series has been regarded as the most primitive series of subgenus Cellia based on egg morphology and the reduced or non-existent cibarial armature of females [57-59], and is thought to have originated in Africa and subsequently disperse eastward to the Oriental and Australasian Regions [52,59]. None of the African species of the Neomyzomyia Series, except for An. nili, are major vectors of malaria. In comparison, most species of the Oriental Leucosphyrus and Australasian Punctulatus Groups of the Neomyzomyia Series are important vectors of both primate and human malarial parasites. The Cellia and Paramyzomyia Series of subgenus Cellia are restricted to the Afrotropical Region, except for An. pharoensis (Cellia Series) and An. multicolor (Paramyzomyia Series) which occur in adjacent arid areas of the Palaearctic (Sahara and Middle East). It seems reasonable to hypothesize that those series that are presently represented by groups in the Afrotropical, Australasian and Oriental Regions arose before eastern Gondwana (Antarctica, India and Australia) fragmented. The Mascarensis, Pauliani and Ranci Groups are confined to Madagascar, which supports the hypothesis that the ancestral forms of at least these groups of the Neomyzomyia Series existed before Madagascar separated from India 100–90 Mya.

Human malaria probably evolved in Africa along with its mosquito hosts and other primates. Modern humans arose in Africa about 200,000 years ago and dispersed into Eurasia [60], reaching Australia about 40,000 years ago. Migration into the New World occurred about 15–20 millennia ago, and most of the Pacific Islands were colonized by four thousand years ago. The point here is that the rise and dispersal of modern humans occurred long after the formation of the continents and the evolution of the major groups of *Anopheles*. Consequently, it seems reasonable to assume that human malarial parasites accompanied humans during their migration out of Africa and were passed on to species of *Anopheles* in other regions that had the ecological, physiological and behavioural attributes required to propagate infections and maintain transmission. These taxa were surely already adapted to feeding on primates, including the ancestors of *Homo sapiens*, and were capable of developing and transmitting the *Plasmodium* species specific to those hosts.

Comprehensive information on the dominant malaria vectors of the world, most of which are presumably recently evolved members of sibling species complexes (Appendix 3), is summarized in a series of publications (and a chapter of this book) by M. Sinka and a team of regional experts and technical advisors – the Americas [61], Africa, Europe and the Middle East [53], the Asia-Pacific Region [54] – that culminated in a thorough review of the principal malaria vector taxa of the world [62]. At present, 96 formally named species of *Anopheles* are members of 26 sibling species complexes (Appendix 4). Twenty of these nominal species actually consist of more than one species, which all together comprise a total of 67 species. Excluding the name-bearing type species, the 58 species, plus five other unnamed species that

are not members of species complexes, a total of 72 species, have yet to be given formal Latin names (Appendix 4).

5. Conclusion

A more robust phylogeny of *Anopheles* mosquitoes than is currently available may be of use in the fight against malaria. Foley et al. [37] suggested that it may help "by elucidating descent relationships of genes for refractoriness, insecticide resistance, and genetically determined ecological and behavioral traits important to malaria transmission." Interrupting the life cycle of malarial parasites by genetically manipulating vector receptiveness to infection is a potential approach to malaria control. A natural classification of Anopheles predictive of biological and ecological traits could facilitate the manipulation of vector genomes by informing the dynamics of introduced genes. Obviously, co-evolutionary studies of parasites and vectors require phylogenies for the mosquitoes. This must far exceed the taxon-limited (exemplar-based) studies conducted to date as they do not provide a basis for gaining insights into interspecific and co-evolutionary relationships of vectors and parasites.

It seems fitting to end here with a comment concerning interspecific hybridization, which was mentioned above in relation to genus Chagasia in the Neotropical Region. Although anopheline species occur in sympatry in most ecosystems, hybridization has only been detected at very low levels between certain members of species complexes in subgenus Cellia, e.g. An. gambiae with both An. arabiensis and An. bwambae in Africa [63,64], An. dirus and An. baimaii in Thailand [65] and An. minimus and An. harrisoni in Vietnam [66]. However, as advocated by Belkin [47], hybridization could provide sufficient genetic variation to permit adaptation to new habitats. Hybridization may occur regularly between some species, particularly widely distributed species that are morphologically similar. It could have played a role in the speciation and evolution of Anopheles mosquitoes and the pathogens they transmit.

Appendix 1 — The internal classification of genus *Anopheles*

Subgenus	Section	Series	Group	Subgroup	Complex	Author
Anopheles						[1]
	Angusticorn					[20]
		Anopheles				[12]
					Claviger	[67]
			Alongensis			[68]
			Aitkenii			[10]
			Atratipes			[69]
			Atratipes			

ubgenus	Section	Series	Group	Subgroup	Complex	Author
			Culiciformis			[20]
			Lindesayi			[20]
					Gigas	[70]
					Lindesayi	[70]
			Maculipennis			[20]
				Maculipennis		[71]
				Quadrimaculatus		[71]
				Freeborni		[71]
			Plumbeus			[20]
			Pseudopunctipen-			[20]
			nis			
			Punctipennis			[20]
					Crucians	[72]
			Stigmaticus			[20]
		Cycloleppteron				[12]
		Lophoscelomyia				[12]
			Asiaticus			[23]
				Asiaticus		[73]
				Interruptus		[73]
	Laticorn					[20]
		Arribalzagia				[74]
		Christya				[75]
		Myzorhynchus				[12]
			Albotaeniatus			[20]
			Bancroftii			[20]
			Barbirostris			[20]
				Barbirostris		[23]
					Barbirostris	[76]
				Vanus		[23]
			Coustani			[20]
			Hyrcanus			[77]
				Lesteri		[78]
				Nigerrimus		[78]

Subgenus	Section	Series	Group	Subgroup	Complex	Author
			Umbrosus			[79]
				Baezai		[73]
				Letifer		[23]
				Separatus		[73]
				Umbrosus		[73]
Baimaia						[15]
.ellia						[80]
		Cellia				[75]
			Squamosus			[21]
		Myzomyia				[75]
			Demeilloni			[22]
			Funestus			[81]
				Aconitus		[82]
				Culicifacies		[81]
				Funestus		[81]
				Minimus		[82]
					Fluviatilis	[83]
					Minimus	[84]
				Rivulorum		[81]
			Marshallii			[22]
					Marshallii	[85]
			Wellcomei			[22]
		Neocellia				[75]
			Annularis			[23]
					Annularis	[86]
					Nivipes	[87]
			Jamesii			[73]
			Maculatus			[88]
				Maculatus	_	[73]
				Sawadwongporni		[73]
		Neomyzomyia				[75]
					Annulipes	[89]

Subgenus	Section	Series	Group	Subgroup	Complex	Author
					Longirostris	[90]
					Lungae	[47]
			Ardensis			[22]
					Nili	[22]
			Kochi			[73]
			Leucosphyrus			[91]
				Hackeri		[92]
				Leucosphyrus		[93]
					Dirus	[94]
					Leucosphyrus	[92]
				Riparis		[93]
			Mascarensis			[26]
			Pauliani			[21]
			Punctulatus			[95]
					Farauti	[96]
			Ranci			[21]
				Ranci		[21]
				Roubaudi		[21]
			Rhodesiensis			[22]
			Smithii			[22]
			Tessellatus			[73]
		Paramyzomyia				[51]
			Cinereus			[22]
			Listeri			[22]
		Pyretophorus				[12]
					Gambiae	[97]
			Ludlowae			[73]
					Sundaicus	[98]
			Subpictus	,	,	[73]
					Subpictus	[99]
Kerteszia						[100]
					Cruzii	[101]

