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The classification of genus *Anopheles* (Diptera: Culicidae): a working hypothesis of phylogenetic relationships

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Abstract

The internal classification of genus *Anopheles* is updated to reflect taxonomic actions published since the classification was last reviewed in 1994. Both formal and informal taxa are included. The classification is intended to aid researchers and students who are interested in analysing species relationships, making group comparisons and testing phylogenetic hypotheses. The genus includes 444 formally named and 40 provisionally designated extant species divided between six subgenera: *Anopheles, Cellia, Kerteszia, Lophopodomyia, Nyssorhynchus* and *Stethomyia*. Subgenera *Anopheles, Cellia* and *Nyssorhynchus* are subdivided hierarchically into nested informal groups of morphologically similar species that are believed to represent monophyletic lineages based on morphological similarity. Changes to the classification include additional species, eliminated species and changes to the hierarchical organization and composition of supraspecific groups, some as a result of molecular studies.

Introduction

The internal classification of genus *Anopheles* Meigen compiled below is a revised, updated version of the classification that appeared in Harbach (1994). Its purpose is the same as before – to provide a foundation for critical studies of evolutionary relationships at specific and supraspecific levels of divergence. As such, the classification presented herein is a working hypothesis that requires further testing.

Anopheline systematics reached the apogee of classical morphological study some years ago and is now dominated by molecular genetic research, but this has had, for the most part, little impact on the internal classification of genus *Anopheles*. As noted by Krzywinski & Besansky (2003), ' ... despite efforts spanning a century, the present system of *Anopheles* classification remains largely untested for its accurate representation of *Anopheles* phylogeny.' With few exceptions (Foley *et al.*, 1998; Sallum *et al.*, 2000, 2002; Krzywinski *et al.*, 2001a,b), studies of evolutionary relationships have focused principally on major vectors of malaria and their closest relatives. Nevertheless, the results of these studies, coupled with the recognition of new species and taxonomic changes published since the classification of *Anopheles* was last reviewed (Harbach, 1994), justify the present paper.

Family Culicidae consists of two principal lineages that are recognized as subfamilies, the Anophelinae and Culicinae (Harbach & Kitching, 1998; Mitchell *et al.*, 2002). The traditional classification of subfamily Anophelinae includes three genera: *Anopheles* (cosmopolitan), *Bironella* Theobald (Australasian) and *Chagasia* Cruz (Neotropical). The majority of anopheline species belong to genus *Anopheles*, which is subdivided into the six subgenera noted above. Sallum *et al.* (2000) proposed synonymy of genus *Bironella* and subgenera *Lophopodomyia* and *Stethomyia* with subgenus *Anopheles* based on a cladistic analysis of morphological criteria, but this action is not accepted because it was put forth prematurely. As noted by Krzywinski & Besansky (2003), the relationships of these taxa hypothesized by Sallum *et al.* are based on homoplastic data and are incongruous with the results of molecular analyses (Besansky & Fahey, 1997; Foley *et al.*, 1998; Krzywinski *et al.*, 2001a,b; Sallum *et al.*, 2002) and

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morphological evidence that supports a sister-group relationship for *Anopheles* and *Bironella* (Harbach & Kitching, 1998). Notwithstanding some indication that subgenera *Anopheles* and *Cellia* may be paraphyletic (Foley *et al.*, 1998; Sallum *et al.*, 2002), the preponderance of available data supports the monophyletic origins of the six subgenera. Considering all lines of evidence, a working hypothesis of higher-level relationships suggests that the ancestral stock of *Anopheles* gave rise to *Stethomyia* and a lineage that subsequently evolved into two clades, one consisting of subgenera *Anopheles* + *Cellia* and the other comprising *Lophopodomyia* + (*Kerteszia* + *Nyssorhynchus*) (Krzywinski & Besansky, 2003).

Most phylogenetic studies of *Anopheles* mosquitoes conducted since the advent of molecular systematics involve lower levels of classification, principally species groups, subgroups and complexes (table 1) that include vectors of human malaria. Considering the taxonomic breadth of the genus, it is obvious that the evolutionary relationships of principal malaria vectors and their closest allies have received more attention than other groups of *Anopheles*. The results of the studies listed in table 1 need not be discussed in detail here since any taxonomic information they contain is noted in the classification detailed below. Most morphologically defined groups thus far studied have been shown to be monophyletic.

The discovery of new species, mainly sibling or cryptic species, seems to be on the increase as a result of DNA analyses (as indicated by the recent work of Cohuet *et al.*, 2003; Kengne *et al.*, 2003; Sedaghat *et al.*, 2003; Wilkerson *et al.*, 2004). The trend now is to develop molecular methods for species identification, which overshadows the need to train a new generation of morphological taxonomists. Ironically, the majority of anopheline species still require morphological identification to group or complex before molecular assays can be applied. The situation is perilous because most molecular systematists do not have the taxonomic expertise to accurately identify species, and the identification of species based on similarity to DNA sequences in GenBank is becoming increasingly common. This is problematical for several reasons. GenBank is an uncurated repository that includes data for a number of species that have been incorrectly identified, sequences of dubious quality, specimens of unknown origin, or a combination of these shortcomings. Additionally, sequences are often submitted for species for which there are no voucher specimens, no collection details, or other data, such as the name of the person who identified the specimens.

Table 1. Phylogenetic studies of *Anopheles* mosquitoes.

Group	Data set	Authors
Anophelinae	Morphology	Harbach & Kitching (1998); Sallum *et al.* (2000)
	DNA: *cyt b, ND5, D2*	Krzywinski *et al.* (2001a)
	ND5, D2, G6pd, white	Krzywinski *et al.* (2001b)
	COI, COII, D2	Sallum *et al.* (2002)
Genus *Anopheles*		
Subgenus *Anopheles*	DNA: *COII*	Foley *et al.* (1998)
Anopheles Series		
Maculipennis Group	Chromosomes	White (1978)
	DNA: *ITS2*	Linton (2004)*, Gordeev *et al.* (2004)
Maculipennis Subgroup	DNA: *ITS2*	Marinucci *et al.* (1999)
Freeborni and Quadrimaculatus Subgroups	DNA: *D2*	Porter & Collins (1996)
Myzorhynchus Series		
Hyrcanus Group	DNA: *ITS2*	Ma & Qu (2002)
Subgenus *Cellia*	Chromosomes	Green (1982); Pape (1992)
	DNA: *COII*	Foley *et al.* (1998)
Myzomyia Series	Chromosomes	Green (1982); Pape (1992)
	DNA: *COII, D3*	Chen *et al.* (2003)
Funestus Group	DNA: *COI, D3, ITS2*	Garros *et al.* (2004a,b)*
Minimus Subgroup	DNA: *COII, D3*	Sharpe *et al.* (2000)
Neocellia Series	Chromosomes	Green *et al.* (1985b)
Maculatus Group	DNA: *ITS2*	Ma *et al.* (2002)
Neomyzomyia Series		
Punctulatus Group	DNA: *ITS2*	Beebe *et al.* (1999)
Pyretophorus Series	Chromosomes	Pape (1992)
	DNA: *COII*	Foley *et al.* (1998)
	Morphology	Anthony *et al.* (1999)*
Gambiae Complex	Chromosomes	Coluzzi *et al.* (1979)
	rDNA, mtDNA	Besansky *et al.* (1994)
	mtDNA	Caccone *et al.* (1996)
Subgenus *Kerteszia*	Morphology	Collucci & Sallum (2003)
Subgenus *Nyssorhynchus*		
Albimanus Section	Morphology	Faran (1980)
Argyritarsis Section	Morphology	Linthicum (1988)

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* and *ND5* from mitochondrial DNA (mtDNA); *D2, D3* and *ITS2* from ribosomal DNA (rDNA); G_6pd and *white* from nuclear DNA.

