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The insupportable validity of mosquito subspecies (Diptera: Culicidae) and their exclusion from culicid classification

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Abstract

Beginning about 80 years ago, the recognition of morphological varieties of mosquitoes was gradually replaced by the recognition of subspecies. As an examination of revisionary and detailed taxonomic studies of mosquitoes clearly shows, subspecies are untenable concepts which have been synonymized with nominotypical forms or recognized as distinct species. Thus, from our perspective, subspecies is not a functional or practical taxonomic rank. Consequently, in this study we critically assessed the taxonomic status of the 120 nominal taxa distinguished as subspecies before now to determine whether they should be recognized as separate species or synonymous names. As a result, 96 subspecies are formally elevated to specific rank, 22 are relegated to synonymy with nominotypical forms, one is considered a *nomen dubium*, one a *species inquirenda* and the names of four nominal species regarded as synonyms are revalidated. The subspecies and their new status are listed in a conspectus. The revalidated species include *Anopheles argentinus* (Brèthes, 1912), from synonymy with *An. pseudopunctipennis* Theobald, 1901c; *An. peruvianus* Tamayo, 1907, from synonymy with *An. pseudopunctipennis* as *nomen dubium*; *Culex major* Edwards, 1935, from synonymy with *Cx. annulioris consimilis* Newstead, 1907; and *Trichoprosopon trichorryes* (Dyar & Knab, 1907), from synonymy with *Tr. compressum* Lutz, 1905. Additionally, the type locality of *Anopheles sergentii* Theobald, 1907 is restricted to El Outaya, Biskra Province, Algeria. A complete list of species to be retained, added to or removed from the Encyclopedia of Life, with a few corrections, is provided.

Key words: classification, morphology, specific rank, synonymy, taxonomic status

Introduction

Theobald (1905a), *Genera Insectorum* Fascicule 26, recognized 464 species of Culicidae. In his fifth volume of *A monograph of the Culicidae or mosquitoes*, Theobald (1910) recognized about 1,050 species and 22 varieties. Slightly more than two decades later, Edwards (1932a), *Genera Insectorum* Fascicule 194, included 1,400 species and 135 varieties in his subfamily Culicinae, the present-day family Culicidae. It is interesting to note that the subspecies category was not recognized for mosquitoes until sometime after 1932.

In his book *Mosquitoes of the Ethiopian Region*, Edwards (1941) described "about 290 species, besides some 40 named subspecies and varieties." He went on to say "In the figures cited above, the word "about" is inserted advisedly, because the mosquitoes form no exception to the rule that the more intensively a group of animals is studied the more difficult it becomes to arrange in exact and satisfactory categories the various types of variation which are found to occur within the groups." After mentioning a number of examples, he stated the following.

> In allotting a status to the forms examined I have thought it best to regard as distinct species forms which differ sharply (even if slightly) in any one of their [life] stages and whose distribution is to a large extent coterminous, [examples]; if intermediates occur or if two forms which differ only slightly occupy different or but slightly overlapping territories [example] I have treated them as varieties or subspecies. It has been the prevalent custom among Dipterists to use the term "variety" in a rather vague and comprehensive sense to indicate any rank below that of species, but is seems desirable to make use of the term "subspecies" for geographically representative and slightly differing forms, leaving "variety" to indicate cases of bridged variation in one area or of colour variation induced by local differences in environment. One reason for making this distinction is that the code of zoological nomenclature lays down the principle that subspecific names have the same status as those of species and are subject to the priority rule, but makes no reference to names of lower categories, which therefore, it has been argued, have no status in nomenclature. Frequently, of course, the data at present available are insufficient to determine whether a given form should correctly be regarded as a species, subspecies or variety, and it may well be that changes in the status allotted to some of the forms described in this book will have to be made at a later date when more information is available.

Acting on provisions of the International *Code of Zoological Nomenclature* (Article 45.6.4), which prohibited the recognition of infrasubspecific taxa after 1961, Harbach & Howard (2007) reviewed the 30 varietal and two infrasubspecific forms of mosquitoes that were recognized at the end of 2006 to determine whether they should be considered as subspecies or infrasubspecific forms. Twenty-nine of the nominal varieties and the two infrasubspecific forms were deemed to be subspecies and one nominal variety was found to be unavailable as a species-group name (Article 45.4) and was excluded from the provisions of the *Code* (Article 1.3.4). Disregarding nominotypical subspecies, the addition of the 31 subspecific forms resulted in the formal recognition of 130 nominal subspecies (incorrectly denoted as 134 in Harbach 2018). Taking into account the number of subspecies that were either synonymized with nominotypical forms or recognized as distinct species before (but overlooked) and after Harbach (2018) and Wilkerson *et al*. (2021) (see below), the number of formally recognized subspecies decreased to the 120 subspecies that are assessed herein to determine whether they should be recognized as separate species or synonyms of the nominotypical forms. *Anopheles aitkenii britanniae* Strickland & Chowdhury, 1931, elevated to subspecific status by Harbach (2018), is dealt with separately. For perspective, the 120 subspecies are constituents of 91 currently recognized species, 50 of which have one or more synonyms, a total of 193 synonymous nominal forms (not including names replaced due to homonymy).