Subgenus	Section	Series	Group	Subgroup	Complex	Author
Lophopodomy	via					[14]
Nyssorhynchus	5					[102]
	Albimanus					[103]
		Albimanus				[24]
		Oswaldoi				[24]
			Oswaldoi			[24]
				Oswaldoi		[24]
					Nuneztovari	[104]
				Strodei		[24]
					Benarrochi	[105]
			Triannulatus		Triannulatus	[24]
	Argyritarsis					[103]
		Albitarsis				[25]
			Albitarsis			[25]
					Albitarsis	[106]
			Braziliensis			[25]
		Argyritarsis				[25]
			Argyritarsis			[25]
			Darlingi			[25]
			Lanei			[25]
			Pictipennis			[25]
	Myzorhynchella					[107]
Stethomyia						[80]

Appendix 2

Alphabetical list of formally named species of *Anopheles* and their position in the classification of the genus. For species Complexes, see Appendices 3 and 4; for authorship of species, visit http://mosquito-taxonomic-inventory.info/valid-species-list.

Species	Subgenus	Section	Series	Group	Subgroup
aberrans	Anopheles	Angusticorn	Anopheles	Aitkenii	

Species	Subgenus	Section	Series	Group	Subgroup
acaci	Anopheles	Angusticorn	Anopheles	Aitkenii	
acanthotorynus	Stethomyia				
aconitus	Cellia		Myzomyia	Funestus	Aconitus
ahomi	Anopheles	Laticorn	Myzorhynchus	Barbirostris	Vanus
ainshamsi	Cellia		Neocellia		
aitkenii	Anopheles	Angusticorn	Anopheles	Aitkenii	
albertoi	Nyssorhynchus	Albimanus	Oswaldoi	Oswaldoi	Strodei
albimanus	Nyssorhynchus	Albimanus	Albimanus		
albitarsis	Nyssorhynchus	Argyritarsis	Albitarsis	Albitarsis	
albotaeniatus	Anopheles	Laticorn	Myzorhynchus	Albotaeniatus	
algeriensis	Anopheles	Angusticorn	Anopheles		
alongensis	Anopheles	Angusticorn	Anopheles	Alongensis	
amictus	Cellia		Neomyzomyia		
anchietai	Anopheles	Laticorn	Arribalzagia		
annandalei	Anopheles	Angusticorn	Lophoscelomyia	Asiaticus	
annularis	Cellia		Neocellia	Annularis	
annulatus	Cellia		Neomyzomyia		
annulipalpis	Anopheles	Angusticorn	Cycloleppteron		
annulipes	Cellia		Neomyzomyia		
anomalophyllus	Nyssorhynchus	Albimanus	Oswaldoi	Oswaldoi	Oswaldoi
antunesi	Nyssorhynchus	Myzorhynchella			
apicimacula	Anopheles	Laticorn	Arribalzagia		
apoci	Cellia		Myzomyia		
aquasalis	Nyssorhynchus	Albimanus	Oswaldoi	Oswaldoi	Oswaldoi
arabiensis	Cellia		Pyretophorus		
arboricola	Anopheles	Angusticorn	Anopheles	Plumbeus	
ardensis	Cellia		Neomyzomyia	Ardensis	
argenteolobatus	Cellia		Cellia		
argyritarsis	Nyssorhynchus	Argyritarsis	Argyritarsis	Argyritarsis	
argyropus	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	
artemievi	Anopheles	Angusticorn	Anopheles	Maculipennis	Maculipennis

Species	Subgenus	Section	Series	Group	Subgroup
arthuri	Nyssorhynchus	Albimanus	Oswaldoi	Oswaldoi	Strodei
aruni	Cellia		Myzomyia	Funestus	Funestus
asiaticus	Anopheles	Angusticorn	Lophoscelomyia	Asiaticus	Asiaticus
atacamensis	Nyssorhynchus	Argyritarsis	Argyritarsis	Pictipennis	
atratipes	Anopheles	Angusticorn	Anopheles	Atratipes	
atroparvus	Anopheles	Angusticorn	Anopheles	Maculipennis	Maculipennis
atropos	Anopheles	Angusticorn	Anopheles	Maculipennis	
aurirostris	Cellia		Neomyzomyia		
austenii	Cellia		Myzomyia	Marshallii	
auyantepuiensis	Kerteszia				
azaniae	Cellia		Myzomyia		
azevedoi	Cellia		Paramyzomyia	Cinereus	
aztecus	Anopheles	Angusticorn	Anopheles	Maculipennis	
baezai	Anopheles	Laticorn	Myzorhynchus	Umbrosus	Baezai
baileyi	Anopheles	Angusticorn	Anopheles	Lindesayi	
baimaii	Cellia		Neomyzomyia	Leucosphyrus	Leucosphyrus
baisasi	Cellia		Neomyzomyia	Leucosphyrus	Leucosphyrus
balabacensis	Cellia		Neomyzomyia	Leucosphyrus	Leucosphyrus
balerensis	Anopheles	Laticorn	Myzorhynchus	Albotaeniatus	
bambusicolus	Kerteszia				
bancroftii	Anopheles	Laticorn	Myzorhynchus	Bancroftii	
barberellus	Cellia		Myzomyia		
barberi	Anopheles	Angusticorn	Anopheles	Plumbeus	
barbirostris	Anopheles	Laticorn	Myzorhynchus	Barbirostris	Barbirostris
barbumbrosus	Anopheles	Laticorn	Myzorhynchus	Barbirostris	Vanus
barianensis	Anopheles	Angusticorn	Anopheles	Plumbeus	
beklemishevi	Anopheles	Angusticorn	Anopheles	Maculipennis	Quadrimaculatus
belenrae	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	
bellator	Kerteszia				
benarrochi	Nyssorhynchus	Albimanus	Oswaldoi	Oswaldoi	Strodei
bengalensis	Anopheles	Angusticorn	Anopheles	Aitkenii	

Species	Subgenus	Section	Series	Group	Subgroup
berghei	Cellia		Myzomyia	Marshallii	
bervoetsi	Cellia		Myzomyia		
boliviensis	Kerteszia				
borneensis	Anopheles	Angusticorn	Anopheles	Aitkenii	
bradleyi	Anopheles	Angusticorn	Anopheles	Punctipennis	
braziliensis	Nyssorhynchus	Argyritarsis	Albitarsis	Braziliensis	
brevipalpis	Anopheles	Laticorn	Myzorhynchus	Umbrosus	
brevirostris	Anopheles	Laticorn	Myzorhynchus	Umbrosus	
brohieri	Cellia		Myzomyia	Marshallii	
brucei	Cellia		Myzomyia	Funestus	Rivulorum
brumpti	Cellia		Cellia		
brunnipes	Cellia		Myzomyia		
bulkleyi	Anopheles	Angusticorn	Lophoscelomyia		
bustamentei	Anopheles	Laticorn	Arribalzagia	,	
buxtoni	Cellia		Neomyzomyia	Ardensis	
bwambae	Cellia		Pyretophorus		
calderoni	Anopheles	Laticorn	Arribalzagia		
caliginosus	Anopheles	Laticorn	Myzorhynchus	Coustani	
cameroni	Cellia		Neomyzomyia	Rhodesiensis	
campestris	Anopheles	Laticorn	Myzorhynchus	Barbirostris	Barbirostris
canorii	Stethomyia		Neomyzomyia	Smithii	
carnevalei	Cellia		Neomyzomyia	Ardensis	
caroni	Cellia				
carteri	Cellia		Myzomyia	Demeilloni	
chiriquiensis	Anopheles	Angusticorn	Anopheles	Pseudopunctipenn	is
chodukini	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	
christyi	Cellia		Pyretophorus		
cinctus	Cellia		Neomyzomyia	Ardensis	
cinereus	Cellia		Paramyzomyia	Cinereus	
claviger	Anopheles	Angusticorn	Anopheles		
clowi	Cellia		Neomyzomyia	Punctulatus	