Obviously, extreme caution must be exercised when GenBank sequences are used as a source of species identification (Linton *et al.*, 2002a; Harbach, 2003).

Little progress has been made in giving formal names to members of species complexes denoted by letter or number designations because 'sibling species pose an especially difficult problem for taxonomists. The process of establishing which available name may apply to a cryptic species is analogous to the identification of human remains by forensic anthropologists, which is sometimes an impossible task' (Harbach, 2003). It should be noted that in those few cases where members of species complexes have been given formal Latin names, notably species of the Nearctic Quadrimaculatus Complex of subgenus *Anopheles* (Reinert *et al.*, 1997) and the Australasian Farauti Complex of subgenus *Cellia* (Schmidt *et al.*, 2001, 2003), there were no junior synonyms of the nominotypical species to consider when naming the species. Obviously, molecular applications 'do not represent a substitute for morphological study because these techniques by themselves cannot be used to resolve formal taxonomic problems. The reason for this is that the entire faunal classification system is based on morphology and the type specimen concept. This does not preclude new species from being described and named on the basis of molecular or genetic data alone [for example see Sedaghat *et al.*, 2003]. It means, however, that the 'modern' techniques must be integrated with classical morphological analysis to determine the correct application of available names for species concepts previously based solely on anatomical characters' (Harbach, 2003).

At the end of July 2004, 444 formally named species and 40 unnamed members of species complexes were recognized as distinct morphological and/or genetic species of *Anopheles*. These species are divided between six subgenera, *Anopheles* (189 species), *Cellia* Theobald (239), *Kerteszia* Theobald (12), *Lophopodomyia* Antunes (6), *Nyssorhynchus* Blanchard (33) and *Stethomyia* Theobald (5). The three largest subgenera are further divided into hierarchical systems of informal taxonomic categories that include sections, series, groups, subgroups and complexes. The history, units and scheme of classification were reviewed in detail by Harbach (1994), and this information is not repeated here. As before, the informal categories of classification are given vernacular names that are printed in Roman type with the first letter capitalized even though the name of a nominal species or other formal taxon precedes the term (capitalized) denoting the level of classification, e.g. Maculipennis Group. Alternatively, in situations where this practice might be unacceptable, an italicized binomen or other scientific name should be used in combination with the term (not capitalized) denoting the level of classification, e.g. *Anopheles maculipennis* group and *Myzomyia* series. In the case of binomina, the generic name or its abbreviation should always be used in the combination as specific names normally should not stand alone.

As previously, taxa are arranged alphabetically within groups, and the groupings at each level of classification are believed to represent phylogenetically related assemblages of species based principally on morphological similarity. However, some groupings contain one or more species of uncertain relationship with members of subordinate groups. These species are listed before the subordinate groups as unassigned members of the higher taxon. The authorities who first introduced or most recently redefined the informal taxonomic groups are indicated by literature citations. References for species complexes are those that include the first mention or treatment of all the species currently recognized within the group.

Only extant species of *Anopheles* are included in the classification. Two described fossil species are omitted. *Anopheles rottensis* Statz from the upper Oligocene of Germany is only tentatively placed in genus *Anopheles* (Statz, 1944). *Anopheles* (*Nyssorhynchus*) *dominicanus* Zavortink & Poinar from Dominican amber is 'unquestionably an *Anopheles*', but its placement in subgenus *Nyssorhynchus* is uncertain (Zavortink & Poinar, 2000).

Changes to the classification

Taxonomic acts published since Harbach (1994) that impact on the classification of *Anopheles* include: (i) the recognition of new taxa and nominal species resurrected from synonymy; (ii) the elimination of species as a result of synonymy, species reduced to subspecies status and species recognized as *nomina dubia*; and (iii) changes to the makeup and structural hierarchy of informal supraspecific groups.

Species added to the classification

Thirty-one new species (23 formally named; eight informally designated) and five species resurrected from synonymy have been added to the classification, as follow.

albitarsis B, provisional designation by Wilkerson *et al.* (1995) (subgenus *Nyssorhynchus*, Argyritarsis Section, Albitarsis Series, Albitarsis Group)

auyantepuiensis Harbach & Navarro, 1996 (subgenus *Kerteszia*)

carnevalaei Brunhes, le Goff & Geoffroy, 1999 (subgenus *Cellia*, Neomyzomyia Series, Ardensis Group, Nili Complex)

comorensis Brunhes, le Goff & Geoffroy, 1997 (subgenus *Cellia*, Pyretophorus Series, Gambiae Complex)

costai Fonseca & Ramos, resurrected from synonymy with *mediopunctatus* (Lutz) by Sallum *et al.* (1999) (subgenus *Anopheles*, Laticorn Section, Arribalzagia Series)

crypticus Coetzee, 1995 (subgenus *Anopheles*, Laticorn Section, Myzorhynchus Series, Coustani Group)

daciae Linton, Nicolescu & Harbach, in Nicolescu *et al.* (2004) (subgenus *Anopheles*, Angusticorn Section, Maculipennis Group, Maculipennis Subgroup)

diluvialis Reinert, in Reinert *et al.* (1997) (subgenus *Anopheles*, Angusticorn Section, Maculipennis Group, Quadrimaculatus Subgroup)

dualaensis Brunhes, le Goff & Geoffroy, 1999 (subgenus *Cellia*, Neomyzomyia Series)

elegans sensu auctorum, new species recognized by Sallum *et al.* (2004) (subgenus *Cellia*, Neomyzomyia Series, Leucosphyrus Group, Hackeri Subgroup)

eouzani Brunhes, le Goff & Bousses, 2003 (subgenus *Cellia*, Neomyzomyia Series, Ardensis Group)

forattinii Wilkerson & Sallum, 1999 (subgenus *Anopheles*, Laticorn Section, Arribalzagia Series)

n. sp. near *gigas* (in Thailand), provisional designation by Rattanarithikul *et al.* (2004) (subgenus *Anopheles*, Anopheles Series, Lindesayi Group, Gigas Complex)

hailarensis Xu & Luo, 1998 (subgenus *Anopheles*, Laticorn Section, Myzorhynchus Series, Hyrcanus Group)

halophylus Silva do Nascimento & Lourenço-de-Oliveira, 2002 (subgenus *Nyssorhynchus*, Albimanus Section, Oswaldoi Series, Triannulatus Group)