The subspecies category has not been universally accepted among mosquito taxonomists. Belkin (1962), in his masterful treatment of the mosquitoes of the South Pacific, bluntly stated that "It may come as a shock to some readers that no subspecies are recognized in this work", and listed four reasons for treating species as the basic taxonomic unit in his study, the most important being "It seems doubtful that subspecies in the classical sense exist in mosquitoes". Colless (1976) made it clear that "Whatever one's views, there is little reason for holding two taxa at subspecies rank if they coexist in the same area, at the same time, without any signs of intergradation". To this it must be added, paraphrasing Belkin, that a basic criterion for determining a taxonomic species should include the constancy of correlated morphological characters. In partial contradiction to Colless, there are many examples where the identity of closely related species is maintained in the face of unambiguous evidence of introgression (gene flow) between incompletely separated species (see below). As Harbach (1988) explained in his treatise on the subgenus *Culex* in southwestern Asia and Egypt, "The species is the taxonomic unit of primary importance…. No subspecies are recognized in this work. Subspecies are largely meaningless biological concepts which have little recognition in modern culicid taxonomy. Most recent workers have either synonymized subspecific names with specific epithets or recognized them for distinct biological species." In the words of the late F. Christian Thompson, formerly of the USDA Systematic Entomology Laboratory located at the Smithsonian National Museum of Natural History in Washington, D.C., "[A subspecies] is not a valid scientific category as it has no real biological/phylogenetic meaning. It is merely a phenetic concept. That was first documented more than a half century ago by Bill Brown and EO Wilson and subsequently supported by numerous other workers." (quoted in Harbach 2012).

In accord with the above researchers, we contend that subspecies are not real or useful taxonomic designations. Furthermore, we agree with Burbrink *et al*. (2022) that the recognition of subspecies is unjustifiable for philosophical, biological and operational reasons, *i.e.* it is indefensible (philosophically) "to accept the existence of subspecies as ontologically distinct entities within a species", (biologically) "to recognize subspecies as arbitrary divisions of clines when such units lack an evolutionary basis and phylogenetic diagnosis" and (operationally) "to use the subspecies category as a pragmatic tool to advance aims such as field guide identifications or conservation policy and management." To corroborate what was mentioned above, Padial & De la Riva (2021) pointed out that recognition of species as phylogenetic lineages has contributed to the elevation of subspecies to species or their rejection as separate taxa. They reviewed the options for retaining subspecies and for practical reasons advocated that biological classification "should emphasise species and reduce the use of subspecies to avoid preserving arbitrary partitions of continuous variation". They also aptly noted that many binomial taxa represent species complexes rather than individual species, which has become increasingly obvious among mosquitoes (see for example the recent discovery of many species complexes in the subgenus of *Kerteszia* Theobald, 1905e of *Anopheles* Meigen, 1818 by Bourke *et al*. 2023).

For practical purposes, we follow herein the definitions of species and subspecies of de Queiroz (1998, 1999, 2005a, 2005b, 2007, 2020, 2021). De Queiroz (2007) reviewed a majority of the species concepts in use and created a rationale for joining those ideas into a "unified species concept". He stated that "Alternative species concepts agree in treating existence as a separately evolving metapopulation lineage as the primary defining property of the species category, but they disagree in adopting different properties acquired by lineages during the course of divergence, e.g. intrinsic reproductive isolation, diagnosability and monophyly, as secondary defining properties (secondary species criteria). A unified species concept can be achieved by treating existence as a separately evolving metapopulation lineage as the **only** [emphasis ours] necessary property of species and the former secondary species criteria as different lines of evidence (operational criteria) relevant to assessing lineage separation." These processes can be uneven genetically, morphologically, behaviorally and spatially. At one end of the spectrum of species definitions, some researchers (*e.g.* Mayr 1942; Dobzhansky 1950, 1970) required "Intrinsic reproductive isolation (absence of interbreeding between heterospecific organisms based on intrinsic properties, as opposed to extrinsic [geographic] barriers)" (de Queiroz 2007: table 1). The absence, or near absence, of interbreeding is not a necessary attribute for an organism to be considered a species according to the unified species concept. This frees us to consider the full spectrum of possible degrees of divergence to define species.

A logical extension of the unified species concept is consideration of how subspecies are defined. In a recent discussion of incompletely separated lineages of copperhead and cottonmouth snakes, de Queiroz (2020, 2021) applied the unified species concept to the subspecies category. The following summarizes his concept of subspecies (de Queiroz 2020).