Species	Subgenus	Section	Series	Group	Subgroup
colledgei	Anopheles	Angusticorn	Anopheles	Stigmaticus	
collessi	Anopheles	Laticorn	Myzorhynchus	Umbrosus	Letifer
comorensis	Cellia		Pyretophorus		
concolor	Anopheles	Angusticorn	Anopheles		
confusus	Cellia		Myzomyia	Funestus	Funestus
corethroides	Anopheles	Angusticorn	Anopheles	Stigmaticus	
costai	Anopheles	Laticorn	Arribalzagia		
coustani	Anopheles	Laticorn	Myzorhynchus	Coustani	
cracens	Cellia		Neomyzomyia	Leucosphyrus	Leucosphyrus
crawfordi	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	Lesteri
cristatus	Cellia		Neomyzomyia	Leucosphyrus	Riparis
cristipalpis	Cellia		Cellia		
crucians	Anopheles	Angusticorn	Anopheles	Punctipennis	
cruzii	Kerteszia				
crypticus	Anopheles	Laticorn	Myzorhynchus	Coustani	
cucphuongensis	Anopheles	Angusticorn	Anopheles	Alongensis	
culicifacies	Cellia		Myzomyia	Funestus	Culicifacies
culiciformis	Anopheles	Angusticorn	Anopheles	Culiciformis	
cydippis	Cellia		Cellia	Squamosus	
daciae	Anopheles	Angusticorn	Anopheles	Maculipennis	Maculipennis
dancalicus	Cellia		Neocellia		
darlingi	Nyssorhynchus	Argyritarsis	Argyritarsis	Darlingi	
daudi	Cellia		Pyretophorus		
deaneorum	Nyssorhynchus	Argyritarsis	Albitarsis	Albitarsis	
deemingi	Cellia		Neomyzomyia	Ardensis	
demeilloni	Cellia		Myzomyia	Demeilloni	
diluvialis	Anopheles	Angusticorn	Anopheles	Maculipennis	Quadrimaculatus
dirus	Cellia		Neomyzomyia	Leucosphyrus	Leucosphyrus
dispar	Cellia		Neocellia	Maculatus	
distinctus	Cellia		Myzomyia	Wellcomei	
domicola	Cellia		Myzomyia		

Species	Subgenus	Section	Series	Group	Subgroup
donaldi	Anopheles	Laticorn	Myzorhynchus	Barbirostris	Barbirostris
dravidicus	Cellia		Neocellia	Maculatus	Maculatus
dthali	Cellia		Myzomyia		
dualaensis	Cellia		Neomyzomyia		
dunhami	Nyssorhynchus	Albimanus	Oswaldoi	Oswaldoi	Oswaldoi
dureni	Cellia		Neomyzomyia	Ardensis	
earlei	Anopheles	Angusticorn	Anopheles	Maculipennis	Freeborni
eiseni	Anopheles	Angusticorn	Anopheles	Pseudopunctipennis	
ejercitoi	Anopheles	Laticorn	Myzorhynchus	Albotaeniatus	
elegans	Cellia		Neomyzomyia	Leucosphyrus	Leucosphyrus
engarensis	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	
eouzani	Cellia		Neomyzomyia	Ardensis	
epiroticus	Cellia		Pyretophorus		
erepens	Cellia		Myzomyia	Wellcomei	
erythraeus	Cellia		Myzomyia		
ethiopicus	Cellia		Myzomyia		
evandroi	Anopheles	Laticorn	Arribalzagia		
evansae	Nyssorhynchus	Albimanus	Oswaldoi	Oswaldoi	Oswaldoi
faini	Cellia		Neomyzomyia	Smithii	
farauti	Cellia		Neomyzomyia	Punctulatus	
fausti	Anopheles	Angusticorn	Anopheles	Plumbeus	
filipinae	Cellia		Myzomyia	Funestus	Aconitus
flavicosta	Cellia		Myzomyia		
flavirostris	Cellia		Myzomyia	Funestus	Minimus
fluminensis	Anopheles	Laticorn	Arribalzagia		
fluviatilis	Cellia		Myzomyia	Funestus	Minimus
fontinalis	Cellia		Myzomyia		
forattinii	Anopheles	Laticorn	Arribalzagia		
fragilis	Anopheles	Angusticorn	Anopheles	Aitkenii	
franciscanus	Anopheles	Angusticorn	Anopheles	Pseudopunctipennis	
franciscoi	Anopheles	Laticorn	Myzorhynchus	Barbirostris	Barbirostris

Species	Subgenus	Section	Series	Group	Subgroup
freeborni	Anopheles	Angusticorn	Anopheles	Maculipennis	Freeborni
freetownensis	Cellia		Myzomyia	Demeilloni	
freyi	Anopheles	Laticorn	Myzorhynchus	Barbirostris	
funestus	Cellia		Myzomyia	Funestus	Funestus
fuscicolor	Anopheles	Laticorn	Myzorhynchus	Coustani	
fuscivenosus	Cellia		Myzomyia	Funestus	Rivulorum
gabaldoni	Anopheles	Laticorn	Arribalzagia		
galvaoi	Nyssorhynchus	Albimanus	Oswaldoi	Oswaldoi	Oswaldoi
gambiae	Cellia		Pyretophorus		
garnhami	Cellia		Myzomyia	Demeilloni	
georgianus	Anopheles	Angusticorn	Anopheles	Punctipennis	
gibbinsi	Cellia		Myzomyia	Marshallii	
gigas	Anopheles	Angusticorn	Anopheles	Lindesayi	
gilesi	Lophopodomyia				
goeldii	Nyssorhynchus	Albimanus	Oswaldoi	Oswaldoi	Oswaldoi
gomezdelatorrei	Lophopodomyia				
gonzalezrinconesi	Kerteszia				
grabhamii	Anopheles	Angusticorn	Cycloleppteron		
grassei	Cellia		Neomyzomyia	Pauliani	
greeni	Cellia		Neocellia	Maculatus	
grenieri	Cellia		Neomyzomyia	Pauliani	
griveaudi	Cellia		Neomyzomyia	Ranci	
guarani	Nyssorhynchus	Myzorhynchella			
guarao	Anopheles	Laticorn	Arribalzagia		
hackeri	Cellia		Neomyzomyia	Leucosphyrus	Hackeri
hailarensis	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	
halophylus	Nyssorhynchus	Albimanus	Oswaldoi	Triannulatus	
hamoni	Cellia		Neomyzomyia	Smithii	
hancocki	Cellia		Myzomyia	Marshallii	
hargreavesi	Cellia		Myzomyia	Marshallii	
harperi	Cellia		Myzomyia	Marshallii	