hervyi Brunhes, le Goff & Geoffroy, 1999 (subgenus *Cellia*, Neocellia Series)
hinesorum Schmidt, 2001, in Schmidt *et al.*, 2001 (subgenus *Cellia*, Neomyzomyia Series, Punctulatus Group, Farauti Complex)
inundatus Reinert, in Reinert *et al.* (1997) (subgenus *Anopheles*, Angusticorn Section, Maculipennis Group, Quadrimaculatus Subgroup)
junlianensis Lei, 1996 (subgenus *Anopheles*, Laticorn Section, Myzorhynchus Series, Hyrcanus Group)
konderi Galvão & Damasceno, resurrected from synonymy with *oswaldoi* Peryassú by Flores-Mendoza *et al.* (2004) (subgenus *Nyssorhynchus*, Oswaldoi Series, Oswaldoi Group, Oswaldoi Subgroup)
maverlius Reinert, in Reinert *et al.* (1997) (subgenus *Anopheles*, Angusticorn Section, Maculipennis Group, Quadrimaculatus Subgroup)
minimus E, provisional designation by Somboon *et al.* (2001) (subgenus *Cellia*, Myzomyia Series, Minimus Group, Minimus Complex)
multicinctus Edwards, resurrected from synonymy with *natalensis* (Hill & Haydon) by Brunhes *et al.* (1998b) (subgenus *Cellia*, Neomyzomyia Series, Ardensis Group)
nimpe Nguyen, Tran & Harbach, in Nguyen *et al.* (2000) (subgenus *Anopheles*, Laticorn Section, Myzorhynchus Series, Hyrcanus Group)
nuneztovari A, provisional designation (Sierra *et al.*, 2004) (subgenus *Nyssorhynchus*, Oswaldoi Series, Oswaldoi Group, Oswaldoi Subgroup, Nuneztovari Complex)
okuensis Brunhes, le Goff & Geoffroy, 1997 (subgenus *Anopheles*, Laticorn Section, Christya Series)
ovengensis Awono-Ambene, Kengne, Simard, Antonio-Nikondjio & Fontenille, 2004 (subgenus *Cellia*, Neomyzia Series, Nili Group)
persiensis Linton, Sedaghat & Harbach, in Sedaghat *et al.* (2003) (subgenus *Anopheles*, Angusticorn Section, Maculipennis Group, Maculipennis Subgroup)
quadriannulatus B, provisional designation by Hunt *et al.*, 1998 (subgenus *Cellia*, Pyretophorus Series, Gambiae Complex)
rageaui Mattingly & Adam, resurrected from synonymy with *smithii* Theobald by Brunhes *et al.* (1999) (subgenus *Cellia*, Neomyzomyia Series, Smithii Group)
rivulorum-like species, provisional designation by Cohuet *et al.* (2003) (subgenus *Cellia*, Myzomyia Series, Funestus Group)
seretsei Abdulla-Khan, Coetzee & Hunt, 1998 (subgenus *Cellia*, Paramyzomyia Series, Listeri Group)
smaragdinus Reinert, in Reinert *et al.* (1997) (subgenus *Anopheles*, Angusticorn Section, Maculipennis Group, Quadrimaculatus Subgroup)
Sumatra species, provisional designation by Peyton (1990), subgenus *Cellia*, Neomyzomyia Series, Leucosphyrus Group, Hackeri Subgroup)
torresiensis Schmidt, in Schmidt *et al.*, 2001 (subgenus *Cellia*, Neomyzomyia Series, Punctulatus Group, Farauti Complex)
trinkae Faran, resurrected from synonymy with *dunhami* Causey by Lounibos *et al.* (1998) (subgenus *Nyssorhynchus*, Albimanus Section, Oswaldoi Series, Oswaldoi Group, Oswaldoi Subgroup)

Species removed from the classification

The following ten nominal species were eliminated from the classification for the reasons indicated.

anthropophagus Xu & Feng, synonymy with *lesteri* Baisas & Hu by Wilkerson *et al.* (2003) (from subgenus *Anopheles*, Laticorn Section, Hyrcanus Group)
arnoulti Grjebine, status changed to *nomen dubium* by Brunhes *et al.* (1998a) (from subgenus *Cellia*, Neomyzomyia Series, Smithii Group)
bervoetsi D'Haenans, to subspecies of *moucheti* Evans (Brunhes *et al.*, 1998b) (from subgenus *Cellia*, Myzomyia Series)
bonneorum Fonseca & Ramos (emended from *bonnei*), synonymy with *costai* Fonsca & Ramos by Sallum *et al.* (1999) (from subgenus *Anopheles*, Laticorn Section, Arribalzagia Series)
courdurieri Grjebine, status changed to *nomen dubium* by Brunhes *et al.* (1998a) (from subgenus *Cellia*, Paramyzomyia Series)
kunmingensis Dong & Wang, synonymy with *liangshanensis* Kang, Tan, Cao, Cheng Yang & Huang by Ma *et al.* (2000) (subgenus *Anopheles*, Laticorn Section, Myzorhynchus Series, Hyrcanus Group)
sicaulti Roubaud, synonymy with *labranchiae* Falleroni by de Zulueta *et al.* (1983) (subgenus *Anopheles*, Angusticorn Section, Anopheles Series, Maculipennis Group)
subalpinus Hackett & Lewis, synonymy with *melanoon* Hackett by Linton *et al.* (2002b) (subgenus *Anopheles*, Angusticorn Section, Anopheles Series, Maculipennis Group)
upemba Lips, status changed to *nomen dubium* by Brunhes *et al.* (1997) (from subgenus *Cellia*, Myzomyia Series, Marshallii Group)
yatsushiroensis Miyazaki, synonymy with *pullus* Yamada by Shin & Hong (2001) (subgenus *Anopheles*, Laticorn Section, Myzorhynchus Series, Hyrcanus Group)

Changes to taxonomic groups

Subgenus Anopheles, *Anopheles Series. Anopheles claviger* (Meigen) and *A. petragnani* del Vecchio, two unassigned members of the Anopheles Series of subgenus *Anopheles*, are recognized as sibling species that comprise the Claviger Complex (Coluzzi *et al.*, 1965). This complex was inadvertently omitted by Harbach (1994).

Rattanarithikul *et al.* (2004) removed *A. kyondawensis* Abraham from the Culiciformis Group and considered it an unassigned species of the Anopheles Series following the discovery of the previously unknown adult and pupal stages. These life stages exhibit unique anatomical features but also share characteristics with both the Aitkenii and Culiciformis Groups.

Subgenus Anopheles, *Anopheles Series, Maculipennis Group.* The classification of the Maculipennis Group is changed to reflect phylogenetic relationships based on the analysis of ITS2 sequence data presented during the 70th annual meeting of the American Mosquito Control Association (Linton, 2004; paper forthcoming). The data for 20 of the 23 recognized species confirm the monophyly of the group and place the Nearctic *A. atropos* Dyar & Knab in a basal relationship to the other species, which comprise three strongly supported clades: the Maculipennis, Quadrimaculatus and Freeborni Subgroups. The Maculipennis Subgroup consists of all Palaearctic members of the group except *A. beklemishevi* Stegnii & Kabanova (known previously as the Maculipennis Complex), the

Quadrimaculatus Subgroup includes *A. beklemishevi* and the five species previously known as the Quadrimaculatus Complex, and the Freeborni Subgroup includes *A. earlei* Vargas, *A. freeborni* Aitken, *A. hermsi* Barr & Guptavanij and *A. occidentalis* Dyar & Knab. The last group of species, along with *A. aztecus* Hoffmann and the former Quadrimaculatus Complex, comprised the previous Maculipennis Subgroup. *Anopheles atropos*, because of its ancestral relationship to the other species, and *A. walkeri* Theobald, because it was not included in Linton's analysis, are retained as unassigned members of the Maculipennis Group. Four museum specimens identified as *A. aztecus* Hoffmann yielded DNA segments corresponding to those of *A. quadrimaculatus* Say, thus raising the question of whether the specimens were misidentified or *A. aztecus* is merely a geographical form of the latter species. Since the status of *A. aztecus* is uncertain, this nominal species is also regarded as an unassigned member of the group pending further study. White (1978) pointed out that *A. lewisi* Ludlow might be the senior synonym of either *A. messeae* Falleroni or *A. beklemishevi*. Until the identity of this nominal species is resolved, it is unassigned to subgroup as well.

Subgenus Anopheles, *Anopheles Series, Punctipennis Group*. The faunal limit of the Crucians Complex was expanded to include all nominal and informally designated species of the Crucians Subgroup recognized by Wilkerson *et al.* (2004) based on incontrovertible rDNA ITS2 sequence data. Consequently, the Crucians Subgroup is no longer recognized in the hierarchical classification of the Punctipennis Group.