> …The point I want to make here is that to be consistent with a modern evolutionary concept of species, the concept of subspecies must be modified so that it is no longer considered a distinct category from that of species. Subspecies are entities of the same fundamental kind as species: they are both population-level lineages. In other words, subspecies **are** [emphasis ours] species... it makes sense to conceptualize subspecies as incompletely separated species (lineages) within a more inclusive species (lineage).
>
> ...Second, under the definition of subspecies as incompletely separated species (lineages) within a more inclusive species (lineage), the subspecies category is no longer being treated as a taxonomic rank and especially not as one indicating something less than a species.... That some species (lineages) are incompletely separated from others is simply a biological fact; it should not be taken to mean that they are anything less than "full" or "good" species (lineages). Related to this point, my proposal also does not depend on the ultimate fate of incompletely separated lineages—that is, whether they subsequently fuse into a single lineage without detectable sublineages, remain partially separated long-term, or eventually become completely separated.
>
> ...*subspecies are incompletely separated lineages within a more inclusive lineage* (note that this definition makes no reference to a taxonomic rank). More precisely, subspecies are not members of a separate and subordinate category relative to species... instead, subspecies are members of the same category as species that are nested within other members of that category.... Trinomials are no longer indicative of the rank of subspecies (because the subspecies category is not a taxonomic rank). Instead, trinomials are simply a representational device that can (but need not) be used to indicate the nesting of incompletely separated lineages within a more inclusive lineage.
>
> ...**Conceptualizing subspecies as incompletely separated species requires that any hypothesized subspecies be supported by the same kinds of evidence that would be required to infer that an entity is a species, as well as evidence that its separation from one or more other species is incomplete** [emphasis ours].

For clarity, we fully agree that in some cases subspecies, given supportive evidence, should be treated as incompletely separated species, indicated as binomina rather than trinomina. Alternatively, available evidence, *e.g.* morphological and genetic distinctions or no evidence of intermixing or hybridization, often indicates that nominal subspecies are completely separated species (see Material and Methods). The bottom line is that subspecies are either species or synonyms of a species. It should be borne in mind that species are hypotheses, which can be tested and modified if proven to be incorrect.

Material and Methods

Original descriptions and all pertinent information available for 91 species (nominotypical forms) and their nominal subspecies (120) were critically examined. Synonyms of the nominal taxa (193 in total) were also examined—most of them are retained as currently assigned but certain ones are treated in more detail where necessary. No mention of synonyms for a specific taxon indicates that it has no synonymous nominal taxa. Type localities, where mentioned, include the present-day names of geographical localities.

Four criteria, gleaned from the sources cited above, are used to consider subspecies as either synonyms or species, summarized as follow.

1. If a subspecies has an allopatric distribution, it is considered a species. As distribution is based on where collectors encountered the taxon rather than where it may occur, this criterion is a bit problematic unless supported by some degree of morphological or genetic distinction.

2. If a subspecies is partially or largely sympatric with the nominotypical form but bears morphological differences in the absence of clinal variation, then it is a species.
3. If a subspecies and the nominotypical form are distinct outside a zone of introgression, indicating that species-specific traits are being selected outside the zone, this is evidence for independent species cohesion, and the two forms are incompletely separated species.
4. If a subspecies does not fit criterion 1, 2 or 3, then it is a synonym of the nominotypical form.

Based on information available in the mosquito literature, only three of de Queiroz's "secondary species criteria", *i.e.* isolation, ecological and diagnosable, are relevant to the issue of species versus synonymy for mosquito subspecies. In most cases, there is little if any specific ecological (*i.e.* different niche or adaptive zone) information for most mosquito subspecies. So, isolation and diagnosability (criteria 1 and 2, respectively) are the two criteria that are applicable in most cases for deciding whether a subspecies is a species or a synonym.

It should be noted that some of the distributions of nominotypical subspecies that are taken from Wilkerson *et al*. (2021) include countries from which the other subspecies have been recorded, and in many cases the type form has not been recorded in those countries. For the most part we have not altered the distributions listed by Wilkerson *et al.*, which for the most part represent the distributions of the species as a whole, *i.e.* the country records for the nominotypical and purported subspecific forms of the species. It is unfortunate that catalogs and some other works give the impression that species include subspecies without indicating in those cases that the nominotypical form is also a subspecies.

The abbreviations used herein for genera and subgenera are taken from Wilkerson *et al*. (2015). The morphological terminology standardized by Harbach & Knight (1980, 1982) and the wing spot terminology established by Wilkerson & Peyton (1990) are used or referred to for clarity.

Status of Subspecies—Species or Synonyms

As indicated in the Introduction, the taxonomic status of 13 nominal taxa was changed either before or after they were listed as subspecies in the reference works of Harbach (2018) and Wilkerson *et al*. (2021). These taxa require no further attention, but it seems advisable to list them here to indicate their current status and source of taxonomic treatment. A fourteenth nominal taxon, *britanniae* Strickland & Chowdhury, 1931, listed as a subspecies by Harbach and Wilkerson *et al*. is also dealt with here.

Aedes (*Hulecoeteomyia*) *japonicus amamiensis* Tanaka, Mizusawa & Saugstad, 1979, *Ae*. (*Hul*.) *japonicus shintienensis* Tsai & Lien, 1950 and *Ae*. (*Hul*.) *japonicus yaeyamensis* Tanaka, Mizusawa & Saugstad, 1979, to specific rank by Wilkerson *et al*. (2022).

Anopheles (*Anopheles*) *gigas simlensis* (James, 1911) (in James & Liston, 1911), to specific rank by Somboon *et al*. (2020b).

Anopheles (*Ano.*) *lindesayi benguetensis* King, 1931, *An.* (*Ano.*) *lindesayi cameronensis* Edwards, 1929b, *An.* (*Ano.*) *lindesayi japonicus* Yamada, 1918 and *An.* (*Ano.*) *lindesayi pleccau* Koidzumi, 1924, to specific rank by Namgay *et al*. (2020).