Species	Subgenus	Section	Series	Group	Subgroup
harrisoni	Cellia		Myzomyia	Funestus	Minimus
hectoris	Anopheles	Angusticorn	Anopheles	Pseudopunctipenni	S
heiheensis	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	
hermsi	Anopheles	Angusticorn	Anopheles	Maculipennis	Freeborni
hervyi	Cellia		Neocellia		
hilli	Cellia		Neomyzomyia		
hinesorum	Cellia		Neomyzomyia	Punctulatus	
hodgkini	Anopheles	Laticorn	Myzorhynchus	Barbirostris	Barbirostris
homunculus	Kerteszia				
hughi	Cellia		Myzomyia	Marshallii	
hunteri	Anopheles	Laticorn	Myzorhynchus	Umbrosus	
hyrcanus	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	
implexus	Anopheles	Laticorn	Christya		
incognitus	Cellia		Neomyzomyia		
indefinitus	Cellia		Pyretophorus	Subpictus	
ininii	Nyssorhynchus	Albimanus	Oswaldoi	Oswaldoi	Oswaldoi
insulaeflorum	Anopheles	Angusticorn	Anopheles	Aitkenii	
intermedius	Anopheles	Laticorn	Arribalzagia		
interruptus	Anopheles	Angusticorn	Lophoscelomyia	Asiaticus	Interruptus
introlatus	Cellia		Neomyzomyia	Leucosphyrus	Leucosphyrus
inundatus	Anopheles	Angusticorn	Anopheles	Maculipennis	Quadrimaculatus
irenicus	Cellia		Neomyzomyia	Punctulatus	
jamesii	Cellia		Neocellia	Jamesii	
janconnae	Nyssorhynchus	Argyritarsis	Albitarsis	Albitarsis	
jebudensis	Cellia		Neomyzomyia	Smithii	
jeyporiensis	Cellia		Myzomyia	Funestus	
judithae	Anopheles	Angusticorn	Anopheles	Plumbeus	
karwari	Cellia		Neocellia		
keniensis	Cellia		Myzomyia	Demeilloni	
kingi	Cellia		Neomyzomyia	Ardensis	
kleini	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	

Species	Subgenus	Section	Series	Group	Subgroup
kochi	Cellia		Neomyzomyia	Kochi	
kokhani	Cellia		Neomyzomyia		
kolambuganensis	Cellia		Neomyzomyia		
koliensis	Cellia		Neomyzomyia	Punctulatus	
kompi	Stethomyia				
konderi	Nyssorhynchus	Albimanus	Oswaldoi	Oswaldoi	Oswaldoi
koreicus	Anopheles	Laticorn	Myzorhynchus	Barbirostris	
kosiensis	Cellia		Myzomyia	Marshallii	
kweiyangensis	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	
kyondawensis	Baimaia				
labranchiae	Anopheles	Angusticorn	Anopheles	Maculipennis	Maculipennis
lacani	Cellia		Neomyzomyia	Ranci	Roubaudi
laneanus	Kerteszia				
lanei	Nyssorhynchus	Argyritarsis	Argyritarsis	Lanei	
latens	Cellia		Neomyzomyia	Leucosphyrus	Leucosphyrus
leesoni	Cellia		Myzomyia	Funestus	Minimus
lepidotus	Kerteszia				
lesteri	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	Lesteri
letabensis	Cellia		Myzomyia	Marshallii	
letifer	Anopheles	Laticorn	Myzorhynchus	Umbrosus	Letifer
leucosphyrus	Cellia		Neomyzomyia	Leucosphyrus	Leucosphyrus
lewisi	Anopheles	Angusticorn	Anopheles	Maculipennis	
liangshanensis	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	
limosus	Cellia		Pyretophorus		
lindesayi	Anopheles	Angusticorn	Anopheles	Lindesayi	
listeri	Cellia		Paramyzomyia	Listeri	
litoralis	Cellia		Pyretophorus		
lloreti	Cellia		Myzomyia	Demeilloni	
longipalpis	Cellia		Myzomyia	Funestus	Funestus
longirostris	Cellia		Neomyzomyia		
lounibosi	Cellia		Neomyzomyia	Rhodesiensis	

Species	Subgenus	Section	Series	Group	Subgroup
lovettae	Cellia		Neomyzomyia	Smithii	
ludlowae	Cellia		Pyretophorus	Ludlowae	
lungae	Cellia		Neomyzomyia		
lutzii	Nyssorhynchus	Myzorhynchella			
macarthuri	Cellia		Neomyzomyia	Leucosphyrus	Riparis
machardyi	Cellia		Neomyzomyia	Ardensis	
maculatus	Cellia		Neocellia	Maculatus	Maculatus
maculipalpis	Cellia		Neocellia		
maculipennis	Anopheles	Angusticorn	Anopheles	Maculipennis	Maculipennis
maculipes	Anopheles	Laticorn	Arribalzagia		
majidi	Cellia		Myzomyia		
malefactor	Anopheles	Laticorn	Arribalzagia		
maliensis	Cellia		Neomyzomyia	Ardensis	
manalangi	Anopheles	Laticorn	Myzorhynchus	Barbirostris	Vanus
mangyanus	Cellia		Myzomyia	Funestus	Aconitus
marajoara	Nyssorhynchus	Argyritarsis	Albitarsis	Albitarsis	
marshallii	Cellia		Myzomyia	Marshallii	
marteri	Anopheles	Angusticorn	Anopheles		
martinius	Anopheles	Angusticorn	Anopheles	Maculipennis	Maculipennis
mascarensis	Cellia		Neomyzomyia	Mascarensis	
mattogrossensis	Anopheles	Laticorn	Arribalzagia		
maverlius	Anopheles	Angusticorn	Anopheles	Maculipennis	Quadrimaculatus
mediopunctatus	Anopheles	Laticorn	Arribalzagia		
melanoon	Anopheles	Angusticorn	Anopheles	Maculipennis	Maculipennis
melas	Cellia		Pyretophorus		
mengalangensis	Anopheles	Angusticorn	Anopheles	Lindesayi	
meraukensis	Cellia		Neomyzomyia		
merus	Cellia		Pyretophorus		
messeae	Anopheles	Angusticorn	Anopheles	Maculipennis	Maculipennis
millecampsi	Cellia		Neomyzomyia	Ardensis	
milloti	Cellia		Neomyzomyia	Pauliani	

Species	Subgenus	Section	Series	Group	Subgroup
minimus	Cellia		Myzomyia	Funestus	Minimus
minor	Anopheles	Laticorn	Arribalzagia		
mirans	Cellia		Neomyzomyia	Leucosphyrus	Hackeri
moghulensis	Cellia		Neocellia		
montanus	Anopheles	Laticorn	Myzorhynchus	Albotaeniatus	
mortiauxi	Cellia		Myzomyia	Marshallii	
moucheti	Cellia		Myzomyia		
mousinhoi	Cellia		Myzomyia	Marshallii	
multicinctus	Cellia		Neomyzomyia	Ardensis	
multicolor	Cellia		Paramyzomyia	Listeri	
murphyi	Cellia		Cellia		
namibiensis	Anopheles	Laticorn	Myzorhynchus	Coustani	
natalensis	Cellia		Neomyzomyia	Ardensis	
nataliae	Cellia		Neomyzomyia		
neivai	Kerteszia				
nemophilous	Cellia		Neomyzomyia	Leucosphyrus	Leucosphyrus
neomaculipalpus	Anopheles	Laticorn	Arribalzagia		
nigerrimus	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	Nigerrimus
nigritarsis	Nyssorhynchus	Myzorhynchella			
nilgiricus	Anopheles	Angusticorn	Anopheles	Lindesayi	
nili	Cellia		Neomyzomyia	Ardensis	
nimbus	Stethomyia				
nimpe	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	
nitidus	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	Nigerrimus
nivipes	Cellia		Neocellia	Annularis	
njombiensis	Cellia		Myzomyia	Marshallii	
noniae	Anopheles	Angusticorn	Lophoscelomyia	Asiaticus	
notanandai	Cellia		Neocellia	Maculatus	Sawadwongporni
notleyi	Cellia		Neomyzomyia	Ranci	Roubaudi
novaguinensis	Cellia		Neomyzomyia		
nuneztovari	Nyssorhynchus	Albimanus	Oswaldoi	Oswaldoi	Oswaldoi