Subgenus Anopheles, *Lophoscelomyia Series, Asiaticus Group*. Rattanarithikul *et al.* (2004) recognized two subgroups within the Asiaticus Group for two species that occur in Thailand: the Asiaticus Subgroup for *A. asiaticus* Leicester and the Interrruptus Subgroup for *A. interruptus* Puri. This action leaves *A. annandalei* Prashad and *A. noniae* Reid as the only unassigned members of the Asiaticus Group. Reid (1968) indicated that the Asiaticus Group included two subgroups, but did not define or name them. It is unknown whether the subgroups recognized by Rattanarithikul *et al.* correspond to Reid's unnamed subgroups.

Subgenus Anopheles, *Myzorhynchus Series, Barbirostris Group*. *Anopheles freyi* Meng and *A. koreicus* Yamada & Watanabe were unassigned species within the Myzorhynchus Series of subgenus *Anopheles* until Lu *et al.* (1997) recognized them as members of the Barbirostris Group. Lu *et al.* did not indicate whether they should be placed in either the Barbirostris or Vanus Subgroup.

Subgenus Anopheles, *Myzorhynchus Series, Hyrcanus Group*. *Anopheles kiangsuensis* Xu & Feng, a previously unassigned species of the Hyrcanus Group, is placed in the Lesteri Subgroup based on the statement of Nguyen *et al.* (1993) that was overlooked by Harbach (1994). Nguyen *et al.* also placed *A. anthropophagus* Xu & Feng in the Lesteri Subgroup, but it is now recognized as a junior synonym of *A. lesteri* Baisas & Hu based on molecular evidence (Wilkerson *et al.*, 2003).

Subgenus Anopheles, *Myzorhynchus Series, Umbrosus Group*. In addition to the Letifer Subgroup (comprised of four species), Rattanarithikul *et al.* (2004) recognized three additional subgroups for three species of the Umbrosus Group that occur in Thailand: the Baezai Subgroup for *A. baezai* Gater, the Separatus Subgroup for *A. separatus* (Leicester) and the Umbrosus Subgroup for *A. umbrosus* (Theobald). Of the 12 species that comprise the Umbrosus Group, five remain unassigned to a subordinate taxon.

Subgenus Cellia, *Myzomyia Series*. Based on combined morphological and molecular studies and phylogenetic analyses, C. Garros, R. Harbach and S. Manguin (paper submitted, preliminary work reported by Garros *et al.*, 2004a,b) propose to unite the Funestus and Minimus Groups (*sensu* Harbach, 1994) into a composite Funestus Group consisting of five subgroups: the Aconitus, Culicifacies, Funestus, Minimus and Rivulorum Subgroups. The Culicifacies Subgroup replaces the Culicifacies Complex, which was previously an unassigned taxon within the Myzomyia Series. *Anopheles jeyporiensis* James, also previously unassigned to group, is now included as a species of uncertain affinity within the new Funestus Group. Rattanarithikul *et al.* (2004) recognized *A. culicifacies* (species B) and *A. jeyporiensis* (cytotypes A, B, C and D) in Thailand as species groups, without explanation, but in light of phylogenetic relationships elucidated by Garros *et al.* these taxa cannot be given group-level status. The Aconitus and Minimus Subgroups were established previously by Chen *et al.* (2003) and independently by Rattanarithikul *et al.* (2004) (as subgroups of the Minimus Group) for the same species included in these groups by Garros *et al.* (2004a,b).

Subgenus Cellia, *Neocellia Series*. *Anopheles jamesii* Theobald, *A. pseudojamesi* Strickland & Chowdhury and *A. splendidus* Koidzumi form a group-level taxon, the Jamesii Group (Rattanarithikul *et al.*, 2004). These three morphologically similar species were previously unassigned members of the Neocellia Series. Rattanarithikul & Green (1987), and many later authors, e.g. Baimai *et al.* (1993b) and Rattanarithikul *et al.* (2004), recognized *A. maculatus* and its closely allied species as a species group rather than a species complex. Since these species exhibit the same degree of morphological differentiation as members of the Annularis Group, they are recognized herein as having an equivalent rank within the Neocellia Series. Rattanarithikul *et al.* (2004) recognized two subgroups for five members of the Maculatus Group that occur in Thailand, the Maculatus and Sawadwongporni Subgroups. They regarded *A. pseudowillmori* (Theobald) and *A. willmori* (James) as unassigned species and did not indicate whether the two Philippine species, *A. dispar* Rattanarithikul & Harbach and *A. greeni* Rattanarithikul & Harbach should be included in one of the subgroups. Chromosomal and morphological data (Green *et al.*, 1985a; Rattanarithikul & Harbach, 1991) indicate that the Philippine species are quite distinct from the mainland members of the group. Consequently, these two species are not assigned to one or the other subgroup.

Subgenus Cellia, *Neomyzomyia Series*. Brunhes *et al.* (1998a) included *A. griveaudi* Grjbeine (formerly Demeilloni Group, Myzomyia Series) with members of the Ranci Group (Neomyzomyia Series) and grouped *A. grassei* Grjebine (formerly Smithii Group, Neomyzomyia Series) with members of the Pauliani Group (Neomyzomyia Series) without explanation. The Kochi Group is recognized for *A. kochi* Dönitz and the Tessellatus Group for *A. tessellatus*

Theobald. These species were previously regarded as unassigned members of the Neomyzomyia Series. Rattanarithikul *et al.* (2004) stated that '*Anopheles kochi* is the only member of this group found in Thailand', thus indicating that other unassigned species of the series also belong to the Kochi Group.

Subgenus Cellia, *Neomyzomyia Series, Leucosphyrus Group.* Peyton's (1990) classification of the Leucosphyrus Group included 14 formally named species, six unnamed species and two geographical forms divided between three subgroups, the Elegans, Leucosphyrus and Riparis Subgroups. Harbach (1994) inadvertently omitted the informally designated 'Sumatra species' from the group. Formal Latin names have been proposed for this and five other new species of the group (Sallum *et al.*, 2004), but because the manuscript by Sallum *et al.* is in press the names are not included herein to avoid the introduction of *nomina nuda.* These authors renamed the Elegans Subgroup as the Hackeri Subgroup because *A. elegans* (James) is synonymous with *A. dirus* species E of the Leucosphyrus Subgroup. They recognize the *A. elegans* of authors as a new species of the Hackeri Group.

Subgenus Cellia, *Paramyzomyia Series.* Sukowati *et al.* (1999) recognized that *A. sundaicus* (Rodenwaldt) is a complex of sibling species based on the reproductive isolation of three sympatric cytological forms in Sumatra and Java that were previously discovered and designated forms A, B and C by Sukowati & Baimai (1996). Linton *et al.* (2001) designated a neotype for *A. sundaicus* from Malaysian Borneo as a foundation for further studies of the complex. Studies of ITS2 rDNA and COI mtDNA sequences have shown that the species represented by the neotype is not the same as species A, B or C (Linton *et al.*, 2001; Dusfour *et al.*, 2004). Recently, Nanda *et al.* (2004) reported the existence of a unique chromosomal form of *A. sundaicus* on Car Nicobar Island, India, that is considered to be a 'geographically segregated population' that requires further study to establish its taxonomic status. Thus, the Sundaicus Complex as currently recognized includes four genetic species, *A. sundaicus* s.s. and *A. sundaicus* species A, B and C, and a cytogenetic variant that may prove to be a fifth species.