Eretmapodites plioleucus brevis Edwards, 1941, to specific rank by da Cunha Ramos *et al*. (1992).

Tripteroides (*Tripteroides*) *bambusa yaeyamensis* Tanaka, Mizusawa & Saugstad, 1979, to specific rank by Toma *et al*. (2019).

Aedes (*Stegomyia*) *mediopunctatus sureilensis* Barraud, 1934, synonymy with the nominotypical form by Huang (1977).

An. (*Ano.*) *saperoi ohamai* Ohama, 1947, synonymy with the nominotypical form by Higa *et al*. (1998).

Armigeres (*Armigeres*) *subalbatus chrysocorporis* Hsieh & Liao, 1956, synonymy with the nominotypical form by Lu *et al*. (1997).

The first 10 nominal taxa are currently listed as species in the Encyclopedia of Life; the last three, being synonymous names, need to be removed from the lists of recognized species.

Anopheles (*Ano.*) *aitkenii britanniae* Strickland & Chowdhury, 1931, as listed in Harbach (2018) and Wilkerson *et al*. (2021), requires explanation. The name *britanniae*, in the original combination *Anopheles* (*Anopheles*) *aitkenii* var. *britanniae*, was considered a *nomen nudum* by Stone *et al.* (1959) and Knight & Stone (1977) (misspelled or emended by them as *brittaniae*). This status was overlooked by Harbach (2018), who recognized the variety as a subspecies of *An*. (*Ano.*) *aitkenii* James, 1903 (in Theobald 1903a) per Article 45.6.4 of the *International Code of Zoological Nomenclature*. Wilkerson *et al.* (2021) continued to consider *britanniae* as a subspecies. Other than Senevet (1958), nominal *britanniae* has not otherwise appeared in the literature, including in comprehensive discussions of the Aitkenii Group (Reid & Knight 1961) by Reid (1968), Harrison & Scanlon (1975), Lee *et al.* (1987) and Harrison *et al.* (1991). We agree with Stone *et al*. (1959) and Knight & Stone (1977) that *britanniae* is a *nomen nudum*. Rationale for this status was not articulated by those authors but we note that the original description is exceptionally brief with the only distinguishing character being a slight difference in the branching of larval seta 3-C. No locality information was given and no exemplar specimens were mentioned, *i.e.* no type specimens or potential type specimens exist.

Disregarding nominotypical forms, the 120 subspecific taxa noted above have been treated as morphological forms of 91 formally recognized species. Those species are listed below in alphabetical order from genus, subgenus, species and subspecies. In essence, the analysis of each species/subspecies taxon was the subject of a separate, in-depth study.

***Aedes* (*Aedimorphus*) *abnormalis* (Theobald)**

subspecies ***abnormalis*** (Theobald, 1909)—original combination: *Bathosomyia abnormalis*. Distribution: Burkina Faso, Central African Republic, Côte d'Ivoire, Ghana, Nigeria, Senegal (Wilkerson *et al*. 2021).

subspecies ***kabwachensis*** Edwards, 1941—original combination: *Aedes* (*Aedimorphus*) *abnormalis* ssp. *kabwachensis*. Distribution: Kenya, Uganda (Wilkerson *et al*. 2021).

Theobald (1909, 1910) described *abnormalis* as the only species in his new genus *Bathosomyia*. The description was based on two males, one unlabelled. Townsend (1990) wrote: "Syntype—Ghana: 1 male [poor condition], Ashanati, Obuasi." A drawing of a slide-mounted clasper [gonostylus] accompanies the description. The male genitalia were remounted by Edwards (1917), who illustrated the opposite side of the Theobald-illustrated structure. Some selected characters for the genus follow. "Head with loose flat scales, except for a few small narrow curved ones in the middle at the base." "Thorax with rather large narrow-curved scales, also the scutellum…." "Male clasper swollen and with large spines and one large apical curved spine. *First posterior cell* [cell R_5] *almost uniform in breath* [emphasis by Theobald]. …this presents a very marked genus on account of the squamose characters of the head, the marked first posterior cell, and the peculiar claspers to the male genitalia." Additional selected characters in the species description Include: "Abdomen brown with basal creamy bands broadened in the middle. Legs uniformly brown, hind tibiae with pale apex." In the male: "Thorax deep brown, clothed with rather large pale creamy narrow-curved scales and brown chaetae [setae]; scutellum ochreous brown with narrow-curved pale creamy scales. …Clasper of genitalia very marked, broadly expanded apically with several large spines and one large curved broad spine at apex. …The genitalia are very peculiar, and the general pale scaled head and thorax, and the large pale basal abdominal patches, should at once separate it."

To our knowledge, the nominotypical subspecies remains known only from those two males. Hopkins (1952) described the larva of *abnormalis* and included it in a key, but his observations were based on larval exuviae of paratypes of subspecies *kabwachensis*. There have been a number of virus isolations from *Ae. abnormalis sensu lato* but no mention has been made about how identifications were carried out (Worth & de Meillon 1960; Mutebi *et al*. 2012).