Species	Subgenus	Section	Series	Group	Subgroup
obscurus	Anopheles	Laticorn	Myzorhynchus		
occidentalis	Anopheles	Angusticorn	Anopheles	Maculipennis	Freeborni
oiketorakras	Lophopodomyia				
okuensis	Anopheles	Laticorn	Christya		
omorii	Anopheles	Angusticorn	Anopheles	Plumbeus	
oryzalimnetes	Nyssorhynchus	Argyritarsis	Albitarsis	Albitarsis	
oswaldoi	Nyssorhynchus	Albimanus	Oswaldoi	Oswaldoi	Oswaldoi
ovengensis	Cellia		Neomyzomyia	Ardensis	
pallidus	Cellia		Neocellia	Annularis	
palmatus	Anopheles	Angusticorn	Anopheles	Aitkenii	
paltrinierii	Cellia		Neocellia		
paludis	Anopheles	Laticorn	Myzorhynchus	Coustani	
pampanai	Cellia		Myzomyia	Funestus	Aconitus
papuensis	Anopheles	Angusticorn	Anopheles	Stigmaticus	
paraliae	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	Lesteri
parangensis	Cellia		Pyretophorus		
parapunctipennis	Anopheles	Angusticorn	Anopheles	Pseudopunctipennis	
parensis	Cellia		Myzomyia	Funestus	Funestus
parvus	Nyssorhynchus	Myzorhynchella			
pattoni	Cellia		Neocellia		
pauliani	Cellia		Neomyzomyia	Pauliani	
peditaeniatus	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	Lesteri
perplexens	Anopheles	Angusticorn	Anopheles	Punctipennis	
persiensis	Anopheles	Angusticorn	Anopheles	Maculipennis	Maculipennis
peryassui	Anopheles	Laticorn	Arribalzagia		
petragnani	Anopheles	Angusticorn	Anopheles		
peytoni	Anopheles	Angusticorn	Anopheles	Aitkenii	
pharoensis	Cellia		Cellia		
philippinensis	Cellia		Neocellia	Annularis	
pholidotus	Kerteszia				
pictipennis	Nyssorhynchus	Argyritarsis	Argyritarsis	Pictipennis	

Species	Subgenus	Section	Series	Group	Subgroup
pilinotum	Anopheles	Angusticorn	Anopheles	Aitkenii	
pinjaurensis	Anopheles	Angusticorn	Anopheles	Aitkenii	
plumbeus	Anopheles	Angusticorn	Anopheles	Plumbeus	
pollicaris	Anopheles	Laticorn	Myzorhynchus	Barbirostris	Barbirostris
powderi	Anopheles	Angusticorn	Anopheles	Plumbeus	
powelli	Anopheles	Angusticorn	Anopheles	Stigmaticus	
pretoriensis	Cellia		Neocellia		
pristinus	Nyssorhynchus	Myzorhynchella			
pseudobarbirostris	Anopheles	Laticorn	Myzorhynchus	Bancroftii	
pseudojamesi	Cellia		Neocellia	Jamesii	
pseudomaculipes	Anopheles	Laticorn	Arribalzagia		
pseudopictus	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	
pseudopunctipennis	Anopheles	Angusticorn	Anopheles	Pseudopunctipennis	
pseudosinensis	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	Nigerrimus
pseudostigmaticus	Anopheles	Angusticorn	Anopheles	Stigmaticus	
pseudosundaicus	Cellia		Pyretophorus		
pseudotibiam aculatu.	s Lophopodomyia				
pseudowillmori	Cellia		Neocellia	Maculatus	
pujutensis	Cellia		Neomyzomyia	Leucosphyrus	Hackeri
pulcherrimus	Cellia		Neocellia		
pullus	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	
punctimacula	Anopheles	Laticorn	Arribalzagia		
punctipennis	Anopheles	Angusticorn	Anopheles	Punctipennis	
punctulatus	Cellia		Neomyzomyia	Punctulatus	
pursati	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	Nigerrimus
quadriannulatus	Cellia		Pyretophorus		
quadrimaculatus	Anopheles	Angusticorn	Anopheles	Maculipennis	Quadrimaculatus
rachoui	Anopheles	Laticorn	Arribalzagia		
radama	Cellia		Neomyzomyia	Pauliani	
rageaui	Cellia		Neomyzomyia	Smithii	
rampae	Cellia		Neocellia	Maculatus	Sawadwongporni

Species	Subgenus	Section	Series	Group	Subgroup
ranci	Cellia		Neomyzomyia	Ranci	Ranci
rangeli	Nyssorhynchus	Albimanus	Oswaldoi	Oswaldoi	Oswaldoi
recens	Cellia		Neomyzomyia	Leucosphyrus	Hackeri
reidi	Anopheles	Laticorn	Myzorhynchus	Barbirostris	Vanus
rennellensis	Cellia		Neomyzomyia	Punctulatus	
rhodesiensis	Cellia		Neomyzomyia	Rhodesiensis	
riparis	Cellia		Neomyzomyia	Leucosphyrus	Riparis
rivulorum	Cellia		Myzomyia	Funestus	Rivulorum
rodhaini	Cellia				
rollai	Kerteszia				
rondoni	Nyssorhynchus	Albimanus	Oswaldoi	Oswaldoi	Strodei
roperi	Anopheles	Laticorn	Myzorhynchus	Umbrosus	Letifer
roubaudi	Cellia		Neomyzomyia	Ranci	Roubaudi
ruarinus	Cellia		Neomyzomyia	Rhodesiensis	
rufipes	Cellia		Neocellia		
sacharovi	Anopheles	Angusticorn	Anopheles	Maculipennis	Maculipennis
salbaii	Cellia		Neocellia		
samarensis	Anopheles	Laticorn	Myzorhynchus	Umbrosus	
sanctielii	Nyssorhynchus	Albimanus	Oswaldoi	Oswaldoi	Oswaldoi
saperoi	Anopheles	Laticorn	Myzorhynchus	Albotaeniatus	
saungi	Cellia		Neomyzomyia		
sawadwongporni	Cellia		Neocellia	Maculatus	Sawadwongporni
sawyeri	Nyssorhynchus	Argyritarsis	Argyritarsis	Argyritarsis	
scanloni	Cellia		Neomyzomyia	Leucosphyrus	Leucosphyrus
schueffneri	Cellia		Neocellia	Annularis	
schwetzi	Cellia		Myzomyia		
separatus	Anopheles	Laticorn	Myzorhynchus	Umbrosus	Separatus
seretsei	Cellia		Paramyzomyia	Listeri	
sergentii	Cellia		Myzomyia	Demeilloni	
seydeli	Cellia		Myzomyia	Marshallii	
shannoni	Anopheles	Laticorn	Arribalzagia		