Subgenus Cellia, *Pyretophorus Series.* Two species groups recognized by Rattanarithikul *et al.* (2004) for members of the Pyretophorus Series are not included in the classification because they suggest evolutionary relationships that are not supported by cladistic analyses of the series based on morphological data (Anthony *et al.*, 1999). Rattanarithikul *et al.* recognized a Ludlowae Group for *A. sundaicus* (Rodenwaldt), and presumably also *A. ludlowae* (Theobald) as implied by the name of the group, and a Subpictus Group for *A. indefinitus* (Ludlow), *A. subpictus* Grassi and *A. vagus* Dönitz. The preferred cladogram of Anthony *et al.* (1999) shows that these species are interspersed within a single clade that includes all Old World members of the series.

Classification of genus *Anopheles*

Additional information is provided for certain taxa in the form of **Notes and comments** that follow the classification. References to **Notes and comments** are indicated in parentheses, e.g. **(see Note 1)**, after those taxa that require supplemental information.

Summary

Subgenus *Anopheles* (cosmopolitan; 189 species)
- Angusticorn Section (94 species)
  - Anopheles Series (Old and New World; 87 species)
  - Cycloleppteron Series (Neotropical; 2 species)
  - Lophoscelomyia Series (Oriental; 5 species)
- Laticorn Section (95 species)
  - Arribalzagia Series (Neotropical; 24 species)
  - Christya Series (Afrotropical; 2 species)
  - Myzorhynchus Series (Old World; 69 species)

Subgenus *Cellia* (Old World; 239 species)
- Cellia Series (Afrotropical; 8 species)
- Myzomyia Series (mainly Afrotropical, also Mediterranean and Oriental; 69 species)
- Neocellia Series (mainly Oriental, also Afrotropical; 33 species)
- Neomyzomyia Series (Afrotropical, Oriental, Australasian; 99 species)
- Paramyzomyia Series (mainly Mediterranean, also east African and north Indian; 6 species)
- Pyretophorus Series (Oriental, Afrotropical; 24 species)

Subgenus *Kerteszia* (Neotropical; 12 species)
Subgenus *Lophopodomyia* (Neotropical; 6 species)
Subgenus *Nyssorhynchus* (Neotropical; 33 species)
- Albimanus Section (19 species)
  - Albimanus Series (1 species)
  - Oswaldoi Series (18 species)
- Argyritarsis Section (10 species)
  - Albitarsis Series (5 species)
  - Argyritarsis Series (5 species)
- Myzorhynchella Section (4 species)

Subgenus *Stethomyia* (Neotropical; 5 species)

Subgenus *Anopheles* Meigen

Angusticorn Section (Reid & Knight, 1961)
- Anopheles Series (Edwards, 1932)
  - *algeriensis* Theobald
  - *concolor* Edwards
  - *kyondawensis* Abraham
  - *marteri* Senevet & Prunnelle
- Claviger Complex (Coluzzi *et al.*, 1965)
  - *claviger* (Meigen)
  - *petragnani* del Vecchio
- Alongensis Group (Phan *et al.*, 1991)
  - *alongensis* Venhuis
  - *cucphuongensis* Vu, Nguyen, Tran & Nguyen
- Aitkenii Group (Reid & Knight, 1961)
  - *aberrans* Harrison & Scanlon
  - *acaci* Baisas
  - *aitkenii* James
  - *bengalensis* Puri
  - *borneensis* McArthur
  - *fragilis* (Theobald)
  - *insulaeflorum* (Swellengrebel & Swellengrebel de Graaf)
  - *palmatus* (Rodenwaldt)
  - *peytoni* Kulasekera, Harrison & Amerasinghe
  - *pilinotum* Harrison & Scanlon
  - *pinjaurensis* Barraud

stricklandi Reid
tigertti Scanlon & Peyton
Atratipes Group (Lee *et al.*, 1987)
atratipes Skuse **(see Note 1)**
tasmaniensis Dobrotworsky
Culiciformis Group (Reid & Knight, 1961)
culiciformis Cogill
sintoni Puri
sintonoides Ho
Lindesayi Group (Reid & Knight, 1961)
Gigas Complex (Harrison *et al.*, 1991) **(see Note 2)**
baileyi Edwards
gigas Giles
gigas s.l. (in Thailand)
Lindesayi Complex (Harrison *et al.*, 1991)
lindesayi Giles
mengalangensis Ma
nilgiricus Christophers
wellingtonianus Alcock
Maculipennis Group (Reid & Knight, 1961)
atropos Dyar & Knab
aztecus Hoffmann
lewisi Ludlow
walkeri Theobald
Maculipennis Subgroup (Linton, 2004)
atroparvus van Thiel
daciae Linton, Nicolescu & Harbach
labranchiae Falleroni
maculipennis Meigen
martinius Shinagarev
melanoon Hackett
messeae Falleroni
persiensis Linton, Sedaghat & Harbach
sacharovi Favre
Quadrimaculatus Subgroup (Linton, 2004)
beklemishevi Stegnii & Kabanova
diluvialis Reinert
inundatus Reinert
maverlius Reinert
quadrimaculatus Say
smaragdinus Reinert
Freeborni Subgroup (Linton, 2004)
earlei Vargas
freeborni Aitken
hermsi Barr & Guptavanij
occidentalis Dyar & Knab
Plumbeus Group (Reid & Knight, 1961)
arboricola Zavortink
barberi Coquillett
barianensis James
fausti Vargas
judithae Zavortink
omorii Sakakibara
plumbeus Stephens
powderi Zavortink
xelajuensis de Leon
Pseudopunctipennis Group (Reid & Knight, 1961)
chiriquiensis Komp
eiseni Coquillett
franciscanus McCracken
hectoris Giaquinto-Mira
parapunctipennis Martini
pseudopunctipennis Theobald
tibiamaculatus (Neiva)
Punctipennis Group (Reid & Knight, 1961)
perplexens Ludlow
punctipennis (Say)
Crucians Complex (Wilkerson *et al.*, 2004)
bradleyi King
crucians Wiedemann (species A, B, C, D and E) **(see Note 3)**
georgianus King
Stigmaticus Group (Reid & Knight, 1961)
colledgei Marks
corethroides Theobald
papuensis Dobrotworsky
powelli Lee
pseudostigmaticus Dobrotworsky
stigmaticus Skuse
Cycloleppteron Series (Edwards, 1932)
annulipalpis Lynch Arribalzaga
grabhamii Theobald
Lophoscelomyia Series (Edwards, 1932)
bulkleyi Causey
Asiaticus Group (Reid, 1968)
annandalei Prashad
noniae Reid
Asiaticus Subgroup (Rattanarithikul *et al.*, 2004)
asiaticus Leicester
Interruptus Subgroup (Rattanarithikul *et al.*, 2004)
interruptus Puri
Laticorn Section (Reid & Knight, 1961)
Arribalzagia Series (Root, 1922)
anchietai Correa & Ramalho
apicimacula Dyar & Knab
bustamentei Galvão
calderoni Wilkerson
costai Fonseca & Ramos
evandroi da Costa Lima
fluminensis Root
forattinii Wilkerson & Sallum
gabaldoni Vargas
guarao Anduze & Capdevielle
intermedius (Peryassú)
maculipes (Theobald)
malefactor Dyar & Knab
mattogrossensis Lutz & Neiva
mediopunctatus (Lutz)
minor da Costa Lima
neomaculipalpus Curry
peryassui Dyar & Knab
pseudomaculipes (Peryassú)
punctimacula Dyar & Knab
rachoui Galvão
shannoni Davis
veruslanei Vargas
vestitipennis Dyar & Knab
Christya Series (Christophers, 1924)
implexus (Theobald)
okuensis Brunhes, le Goff & Geoffroy
Myzorhynchus Series (Edwards, 1932)
obscurus (Grünberg)
Albotaeniatus Group (Reid & Knight, 1961)
albotaeniatus (Theobald)
balerensis Mendoza
ejercitoi Mendoza
montanus Stanton & Hacker
saperoi Bohart & Ingram