Edwards (1941) described subspecies *kabwachensis* based on reared specimens from Kabwach, Kenya. He designated a male as the holotype and provided brief descriptions of the male, female and pupa. Hopkins (1952), as noted above, described the larva as *Ae. abnormalis*. Townsend (1990) wrote [square brackets from original]: "***kabwachensis*** Edwards, 1941: 181–182, 395, 432 (*Aedes (Aedimorphus) abnormalis* subsp.). Holotype male [P & L skins on slide]—Kenya: [Kavirondoj], Kabwach Forest, [Kisii]. Paratypes (7)—Kenya: 7 female. …Edwards labelled the male as holotype, but the label was obscured beneath the locality label. Mattingly's (1956b: 38–39) lectotype designation is therefore invalid. I have removed Mattingly's and Edwards' labels and replaced them with a standard BMNH 'holotype' label. The genitalia of paratypes on two pinned mounts are supernumerary to pinned series."

The hindfemora of subspecies *kabwachensis* and *abnormalis* lack an apical pale spot. The two differ in that *abnormalis* has all three scutellar lobes with narrow scales whereas *kabwachensis* has broad scales on the lateral lobes and narrow scales on the middle lobe; and the vertex of *abnormalis* has mostly broad decumbent scales, while *kabwachensis* has the vertex with mostly narrow decumbent scales. Since the female of *abnormalis* is not known it is possible that these differences are due to sexual dimorphism.

Edwards (1941) redescribed the male genitalia of *abnormalis* as follows: "Style [gonostylus] with slender stem and greatly expanded distal portion, with a fairly long horn [gonostylar claw], a row of five sharp-pointed spines on the terminal margin, and a stronger spine adjacent to which is a small pubescent point, lower part of expanded portion bare; coxite [gonocoxite] broad in middle." For *kabwachensis*: "almost as in the type of *A. abnormalis*, the only obvious difference being in the shape of the expanded portion of the style." The drawings provided by Edwards (fig. 52a, type form; fig. 52c, *kabwachensis*) show that the shape of the apical structures of the gonostylus of both are similar, as described. The stem [stalk, basal portion of the gonostylus] of the type form, however, appears much narrower than for *kabwachensis*, and the median expansion of the gonocoxite is broader and more rounded in *kabwachensis* than in the type form. Although not discussed, it appears to us from the drawings that the basal piece of the phallosome is much narrower and almost pointed in the type form, broader in *kabwachensis*, and tergum IX of the type form is concave posteriorly while in *kabwachensis* it is narrowed anteriorly and posteriorly. Other features shown in the illustrations of the male genitalia are not distinct enough for comparison.

It is not clear, except for similar adult morphology, why Edwards thought the two forms should be subspecies rather than full species. There is immense geographical distance between the two forms, type form from far western Africa, *kabwachensis* from eastern Africa. This of course could be an artefact of so few specimens available for study. For comparisons, only the males are known for both. The larval and pupal exuviae of the holotype and paratypes of *kabwachensis* exist but only the male has been described in any detail. However, we think the few characters that separate males of the two forms are significant and indicate two genetically independent species. For this reason, we hereby elevate *kabwachensis* to species status: ***Aedes* (*Aedimorphus*) *kabwachensis* Edwards, 1941**. *Aedes kabwachensis* is currently listed as a species in the Encyclopedia of Life.

As an aside, Wigglesworth (1929), accepting the identification by Edwards, described and illustrated the larva and pupa of what they both thought was *abnormalis,* but which later was recognized by Edwards as a misidentification of a new species, which he named *Aedes* (*Aedimorphus*) *wigglesworthi* Edwards, 1941. No subsequent taxonomic catalog has recognized the misidentification or that Wigglesworth (1929) was the source of the description of the species named in his honor.

Aedes (*Aedimorphus*) *cumminsii* (Theobald)

subspecies ***cumminsii*** (Theobald, 1903a)—original combination: *Culex cumminsii*. Distribution: Angola, Benin, Burkina Faso, Cameroon, Central African Republic, Côte d'Ivoire, Democratic Republic of the Congo, Ethiopia, Ghana, Kenya, Liberia, Mali, Mozambique, Nigeria, Senegal, Sierra Leone, South Africa, South Sudan, Sudan, Uganda, Zambia (Wilkerson *et al*. 2021).

subspecies ***mesostictus*** Harbach, 2018—original combination: *Aedes* (*Aedimorphus*) *mesostictus* [*nomen novum* for *mediopunctata* Theobald, 1909; formerly *Aedes cumminsii mediopunctatus* (Theobald, 1909); subspecific status by Harbach & Howard, 2007]. Distribution: Ghana, Nigeria (Wilkerson *et al*. 2021).

The taxa under review here are placed in the *Aedes* (*Aedimorphus*) *dentatus* group of Edwards (1941) and McIntosh (1975), which also includes *bevisi* (Edwards, 1915), *dentatus* (Theobald, 1904), *holocinctus* Edwards, 1941, *pachyurus* Edwards, 1936 and *subdentatus* Edwards, 1936. According to McIntosh (1975) the *dentatus* group is "Similar to *leesoni* group except: scutellar scales always narrow; hind posttarsal claws armed; basal mesal lobe well developed; gonostylus expanding gradually towards apex and therefore without a contrastingly narrow arm; a single strong gonostylar claw present; comb with spines." We think the similarities in the male genitalia of these species, especially the form of the gonostylus, are evidence of a monophyletic ("natural") grouping.