Species	Subgenus	Section	Series	Group	Subgroup
similissimus	Anopheles	Laticorn	Myzorhynchus	Umbrosus	
sinensis	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	
sineroides	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	
sintoni	Anopheles	Angusticorn	Anopheles	Culiciformis	
sintonoides	Anopheles	Angusticorn	Anopheles	Culiciformis	
smaragdinus	Anopheles	Angusticorn	Anopheles	Maculipennis	Quadrimaculatus
smithii	Cellia		Neomyzomyia	Smithii	
solomonis	Cellia		Neomyzomyia		
somalicus	Cellia		Neomyzomyia	Ardensis	
splendidus	Cellia		Neocellia	Jamesii	
squamifemur	Lophopodomyia				
squamosus	Cellia		Cellia	Squamosus	
stephensi	Cellia		Neocellia		
stigmaticus	Anopheles	Angusticorn	Anopheles	Stigmaticus	
stookesi	Cellia		Neomyzomyia		
stricklandi	Anopheles	Angusticorn	Anopheles	Aitkenii	
strodei	Nyssorhynchus	Albimanus	Oswaldoi	Oswaldoi	Strodei
subpictus	Cellia		Pyretophorus	Subpictus	
sulawesi	Cellia		Neomyzomyia	Leucosphyrus	Hackeri
sundaicus	Cellia		Pyretophorus	Ludlowae	
superpictus	Cellia		Neocellia		
swahilicus	Cellia		Cellia		
symesi	Anopheles	Laticorn	Myzorhynchus	Coustani	
takasagoensis	Cellia		Neomyzomyia	Leucosphyrus	Leucosphyrus
tasmaniensis	Anopheles	Angusticorn	Anopheles	Atratipes	
tchekedii	Cellia		Myzomyia		
tenebrosus	Anopheles	Laticorn	Myzorhynchus	Coustani	
tessellatus	Cellia		Neomyzomyia	Tessellatus	
theileri	Cellia		Myzomyia	Wellcomei	
theobaldi	Cellia		Neocellia		
thomasi	Stethomyia				

Species	Subgenus	Section	Series	Group	Subgroup
tibiamaculatus	Anopheles	Angusticorn	Anopheles	Pseudopunctipennis	
tigertti	Anopheles	Angusticorn	Anopheles	Aitkenii	
torresiensis	Cellia		Neomyzomyia	Punctulatus	
triannulatus	Nyssorhynchus	Albimanus	Oswaldoi	Triannulatus	
trinkae	Nyssorhynchus	Albimanus	Oswaldoi	Oswaldoi	Oswaldoi
turkhudi	Cellia		Paramyzomyia	Cinereus	
umbrosus	Anopheles	Laticorn	Myzorhynchus	Umbrosus	Umbrosus
vagus	Cellia		Pyretophorus	Subpictus	
vaneedeni	Cellia		Myzomyia	Funestus	Funestus
vanhoofi	Cellia		Neomyzomyia	Smithii	
vanus	Anopheles	Laticorn	Myzorhynchus	Barbirostris	Vanus
vargasi	Lophopodomyia				
varuna	Cellia		Myzomyia	Funestus	Aconitus
vernus	Cellia		Neomyzomyia	Ardensis	
veruslanei	Anopheles	Laticorn	Arribalzagia		
vestitipennis	Anopheles	Laticorn	Arribalzagia		
vietnamensis	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	Lesteri
vinckei	Cellia		Neomyzomyia	Ardensis	
walkeri	Anopheles	Angusticorn	Anopheles	Maculipennis	
walravensi	Cellia		Myzomyia		
watsonii	Cellia		Neomyzomyia		
wellcomei	Cellia		Myzomyia	Wellcomei	
wellingtonianus	Anopheles	Angusticorn	Anopheles	Lindesayi	
whartoni	Anopheles	Laticorn	Myzorhynchus	Umbrosus	Letifer
willmori	Cellia		Neocellia	Maculatus	
wilsoni	Cellia		Neomyzomyia	Smithii	
xelajuensis	Anopheles	Angusticorn	Anopheles	Plumbeus	
xui	Anopheles	Laticorn	Myzorhynchus	Hyrcanus	
yaeyamaensis	Cellia		Myzomyia	Funestus	Minimus
ziemanni	Anopheles	Laticorn	Myzorhynchus	Coustani	

Appendix 3

Sibling species complexes of Anopheles - formally named and unnamed species. The Maculatus, Maculipennis and Punctulatus Complexes are now considered to be super-complexes referred to as "Groups" with subordinate complexes. Likewise, the Culicifacies Complex is considered to be a Subgroup.

Barbirostris Complex [76] barbirostris annularis A complex [86] barbirostris annularis A complex [86] claviger complex [87] claviger pellithas Genotype B perragnani Crucians Complex [72] bradleyi pollithas Genotype CI crucians A annulipes A Genotype CI crucians A annulipes A Genotype CI crucians B annulipes A Genotype E subpictus A subpictus A crucians B annulipes B Genotype E subpictus A subpictus Complex [87] crucians B annulipes B Genotype G sundaicus Complex [87] crucians B annulipes C Genotype G Sundaicus Complex [87] crucians D annulipes C Genotype G Sundaicus Complex [87] crucians D annulipes G lungae sundaicus B sundaicus C sundaicus B sundaicus C sundaicus B sundaicus B sundaicus C sundaicus B sundaicus B sundaicus C sundaicus C sundaicus C sundaicus B sundaicus B sundaicus C su	Subgenus Anopheles	Subgenus Cellia	latens	farauti 5
barbirostris Claviger Opplex [67] annularis B Genotype A irenicus claviger petragmani pellidus Genotype Glaviger petragmani philippinensis Genotype C2 subpicus Complex [95] crucians Complex [72] schneffineri Genotype C2 subpicus Complex [95] crucians Complex [72] schneffineri Genotype C2 subpicus Complex [95] crucians A annulipes A Genotype E subpicus C crucians B annulipes A Genotype G Sundaicus Complex [97] crucians C annulipes C Genotype G Sundaicus Complex [97] crucians E annulipes C Genotype G Sundaicus Complex [97] crucians E annulipes G lungae Complex [47] sundaicus C gigas Complex [70] annulipes H natation sundaicus C gigas S.I. annulipes I solomonis gigas s.I. annulipes K dispur sundaicus D sulficias C annulipes M natation sundaicus C annulipes M natation sundaicus C annulipes M natation sundaicus C gigas S.I. annulipes K dispur sundaicus B gigas s.I. annulipes C gray annulipes M natation sundaicus C annulipes M natulius Group [88] sundaicus D sundaicus D sundaicus C sundaicus C sundaicus Complex [97] sundaicus C genotype G Genotype G Genotype G Genotype G Genotype G Sundaicus Complex [97] subpicus C sundaicus Complex [97] sundaicus C sund	Daubinastnia Commley [76]	Americania Complex [96]	leucosphyrus	farauti 6
Clavieger Complex [67] annularis B Genotype A irenicus claviege petragnani philippinensis Genotype C1 subpicus Complex [95] pradicy A numlipes Complex [89] Genotype C2 subpicus Complex [95] subpicus Complex [95] pradicy A numlipes Complex [89] Genotype D subpicus B crucians B annulayes B Genotype E subpicus B crucians B annulayes B Genotype G enotype G crucians B annulayes B Genotype G enotype G crucians D annulayes D Genotype G enotype G crucians D annulayes D Genotype G enotype G enotype G enotype [97] enotype Crucians D annulayes G lingae sundaicus Subgroup Gigas of annulayes G lingae sundaicus Subgroup [170] annulayes H nataliae sundaicus C balleyi annulayes I solomonis sundaicus C sundaicus C mumlipes I solomonis sundaicus C sundaicus C mumlipes I solomonis sundaicus C sundaicus C lindaesayi dinayes I solomonis sundaicus E sigas s. L. Lindaesayi Complex [70] annulayes L greeni Complex [10] lindesayi annulayes A pseudowillmori susperpictus B magalangensis annulayes A pseudowillmori susperpictus B milgiricus wellingtonianus annulayes A manulayes A subgroup Grupi Grupi B subgroup [173] crucii B culicifacies A culicifacies A culicifacies A culicifacies B annulayes A culicifacies B annulaye				
claviger petragmani philippinensis Genotype C1 Subpicus Complex [95] Crucians Complex [72] schneffneri Genotype C2 subpicus C crucians A annulipes A Genotype D subpicus C crucians A annulipes B Genotype E subpicus C crucians C annulipes B Genotype E subpicus C crucians C annulipes C Genotype F subpicus C crucians C annulipes D Genotype G sundaicus Complex [97] crucians E annulipes B Genotype G sundaicus Complex [97] crucians E annulipes G figure Complex [47] sundaicus gigas complex [70] annulipes A financia Gigas Complex [70] annulipes I nataliae sundaicus C annulipes C finantinipes I solomonis sundaicus D sundaicus D sundaicus D sundaicus C sun				
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baisasi [94,109] halophylus				
	occidentalis			
halahacensis tarauti triannulatus				
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introlatus farauti 4 triannulatus C		introlatus	farauti 4	triannulatus C