Bancroftii Group (Reid & Knight, 1961)
bancroftii Giles
pseudobarbirostris Ludlow
Barbirostris Group (Reid & Knight, 1961)
freyi Meng
koreicus Yamada & Watanabe
Barbirostris Subgroup (Reid, 1968)
barbirostris van der Wulp **(see Note 4)**
campestris Reid
donaldi Reid
franciscoi Reid
hodgkini Reid
pollicaris Reid
Vanus Subgroup (Reid, 1968)
ahomi Chowdhury
barbumbrosus Strickland & Chowdhury
manalangi Mendoza
reidi Harrison
vanus Walker
Coustani Group (Reid & Knight, 1961)
caliginosus de Meillon
coustani Laveran
crypticus Coetzee
fuscicolor van Someren
namibiensis Coetzee
paludis Theobald
symesi Edwards
tenebrosus Dönitz
ziemanni Grünberg
Hyrcanus Group (Reid, 1953)
argyropus (Swellengrebel) **(see Note 5)**
chodukini Martini
changfus Ma
dazhaius Ma
engarensis Kanda & Oguma
hailarensis Xu & Luo
heiheenis Ma
hyrcanus (Pallas)
junlianensis Lei
kweiyangensis Yao & Wu
liangshanensis Kang, Tan, Cao, Cheng Yang & Huang
nimpe Nguyen, Tran & Harbach
pseudopictus Grassi
pullus Yamada
sinensis Wiedemann **(see Note 6)**
sineroides Yamada
xiaokuanus Ma
Lesteri Subgroup (Harrison, 1972)
crawfordi Reid **(see Note 7)**
kiangsuensis Xu & Feng
lesteri Baisas & Hu
paraliae Sandosham
peditaeniatus (Leicester)
vietnamensis Nguyen, Tran & Nguyen
Nigerrimus Subgroup (Harrison, 1972)
nigerrimus Giles **(see Note 8)**
nitidus Harrison, Scanlon & Reid
pseudosinensis Baisas
pursati Laveran
Umbrosus Group (Reid, 1950)
brevipalpis Roper
brevirostris Reid
hunteri (Strickland)
samarensis Rozeboom
similissimus Strickland & Chowdhury
Baezai Subgroup (Rattanarithikul *et al.*, 2004)
baezai Gater
Letifer Subgroup (Reid, 1968)
collessi Reid
letifer Sandosham
roperi Reid
whartoni Reid
Separatus Subgroup (Rattanarithikul *et al.*, 2004)
separatus (Leicester)
Umbrosus Subgroup (Rattanarithikul *et al.*, 2004)
umbrosus (Theobald)

Subgenus *Cellia* Theobald

Cellia Series (Christophers, 1924)
argenteolobatus (Gough)
brumpti Hamon & Rickenbach
cristipalpis Service
murphyi Gillies & de Meillon
pharoensis Theobald
swahilicus Gillies
Squamosus Group (Grjebine, 1966)
cydippis de Meillon
squamosus Theobald
Myzomyia Series (Christophers, 1924)
apoci Marsh
azaniae Bailly-Choumara
barberellus Evans
brunnipes (Theobald)
domicola Edwards
dthali Patton
erythraeus Corradetti
ethiopicus Gillies & Coetzee
flavicosta Edwards
fontinalis Gillies & de Meillon
longipalpis (Theobald)
majidi Young & Majid
moucheti Evans
schwetzi Evans
tchekedii de Meillon & Leeson
walravensi Edwards
Demeilloni Group (Gillies & de Meillon, 1968)
carteri Evans & de Meillon
demeilloni Evans
freetownensis Evans
garnhami Edwards
keniensis Evans
lloreti Gil Collado
sergentii (Theobald)
Funestus Group (Garros *et al.*, 2004a,b, unpublished data)
jeyporiensis James **(see Note 9)**
Aconitus Subgroup (Chen *et al.*, 2003)
aconitus Dönitz **(see Note 10)**
filipinae Manalang
mangyanus (Banks)
pampanai Büttiker & Beales
varuna Iyengar
Culicifacies Subgroup (Garros *et al.*, 2004a,b, unpublished data)

culicifacies Giles (species A, B, C, D and E) (Kar, 1999)
Funestus Subgroup (Garros *et al.*, 2004a,b, unpublished data)
aruni Sobti
confusus Evans & Leeson
funestus Giles
parensis Gillies
vaneedeni Gillies & Coetzee
Minimus Subgroup (Chen *et al.*, 2003)
flavirostris (Ludlow)
leesoni Evans
Fluviatilis Complex (Sarala *et al.*, 1994)
fluviatilis James (species T and U) **(see Note 11)**
Minimus Complex (Green *et al.*, 1990)
minimus Theobald (species A and C) **(see Note 12)**
minimus E (Somboon *et al.*, 2001)
Rivulorum Subgroup (Garros *et al.*, 2004a,b, unpublished data)
brucei Service
fuscivenosus Leeson
rivulorum Leeson
rivulorum-like species (Cohuet *et al.*, 2003)
Marshallii Group (Gillies & de Meillon, 1968)
austenii (Theobald)
berghei Vincke & Leleup
brohieri Edwards
gibbinsi Evans
hancocki Edwards
hargreavesi Evans
harperi Evans
mortiauxi Edwards
mousinhoi de Meillon & Pereira
njombiensis Peters
seydeli Edwards
Marshallii Complex (Gillies & Coetzee, 1987)
hughi Lambert & Coetzee
kosiensis Coetzee, Segerman & Hunt
letabensis Lambert & Coetzee
marshallii (Theobald) **(see Note 13)**
Wellcomei Group (Gillies & de Meillon, 1968)
distinctus (Newstead & Carter)
erepens Gillies
theileri Edwards
wellcomei Theobald
Neocellia Series (Christophers, 1924)
dancalicus Corradetti
hervyi Brunhes, le Goff & Geoffroy
karwari (James) **(see Note 14)**
maculipalpis Giles
moghulensis Christophers
paltrinierii Shidrawi & Gillies
pattoni Christophers
pretoriensis (Theobald)
pulcherrimus Theobald
rufipes (Gough)
salbaii Maffi & Coluzzi
stephensi Liston
superpictus Grassi
theobaldi Giles
Annularis Group (Reid, 1968)
annularis van der Wulp
pallidus Theobald
philippinensis Ludlow
schueffneri Stanton
Nivipes Complex (Green *et al.*, 1985b; Harrison *et al.*, 1991)
nivipes (Theobald) (2 cytogenetic species in Thailand)
Jamesii Group (Rattanarithikul *et al.*, 2004)
jamesii Theobald **(see Note 15)**
pseudojamesi Strickland & Chowdhury
splendidus Koidzumi
Maculatus Group (Rattanarithikul & Green, 1987) **(see Note 16)**
dispar Rattanarithikul & Harbach
greeni Rattanarithikul & Harbach
pseudowillmori (Theobald)
willmori (James)
Maculatus Subgroup (Rattanarithikul *et al.*, 2004)
dravidicus Christophers
maculatus Theobald
Sawadwongporni Subgroup (Rattanarithikul *et al.*, 2004)
notanandai Rattanarithikul & Green
sawadwongporni Rattanarithikul & Green
Neomyzomyia Series (Christophers, 1924)
amictus Edwards
annulatus de Rook
annulipes Walker (species A, B, C, D, E, F and G) (Booth & Bryan, 1986) **(see Note 17)**
aurirostris (Watson)
dualaensis Brunhes, le Goff & Geoffroy
hilli Woodhill & Lee
incognitus Brug
kolambuganensis Baisas
longirostris Brug
meraukensis Venhuis
novaguinensis Venhuis
saungi Colless
stookesi Colless
watsonii (Leicester)
Lungae Complex (Belkin, 1962)
lungae Belkin & Schlosser
nataliae Belkin
solomonis Belkin, Knight & Rozeboom
Ardensis Group (Gillies & de Meillon, 1968)
ardensis (Theobald)
buxtoni Service
cinctus (Newstead & Carter)
deemingi Service
dureni Edwards
kingi Christophers
machardyi Edwards
maliensis Bailly-Choumara & Adam
millecampsi Lips
multicinctus Edwards
natalensis (Hill & Haydon)
eouzani Brunhes, le Goff & Bousses
vernus Gillies & de Meillon
vinckei de Meillon
Nili Complex (Gillies & de Meillon, 1968) **(see Note 18)**
carnevalaei Brunhes, le Goff & Geoffroy
nili (Theobald)