The nominotypical form was described from a single female, "perfect except for the ends of the hindlegs", collected in Bahr-el-Ghazal, Central Africa [north-central South Sudan]. Theobald (1903a) wrote that "It is a large and handsome species, unlike anything I have seen from Africa." He illustrated the head, a prothoracic lobe and anterior-most part of the scutum. Selected portions of the description follow: "Head deep brown, with narrow-curved, pale golden scales and numerous long, black, upright forked scales, and small, flat, paler scales at the sides; palpi and proboscis deep brown, covered with blackish-brown scales… clypeus deep brown; antennae deep brown, with pale pubescence and deep brown verticillate hairs, basal joint testaceous, with a few pale scales, second joint also testaceous at the base, with a few pale scales on the inside…. Thorax deep rich brown, covered with narrow, hair-like, curved golden scales, with two small patches just in front of the scutellum; scutellum pale brown, with narrow-curved, creamy scales… pleurae brown… with numerous flat creamy-white scales…. Abdomen deep brown, unbanded, with large basal, white, lateral spots… venter paler than the dorsum, with ochraceous hue, with pale creamy scales and the apical borders of the segments dark. Legs deep brown, coxae brown, base and venter of femora pale…. Halteres pallid."

The synonym of *cumminsii*, *Culicada fuscopalpalis* Theobald, 1909, along with subspecies *mesostictus* Harbach (as *Culicada mediopunctata* Theobald, 1909) were described from Obuasi [Ashanti Region, Ghana]; *fuscopalpalis* from a single male and *mediopunctata* from a single female. In general, both seem similar to *cumminsii*, but there is no mention by Theobald of resemblance to either. Synonym *fuscopalpalis* has the "Abdomen deep brown with black scales and basal bands of creamy scales, long golden brown lateral hairs [setae]; venter pale ochreous with narrow black apical bands… a yellow spot at the apex of the hind tibiae…. This well-marked Culicada [*sic*] can at once be told by the male claspers…. No ♀ was found in the collection." If it becomes a valid name, since this describes a male, characters of a corresponding female could differ. Subspecies *mesostictus* (= *mediopunctata*) has "a dense bright golden border of scales around the eyes…. Abdomen deep blackish-brown, almost black, the segments, except the basal one, with median basal dull-white patches; border bristles [setae] golden; laterally are pale creamy basal lateral patches; venter yellow scaled, except at the apex, where they are creamy, each segment with a narrow dark scaled apical border… apex of hind tibiae with a prominent white band…. Halteres with pale stem and fuscous knob… easily told by the basal central pale abdominal spots." Therefore, the abdomen of both *cumminsii* and *mediopunctatus* (= *mesostictus*) has basolateral pale patches and *mediopunctatus* (= *mesostictus*) also has mesal pale spots.

Also associated with *cumminsii sensu lato* is a currently recognized synonym of *mesostictus*, *Aedes* (*Aedimorphus*) *cumminsi* (*sic*) var. *daruensis* Evans, 1925 from Moa River, Daru, Sierra Leone. Evans described *daruensis* by briefly comparing it with *cumminsii*. She noted: "*Abdomen* with small, but well-defined median, basal, pale spots on the third to seventh segments." Evans provided an illustration of the male genitalia, which are characteristic of other species related to *cumminsii*.

Edwards (1941) reviewed what was known about this group and included *cumminsii* and *mediopunctatus* (= *mesostictus*), as a subspecies of *cumminsii*, in a key. Confusingly, he stated that *cumminsii* had the "Abdomen all dark above." and *mediopunctatus* (= *mesostictus*) "Differs from the typical form chiefly if not solely in possessing small median basal whitish spots on the abdominal tergites [terga] in both sexes."

Adding to the overall confusion concerning the concept of *cumminsii sensu stricto*, except for the illustration of the head by Theobald (1903a) and various depictions of the male genitalia, none of which show obvious differences, there are no illustrations of any adult characters except for recent color photographs of *cumminsii sensu lato* from South Africa (Guarido *et al*. 2021). Thoracic and abdominal characters in these photographs are sufficient to see resemblances and differences with known descriptions of *cumminsii sensu lato.*

Hopkins (1952) described and illustrated, in detail, the larva of *cumminsii* from Uganda but did not associate it with adult characters nor make mention of *mediopunctatus* (= *mesostictus*) or other names associated with *cumminsii*. The larva he described would be easily recognized since it has the integument of the thorax and abdomen with numerous small, chitinous plates. We have found no characterizations of the pupal stage.

In an ecological study of *Aedes* species in northeastern South Africa, Guarido *et al*. (2021), using the *COI* "barcode" gene (Hebert *et al.* 2003), added to the questions surrounding the identity of *cumminsii sensu lato*. "Species belonging to *Aedimorphus* subgenera [*sic*] were recovered in different clusters [in their phylogenetic trees], suggesting that this subgenus is not monophyletic in this study. Sequences produced here from mosquitoes which were identified morphologically as *Ae. cumminsii*… clustered with *Ae. pachyurus* (of the same group) and *Ae. quasiunivittatus* (of another group within the same subgenus) and did not cluster together with sequences from *Ae. cumminsii* from Kenya…. This species was originally described in Ghana and is widely distributed in Africa. Subspecies based on subtle differences in abdomen scaling have been described, such as ssp. *mediopunctatus* (Theobald)… and it is not surprising that specimens from South Africa are different. *Aedes cumminsii* likely represents a complex of species which will require further studies to elucidate their taxonomy".