Appendix 4

Unnamed and provisionally designated members of species complexes and their position in the classification of genus *Anopheles* (Sections of subgenera *Anopheles* and *Nyssorhynchus* are omitted). Excluding nominotypical members, the list includes 72 species that require formal Latin names.

Species	Authors	Subgenus	Series	Group	Subgroup	Complex
albitarsis sp. F,G,H,I	[114,115]	Nyssorhynchus	Albitarsis	Albitarsis		Albitarsis
annularis sp. A,B	[86]	Cellia	Neocellia	Annularis		Annularis
annulipes sp. A-Q	[89]	Cellia	Neomyzomyia			Annulipes
Anopheles CP Form	[116]	Nyssorhynchus	Oswaldoi	Oswaldoi	Strodei	
barbirostris clades I-IV	[117]	Anopheles	Barbirostris	Barbirostris	Barbirostris	Barbirostris
benarrochi sp. B	[105]	Nyssorhynchus	Oswaldoi	Oswaldoi	Strodei	Benarrochi
crucians sp. A-E	[72]	Anopheles	Anopheles	Punctipennis		Crucians
cruzii sp. A,B,C	[118]	Kerteszia				
culicifacies sp. A-E	[108]	Cellia	Myzomyia	Funestus	Culicifacies	Culicifacies
farauti sp. 4,5,6	[109,119]	Cellia	Neomyzomyia	Punctulatus		Farauti
fluviatilis sp. S,T,U	[83]	Cellia	Myzomyia	Funestus	Minimus	Fluviatilis
funestus-like sp.	[120]	Cellia	Myzomyia	Funestus	Funestus	
gigas s.l. (Thailand)	[70]	Anopheles	Anopheles	Lindesayi		Gigas
hyrcanus sp _{IR}	[121]	Anopheles		Hyrcanus		
janconnae, lineage nr	[122]	Nyssorhynchus	Albitarsis	Albitarsis		Albitarsis
longipalpis Type A	[123]	Cellia	Myzomyia	Funestus	Minimus	
longipalpis Type C	[123]	Cellia	Myzomyia	Funestus	Funestus	
longirostris Genotypes A,B,C1,C2,D,E,F,G,H	[90]	Cellia	Neomyzomyia			Longirostris
marajoara lineages 1,2	[124]	Nyssorhynchus	Albitarsis	Albitarsis		Albitarsis
nivipes (2 cytotypes)	[87]	Cellia	Neocellia	Annularis		Nivipes
nuneztovari sp. A	[125]	Nyssorhynchus	Oswaldoi	Oswaldoi	Oswaldoi	Nuneztovari
nuneztovari B/C	[104]	Nyssorhynchus	Oswaldoi	Oswaldoi	Oswaldoi	Nuneztovari
punctulatus, sp. nr	[126]	Cellia	Neomyzomyia	Punctulatus		

Species	Authors	Subgenus	Series	Group	Subgroup	Complex
quadriannulatus sp. B	[127]	Cellia	Pyretophorus			Gambiae
subpictus sp. A-D	[99]	Cellia	Pyretophorus	Subpictus		Subpictus
sundaicus sp. B-E	[98,128]	Cellia	Pyretophorus	Ludlowae		Sundaicus
superpictus sp. A,B	[110,129]	Cellia	Neocellia			Superpictus
takasagoensis, aff.	[130]	Cellia	Neomyzomyia	Leucosphyrus	Leucosphyrus	Dirus
triannulatus sp. C	[113]	Nyssorhynchus	Oswaldoi	Triannulatus		Triannulatus

Appendix 5

Phylogenetic studies of Anopheles mosquitoes. Groups included in the table are those recognized herein. None of the studies included all taxa that comprise the group investigated, but those marked with an asterisk (*) included the majority of species. Nucleotide sequences include COI, COII, cyt b, ND4, ND5 and ND6 from mitochondrial DNA (mtDNA); D2, D3, 18S, ITS1 and ITS2 from ribosomal DNA (rDNA); EF-1 α , G_6pd and white from nuclear DNA.

Group	Data set	Authors
Genus Anopheles	Morphology	[40] [36]
	cyt b, ND5, D2 ND5, D2, G₅pd, white COI, COII, D2 18S	[38] [39] [41] [131]
Subgenus <i>Anopheles</i>	Morphology <i>COII</i>	[42] [37]
Anopheles Series		
Maculipennis Group	Chromosomes	[132] [71]* [133,134]
Maculipennis Subgroup	ITS2	[135]
Freeborni and Quadri- maculatus Subgroups	D2	[136]
Myzorhynchus Series Barbirostris Complex	ITS2, COI, COII ITS2, COI	[137,139] [117]
Hyrcanus Grou	ITS2	[139,140] [141]*