ovengensis Awano-Ambene, Kengne, Simard, Antonio-Nkondjio & Fontenille
somalicus Rivola & Holstein
Kochi Group (Rattanarithikul *et al.*, 2004)
kochi Dönitz
Leucosphyrus Group (Reid, 1949)
Hackeri Subgroup (Sallum *et al.*, 2004)
elegans sensu auctorum
hackeri Edwards
pujutensis Colless
sulawesi Waktoedi
Sumatra species (Peyton, 1990)
Leucosphyrus Subgroup (Peyton, 1990)
baisasi Colless
Dirus Complex (Peyton & Ramalingam, 1988)
dirus Peyton & Harrison (species A)
dirus B, C and D
elegans (James) (species E)
nemophilous Peyton & Ramalingam
takasagoensis Morishita
Leucosphyrus Complex (Peyton, 1990)
balabacensis Baisas
introlatus Colless
leucosphyrus Dönitz (species A and B) (Baimai *et al.*, 1988)
Riparis Subgroup (Peyton, 1990)
cristatus King & Baisas
macarthuri Colless
riparis King & Baisas
Mascarensis Group (Harbach, 1994)
mascarensis de Meillon
Pauliani Group (Grjebine, 1966)
grassei Grjebine
grenieri Grjebine
milloti Grjebine & Lacan
pauliani Grjebine
radama de Meillon
Punctulatus Group (Schmidt *et al.*, 2001)
clowi Rozeboom & Knight
koliensis Owen
punctulatus Dönitz
rennellensis Taylor & Maffi
sp. near *punctulatus* (Foley *et al.*, 1995)
Farauti Complex (Schmidt *et al.*, 2003)
farauti Laveran
farauti 4, 5 and 6 (Foley *et al.*, 1993)
hinesorum Schmidt
irenicus Schmidt
torresiensis Schmidt
Ranci Group (Grjebine, 1966)
griveaudi Grjebine
Ranci Subgroup (Grjebine, 1966)
ranci Grjebine
Roubaudi Subgroup (Grjebine, 1966)
lacani Grjebine
notleyi van Someren
roubaudi Grjebine
Rhodesiensis Group (Gillies & de Meillon, 1968)
cameroni de Meillon & Evans
lounibosi Gillies & Coetzee
rhodesiensis Theobald
rodhaini Leleup & Lips
ruarinus Edwards
Smithii Group (Gillies & de Meillon, 1968)
caroni Adam
faini Leleup
hamoni Adam
jebudensis Froud
lovettae Evans
rageaui Mattingly & Adam
smithii Theobald
vanhoofi Manson & Lebied
wilsoni Evans
Tessellatus Group (Rattanarithikul *et al.*, 2004)
tessellatus Theobald
Paramyzomyia Series (Christophers & Barraud, 1931)
Cinereus Group (Gillies & de Meillon, 1968)
azevedoi Ribeiro
cinereus Theobald
turkhudi Liston
Listeri Group (Gillies & de Meillon, 1968)
listeri de Meillon
multicolor Cambouliu
seretsei Abdulla-Khan, Coetzee & Hunt
Pyretophorus Series (Edwards, 1932)
christyi (Newstead & Carter)
daudi Coluzzi **(see Note 19)**
indefinitus (Ludlow)
limosus King
litoralis King
ludlowae (Theobald)
parangensis (Ludlow)
vagus Dönitz **(see Note 20)**
Gambiae Complex (White, 1985)
arabiensis Patton
bwambae White
comorensis Brunhes, le Goff & Geoffroy
gambiae Giles
melas Theobald
merus Dönitz
quadriannulatus Theobald
quadriannulatus B (Hunt *et al.*, 1998)
Subpictus Complex (Suguna *et al.*, 1994)
subpictus Grassi (species A, B, C and D) **(see Note 21)**
Sundaicus Complex (Sukowati *et al.*, 1999)
sundaicus (Rodenwaldt)
sundaicus A, B and C

Subgenus *Kerteszia* Theobald

auyantepuiensis Harbach & Navarro
bambusicolus Komp
bellator Dyar & Knab
boliviensis (Theobald)
cruzii Dyar & Knab
gonzalezrinconesi Cova García, Pulido F. & Escalante de Ugueto
homunculus Komp
laneanus Correa & Cerqueira
lepidotus Zavortink
neivai Howard, Dyar & Knab
pholidotus Zavortink
rollai Cova García, Pulido F. & Escalante de Ugueto

Subgenus *Lophopodomyia* Antunes

gilesi (Peryassú)
gomezdelatorrei Levi-Castillo
oiketorakras Osorno-Mesa
pseudotibiamaculatus Galvão & Barretto
squamifemur Antunes
vargasi Gabaldón, Cova García & Lopez

Subgenus *Nyssorhynchus* Blanchard

Albimanus Section (Levi Castillo, 1949)
Albimanus Series (Faran, 1980)
albimanus Wiedemann
Oswaldoi Series (Faran, 1980)
Oswaldoi Group (Faran, 1980)
Oswaldoi Subgroup (Faran, 1980)
anomalophyllus Komp
aquasalis Curry
dunhami Causey
evansae (Brèthes)
galvaoi Causey
ininii Senevet & Abonnenc
konderi Galvão & Damasceno
oswaldoi (Peryassú) **(See Note 22)**
rangeli Gabaldón, Cova Garcia & Lopez
sanctielii Senevet & Abonnenc
trinkae Faran
Nuneztovari Complex (Conn *et al.*, 1993; Sierra *et al.*, 2004) **(see Note 23)**
nuneztovari Gabaldón (cytotypes B/C)
nuneztovari A
Strodei Subgroup (Faran, 1980)
benarrochi Gabaldón
rondoni (Neiva & Pinto)
strodei Root
Triannulatus Group (Faran, 1980)
halophylus Silva do Nascimento & Lourenço-de-Oliveira
triannulatus (Neiva & Pinto)
Argyritarsis Section (Levi Castillo, 1949)
Albitarsis Series (Linthicum, 1988)
Albitarsis Group (Linthicum, 1988)
albitarsis Lynch Arribalzaga
albitarsis B (Wilkerson *et al.*, 1995)
deaneorum Rosa-Freitas
marajoara Galvão & Damasceno
Braziliensis Group (Linthicum, 1988)
braziliensis (Chagas)
Argyritarsis Series (Linthicum, 1988)
Argyritarsis Group (Linthicum, 1988)
argyritarsis Robineau-Desvoidy
sawyeri Causey, Deane, Deane & Sampaio
Darlingi Group (Linthicum, 1988)
darlingi Root
Lanei Group (Linthicum, 1988)
lanei Galvão & Lane
Pictipennis Group (Linthicum, 1988)
pictipennis (Philippi)
Myzorhynchella Section (Peyton *et al.*, 1992)
antunesi Galvão & Amaral
lutzii Cruz
nigritarsis (Chagas)
parvus (Chagas)