The nominal taxa discussed here clearly represent a species complex that will require much more effort to resolve, but there is no indication that *mesostictus* (= *mediopunctatus*) is other than a valid species related to *cumminsii*. We therefore elevate it to species status: ***Aedes* (*Aedimorphus*) *mesostictus* Harbach, 2018**. *Aedes mesostictus* is currently listed as a species (as *Ae. mediopunctatus*, incorrectly attributed to Theobald 1905d), in the Encyclopedia of Life.

We do not think there is enough known about this group to place the two junior subjective synonyms (*fuscopalpalis* and *daruensis*) with either *Ae. cumminsii* or *Ae. mesostictus*. We therefore choose to list them, for now, as synonyms of *cumminsii*.

***Aedes* (*Aedimorphus*) *durbanensis* (Theobald)**

subspecies ***angolae*** Ribeiro & Ramos, 1974—original combination: *Aedes durbanensis angolae*. Distribution: Angola (Ribeiro & Ramos 1974).

subspecies ***durbanensis*** (Theobald, 1903a)—original combination: *Grabhamia durbanensis*. Distribution: Angola, Congo, Democratic Republic of the Congo, Ethiopia, Madagascar, Mozambique, South Africa, Tanzania (Wilkerson *et al*. 2021).

The nominotypical subspecies was described from a single female from Durban, South Africa [KwaZulu-Natal Province]. It was characterized as follows (after Theobald 1903a): Head with silvery gray narrow curved scales; clypeus black, with a tubercle on each side near base; proboscis pale brownish yellow overall, apex and base black; maxillary palpus densely scaled, brown basally, white at apex; antenna deep brownish yellow with first 3 flagellomeres dull brick red, first flagellomere with white scales, second and third with dark scales; thorax with rich brown ornamentation, to some extent forming ornamentation at the sides, scutellum with pale narrow curved scales, pleura brown with gray scales; femora and tibiae mottled with pale scales, tarsomeres with narrow pale basal bands; wing mottled with pale and dark scales; abdomen black, with basal white bands and apicolateral yellow spots. Theobald emphasized that "It can be at once told by the thoracic ornamentation, peculiar mottled wings, and basal abdominal banding, and apical yellow lateral spots."

The male genitalia of the type form were described and illustrated by Edwards (1941), who noted: "Style [gonostylus] with a row of long curved hairs [setae] on distal margin and many more hairs on the surface, spine [gonostylar claw] inserted well before tip at broadest part of style; no apical hair-tuft on coxite [gonocoxite], basal lobe [basal mesal lobe] peculiar in having a regular row of hairs on its margin." These features were also reported by Ribeiro & Ramos (1974) and Jupp (1996). The pupal stage of *durbanensis* was very briefly described and the trumpet and paddle illustrated by de Meillon *et al*. (1945). The egg was described in detail by Linley & Service (1994).

Subspecies *angolae* was described and illustrated in direct comparison with *durbanensis* by Ribeiro & Ramos (1974) using female, male and larval specimens of *angolae* from Moçâmedes, Namibe Province, coastal Angola, 15º 12′ S, 12º 09′ E [verbatim coordinates not verified]. Specimens of *durbanensis* used in the description were from Natal, South Africa and Lourenço Marques, Mozambique. The authors stated: "In the female sex, *Ae*. *durbanensis angolae* subsp. nov. cannot be distinguished from the nominate subspecies." However, they pointed out diagnostic characters in the male genitalia and larva (see below). Note that Ribeiro & Ramos were motivated to sort out the identity of these taxa, along with a similar species found on the Angolan coast, *Ae*. *natronius* Edwards, 1932b: "it became clear not only that the description of the larva, given by Rebelo and Pereira (1) [1943, not seen by us] and taken by Hopkins (2) [1952], was not a satisfactory one but also that a subspecific treatment might be given to the angolan [*sic*] population of *Ae*. *durbanensis*." For us, the larva of putative *durbanensis* described and illustrated by Hopkins (1952) is another, yet to be determined, species. It exhibits an incomplete saddle, short anal papillae (as in *angolae*), a straight row of comb scales and very short pecten spines.

Males of the two forms differ, according to Ribeiro & Ramos (1974), as follow [figure numbers refer to the original publication]: "Males of both subspecies, however, can be readily separated on the basis of genitalic characters. While *Ae. durbanensis angolae* subsp. nov. (Fig. 4) has a row of l0–12 setae along the distal margin of basal lobe of coxite [gonocoxite] and has only subequal, small setae on the lateral surface of style [gonostylus], the nominate subspecies (Fig. 1) has only 5 or 6 setae along distal margin of basal lobe of coxite and the 2 or 3 most basal setae of its style are unusually long, about 1/3 or more the length of the style itself." Other differences are illustrated but we did not undertake further study.