Group	Data set	Authors	
	ITS2, COI	[142]	
Subgenus <i>Cellia</i>	Chromosomes	[143,144]	
	COII	[37]	
Myzomyia Series	Chromosomes	[143,144]	
	COII, D3	[82]	
Funestus Group	ITS2, COII, D3	[55]*	
	COII, D3	[81]*	
Minimus Subgroup	COII, D3	[145]	
Minimus Complex	D3, ITS2	[146]*	
Neocellia Series	Chromosomes	[87]	
Annularis Group	ITS2, COII, D3, ND5	[147]	
	D3, ITS2	[148]	
Maculatus Group	ITS2, COII, D3	[149–151]	
Neomyzomyia Series	ITS2, COI, COII, EF-1α	[89]	
Annulipes Complex	COI, ND6	[152]	
Leucosphyrus Group			
Punctulatus Group	ITS2	[153]	
	185	[154]	
Farauti Complex	ITS1	[109]	
Pyretophorus Series	Morphology	[56]*	
	Chromosomes	[144]	
	COII	[37]	
Gambiae Complex	Chromosomes	[155]	
	rDNA, mtDNA	[156]	
Sundaicus Complex	mtDNA	[157]	
	ITS2, D2, COI, ND4	[158]	
	white	[114]	
	cyt b, ITS2, COI	[128]	
Subgenus Kerteszia	Morphology	[44]	
Subgenus Nyssorhynchus	ITS2	[159]	
Albimanus Section	Morphology	[24]	
Argyritarsis Section	Morphology	[25]	
Myzorhynchella Section	ITS2, COI, white	[160]	

Appendix 6

Unassigned - (17) Lesteri Subgroup - (5) Nigerrimus Subgroup - (4)

Summary of the formal and informal group taxa (species complexes omitted) of genus Anopheles. The zoogeographic distribution and the number of formally named and informally designated species (in parentheses) are given for each taxon. Minor extensions of one or more species of a group into an adjacent zoogeographic region are disregarded. C = cosmopolitan; NW = New World; OW = Old World; Af = Afrotropical; Au = Australasian; Ne = Nearctic; Nt = Neotropical; Or = Oriental; Pa = Palaearctic.

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Subgenus Anopheles-C (191)
                                               Umbrosus Group – Or (12)
                                                                                           Mascarensis Group - Af (1)
Angusticorn Section - OW, NW (95)
                                                                                              Pauliani Group - Af (5)
                                                  Unassigned – (5)
 Anopheles Series - OW and
                                                  Baezai Subgroup – (1)
                                                                                              Punctulatus Group - Au (13)
                                                  Letifer Subgroup – (4)
         NW (88)
                                                                                              Ranci Group - Af (5)
   Alongensis Group - Or (2)
                                                  Separatus Subgroup – (1)
                                                                                                Unassigned - (1)
   Aitkenii Group - Or (13)
                                                  Umbrosus Subgroup – (1)
                                                                                                 Ranci Subgroup - (1)
                                                                                                 Roubaudi Subgroup - (3)
   Atratipes Group - Au (2)
   Culiciformis Group - Or (3)
                                             Subgenus Baimaia- Or (1)
                                                                                              Rhodesiensis Group - Af (5)
   Lindesayi Group - Or (7)
                                                                                              Smithii Group - Af (9)
   Maculipennis Group - Ne, Pa (20)
                                              Subgenus Cellia— OW (233)
                                                                                              Tessellatus Group - Or (1)
                                               Cellia Series - Af (8)
    Maculipennis Subgroup -
                                                                                             Paramyzomyia Series – Af, Pa (6)
          Pa (10)
                                                Unassigned - (6)
                                                                                              Cinereus Group - Af (2), Pa (1)
    Quadrimaculatus Subgroup -
                                                Squamosus Group – (2)
                                                                                              Listeri Group - Af (2), Pa (1
                                               Myzomyia Series – Af, Or (71)
                                                                                            Pyretophorus Series - Af (10),
          Ne (5), Pa (1)
    Freeborni Subgroup - Ne (4)
                                                Unassigned - Af (16)
                                                                                                    Or (12)
                                                Demeilloni Group – Af (7)
Funestus Group – Af, Or (29)
   Plumbeus Group - Ne (2), Nt (4),
         Pac (3)
                                                                                           Subgenus Kerteszia- Nt (14)
                                                  Unassigned – (1)
   Pseudopunctipennis Group -
          Ne (7)
                                                  Aconitus Subgroup - Or (5)
                                                                                           Subgenus Lophopodomyia- Nt (6)
   Punctipennis Group - Ne (9)
                                                  Culicifacies Subgroup - Or (5)
                                                                                           Subgenus Nyssorhynchus- Nt (38)
   Stigmaticus Group – Au (6)
                                                  Funestus Subgroup – Af (7)
 Cycloleppteron Series - Ne (2)
                                                  Minimus Subgroup - Af (1),
                                                                                           Albimanus Section - (24)
 Lophoscelomyia Series - Or (4)
                                                       Or (6)
                                                                                             Albimanus Series – (1)
   Unassigned – (1)
                                                  Rivulorum Subgroup – Af (4)
                                                                                            Oswaldoi Series - (23)
                                                  Marshallii Group - Af (15)
                                                                                              Oswaldoi Group - (21)
   Asiaticus Group – (4)
    Unassigned – (2)
                                                 Wellcomei Group - Af (4)
                                                                                               Oswaldoi Subgroup - (14)
    Asiaticus Subgroup – (1)
                                               Neocellia Series - Af, Or, Pal (24)
                                                                                               Strodei Subgroup – (7)
    Interruptus Subgroup - (1)
                                                Unassigned - Af, Or, Pa (14)
                                                                                              Triannulatus Group – (3)
Laticorn Section - Af, Au, Nt, Or,
                                                 Annularis Group – Or (7)
                                                                                           Argyritarsis Section – (14)
                                                Jamesii Group – Or (3)
         Pa (96)
                                                                                            Albitarsis Series - (8)
 Arribalzagia Series - Ne (24)
                                                Maculatus Group - Or (9)
                                                                                              Albitarsis Group - (7)
 Christya Series - Af (2)
                                                  Unassigned – (4)
                                                                                              Braziliensis Group - (1)
 Myzorhynchus Series - Af, Au, Or,
                                                  Maculatus Subgroup - (2)
                                                                                             Argyritarsis Series – (6)
         Pa (70)
                                                  Sawadwongporni Subgroup – (3)
                                                                                              Argyritarsis Group – (2)
   Albotaeniatus Group - Or (4),
                                               Neomyzomyia Series - Af, Au,
                                                                                              Darlingi Group – (1)
         Pa (1)
                                                      Or (121)
                                                                                              Lanei Group - (1)
   Bancroftii Group - Au/Or (2)
                                                Unassigned - Af, Au, Or (42)
                                                                                              Pictipennis Group – (2)
   Barbirostris Group - Or (16)
                                                Ardensis Group - Af (18)
                                                                                           Myzorhynchella Section – (6)
    Unassigned - (2)
                                                Kochi Group - Or (1)
     Barbirostris Subgroup – (9)
                                                Leucosphyrus Group - O (21)
                                                                                           Subgenus Stethomyia- Ne (5)
    Vanus Subgroup – (5)
                                                  Hackeri Subgroup – (5)
   Coustani Group - Af (9)
                                                  Leucosphyrus Subgroup - (13)
   Hyrcanus Group - Pa (26)
                                                  Riparis Subgroup - (3)
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Three new species of *Anopheles* were formally described and named while the book was in press: *An.* (*Anopheles*) vanderwulpi (= *An. barbirostris* clade II) [161]; *An.* (*Cellia*) amharicus (= *An. quadriannulatus* sp. B) and *An.* (*Cellia*) coluzzii (= molecular M form of *An. gambiae*) [162]. *Anopheles* (*Anopheles*) kunmingensis (Laticorn Section, Myzorhynchus Series, Hyrcanus Group) was inadvertently omitted from Appendix 2 during preparation of the chapter. Thus, the genus now includes 469 formally named species and 70 species that require formal Latin names.

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