Subgenus *Stethomyia* Theobald

acanthotorynus Komp
canorii Flock & Abonnenc
kompi Edwards
nimbus (Theobald)
thomasi Shannon

Notes and comments

1. Harrison & Scanlon (1975) suggested that *A. atratipes* belongs in the Stigmaticus Group.
2. Lu *et al.* (1997) included Harrison *et al.* (1991) in their list of literature cited, but did not mention this publication when they recognized the Gigas Complex as the '*An. gigas* group'. Inasmuch as Lu *et al.* treated *A. baileyi* as a subspecies of *A. gigas*, apparently without noticing that Harrison *et al.* had elevated it to species status, it makes no sense to recognize a single species (with its subspecies) as a species group.
3. Based on rDNA ITS2 sequence, the Crucians Complex includes *A. bradleyi* and five species provisionally designated as *A. crucians* A, B, C, D and E (Wilkerson *et al.*, 2004). It is not known which of the species bearing letter designations might be *A. crucians* s.s., *A. georgianus* or unnamed species. For this reason, *A. georgianus* is listed as a separate species of the complex although it may be conspecific with one of the unnamed species.
4. Four karyotypic forms of *A. barbirostris* (forms A, B, C and D) were reported by Baimai *et al.* (1995). Forms A, B and C are known from Thailand and form D occurs in Indonesia (Java). It is not known whether the forms in Thailand represent the same or different species. Form D, however, 'may represent ... a distinct species'.
5. Two karyotypic forms of *A. argyropus* (forms A and B) occur in Thailand (Baimai *et al.*, 1993a).
6. Two karyotypic forms of *A. sinensis* (forms A and B) occur in both Thailand and Taiwan (Baimai *et al.*, 1993a).
7. Two karyotypic forms of *A. crawfordi* (forms A and B) occur in Thailand (Baimai *et al.*, 1993a).
8. Baimai *et al.* (1993a) found two karyotypic forms of *A. nigerrimus* (forms A and B) in Thailand. Form A also occurs in Indonesia.
9. Four karyotypic forms of *A. jeyporiensis* (forms A, B, C and D) occur in Thailand (Baimai *et al.*, 1996a).
10. Three karyotypic forms of *A. aconitus* (forms A, B and C) occur in Thailand and a fourth (form D) occurs on the Indonesian island of Java (Baimai *et al.*, 1996a).
11. Sarala *et al.* (1994) originally recognized three species within *A. fluviatilis* (provisionally designated species S, T and U) based on the banding patterns of polytene chromosomes. Manonmani *et al.* (2001) developed a PCR assay from rDNA ITS2 sequence differences that identified two of these species, which in the absence of chromosomal data were referred to as species X and Y. In a follow-on study, Manonmani *et al.* (2003) correlated the results of chromosomally and PCR identified mosquitoes and showed that species X and Y correspond to species S and T, respectively. Comparison of nucleotide sequences in GenBank reveals that the conserved 28S unit of rDNA from species S (Singh *et al.*, 2004) is homologous with that of *A. minimus* C (Chen

Bin and C. Garros, independent personal communications). Furthermore, recent unpublished molecular studies involving samples of *A. fluviatilis* S from Orissa, India, where this taxon was originally discovered (Chen Bin, personal communication), reinforce the genetic homology of these two reputed species. Therefore, *A. fluviatilis* species S is conspecific with *A. minimus* species C (this taxon was named earlier than the former and is the senior synonym). Consequently, the Fluviatilis Complex includes only two species, species T and U.

12. Green *et al.* (1990) referred to the second species as 'species C' so it would not be confused with the 'form B' reported from Hainan Island by Yu & Li (1984) and Yu (1987). Chen *et al.* (2002) showed that form B is merely a morphological variant of species A.
13. Hunt & Coetzee (1991) provided cytogenetic evidence for two species of *A. marshallii*.
14. Three karyotypic forms of *A. karwari* (forms A, B and C) occur in Thailand (Baimai *et al.*, 1994).
15. Two karyotypic forms of *A. jamesii* (forms A and B) occur in Thailand (Baimai *et al.*, 1994).
16. Baimai (1989) and Baimai *et al.* (1993a) recognized three chromosomal forms of *A. maculatus* (B, E and K). Forms B and E are currently regarded as cytotypes of *A. maculatus*. As noted by Green *et al.* (1985a), either these forms are sibling species or they represent geographic variation within *A. maculatus*. In general, form B occurs through most of Thailand and is replaced by form E in southern Thailand and peninsular Malaysia. Cross-mating studies found no evidence of post-mating reproductive incompatibility between the two cytotypes (Baimai *et al.*, 1984). However, the fact that the two forms can be distinguished by their cuticular hydrocarbon profiles (Kittayapong *et al.*, 1990), which also provide indirect evidence for their sympatric occurrence in areas of peninsular Malaysia (Kittayapong *et al.*, 1993), suggests that they may be distinct species. Likewise, the morphological distinctions observed in form K suggest that it is also another species of the Maculatus Group.
17. Booth & Bryan (1986) presented evidence for three additional species within the Annulipes Complex, but these were not recognized with letter designations.
18. Kengne *et al.* (2003) and Awomo-Ambene *et al.* (2004) referred to the Nili Complex as the '*Anopheles nili* group' of species. This usage, denoting an assemblage of closely related species, unjustifiably recognizes a new group-level unit of classification that would prematurely exclude the Nili Complex from the Ardensis Group.
19. Colluzi (in Gillies & Coetzee, 1987) stated that he believed *A. daudi* is merely a 'melanic mutant of some member of the *gambiae* complex'.
20. Two karyotypic forms of *A. vagus* (forms A and B) occur in Thailand (Baimai *et al.*, 1996b).
21. Three karyotypic forms of *A. subpictus* (forms A, B, C and C) are known in Southeast Asia: form A occurs in Indonesia and the Philippines, form B occurs in Thailand, Indonesia and the Philippines, and forms C and D occur in Thailand (Baimai *et al.*, 1996b). It is not known whether any of these forms correspond with one or other of the four species that comprise the Subpictus Complex in India.
22. Sequence data for the second internal transcribed spacer (ITS2) of rDNA provide evidence that *A. oswaldoi* may be a species complex (Marrelli *et al.*, 1999).
23. Conn *et al.* (1993: p. 300) introduced the concept of a Nuneztovari Complex for three cytological forms, which they referred to as *A. nuneztovari* A, B and C. Whereas Harbach (1994) inferred that the letter designations connoted three cytogenetic species, it is clear that the authors used them to denote three distinctive cytotypes of a single species. Having said this, recent DNA studies indicate that cytotypes B and C in Venezuela and Colombia are merely cytological forms of a single species (Sierra *et al.*, 2004), which is genetically distinct from cytotype A and another form, probably a new species, in the Brazilian Amazon (Fritz *et al.*, 1994; Conn *et al.*, 1998).

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