Distinguishing differences of larvae are summarized as follow. In *durbanensis*: Comb scales asymmetrical, 7 or 8 (6–19) in a single row; siphon longer, index 2.2–2.5 (2.4); pecten spines moderately long and pointed, longest spine 5 or 6 times longer than width at base, mostly asymmetrical with a few basal denticles, distal 2 or 3 spines unequally spaced; anal papillae slightly longer than saddle, with round lanceolate apices. In *angolae*: Comb scales symmetrical, about 10 (8–20) arranged in 1 or 2 irregular rows; siphon shorter, index 1.7–2.0 (1.9); pecten spines very long, finely drawn out, longest spine about 7 to 10 time longer than width at base, also with a few basal denticles, spines equally spaced on siphon; anal papillae not or only slightly longer than saddle, ovoid or round lanceolate.

Based on the above diagnostic characters, and the great distance between the type localities, without evidence of intermediate forms, we think the two nominal taxa are separate species and here elevate *angolae* to species status: ***Aedes* (*Aedimorphus*) *angolae* Ribeiro & Ramos, 1974**. *Aedes angolae* is currently listed as a species in the Encyclopedia of Life; however, the authorship is incorrectly attributed to only the first author.

Synonym *Grabhamia ocellata* Theobald, 1910 was described from four females and three males from Maputo Bay ('Delagoa Bay') [Townsend 1990]. Theobald (1910) listed the collection site as "*Habitat*.—Lourenco Marques." Maputo is the capital of Mozambique, which has the official name of Lourenço Marques. Geographically, the type localities of *durbanensis* and *ocellata* are very close. We think the description of the female of *ocellata* does not differ significantly from that of *durbanensis,* except for two prominent black spots on the thorax in *ocellata*, presumably on the scutal fossae. We have not examined the syntype series to verify this. However, for some reason, Theobald did not compare *ocellata* with *durbanensis*. Edwards (1911b) stated "The type of *G. durbanensis* is a small specimen, but evidently the same as *G. ocellata*." This implied synonymy has been followed since. However, the lack of comment from Theobald, the distinctive dark eye-like thoracic spots and Theobald's statement that "The genitalia [of *ocellata*] are very marked.", referring to the large paddle-shaped gonostylus, also seen in later treatments of *durbanensis*, indicate that a closer look is needed to verify its status. For now, we retain it as a synonym of *Ae*. (*Aed*.) *durbanensis* (Theobald).

***Aedes* (*Aedimorphus*) *hirsutus* (Theobald)**

subspecies ***adenensis*** Edwards, 1941—original combination: *Aedes* (*Aedimorphus*) *hirsutus* var. *adenensis* (as ssp. in Pao & Knight 1970, explicitly elevated to ssp. by White 1975). Distribution: Yemen (Edwards 1941).

subspecies ***hirsutus*** (Theobald, 1901a)—original combination: *Culex hirsutum* [*sic*]. Distribution: Benin, Burkina Faso, Côte d'Ivoire, Ethiopia, Kenya, Madagascar, Mali, Mauritania, Namibia, Nigeria, Senegal, South Africa, South Sudan, Sudan, Togo, Zambia, Zimbabwe (Wilkerson *et al*. 2021).

The nominotypical subspecies was described from a female and a male from Salisbury, Mashonaland [Harare, Zimbabwe]. The detailed description has a separate color illustration. Theobald's (1901a) diagnosis follows here (after Theobald 1901a [plates]): fig. 80, pl. XX): "Thorax dark chestnut-brown, with dull creamy scales forming a broad median line and four creamy spots. Abdomen dark umber-brown, with basal yellowish-white bands and with two large dull yellow apical spots on the fifth and sixth segments; venter mottled with black, yellow and white scaled patches. Legs with broad basal white bands, femora, tibiae and metatarsi [tarsomere 1] hirsute, bases of the femora pale, remainder black, with a few pale scales." Also, "palpi short, dark brown, with numerous pale scales at the apex". Subsequent authors (Edwards 1911b, 1912b, 1941; Jupp 1996) noted that there is a white costal fringe on the distal part of the wing, which was not mentioned or illustrated by Theobald (1901a).

Theobald (1903a) described a similar taxon, *Culex transvaalensis*, but he did not note a similarity with *hirsutus*. In the collection of the Natural History Museum, London, Townsend (1990) found three syntype females from South Africa [Transvaal], Pretoria, and a male labelled "type", which he stated had no type status since only the female was described. Without comment Edwards (1911b) reduced *transvaalensis* to a synonym of *hirsutum*. Theobald (1913a) distinguished the two species in a key: "Abdomen basally banded" for *transvaalensis* and "Abdomen with two apical spots on 5th and 6th segments as well as bands" for *hirsutum*. He also stated: "Edwards considers this [*hirsutum*] the same as *Culex transvaalensis*, Theobald. The two marked apical spots on both fifth and sixth abdominal segments in *Culex hirsutum* never occur in *Culex transvaalensis* and the thorax is differently ornamented. The type has either been altered or this young writer has been unable to appreciate the distinctive characters." He further added: "As pointed out under *C. hirsutum*, Theobald, Edwards is in complete error in vaguely assuming this [*transvaalensis*] is the same as that marked species." The discussion was apparently put to rest by Edwards (1915), who stated: "Theobald... has criticised my statement that his *Culex hirsutum* and *C. transvaalensis* are one and the same species. I have re-examined the specimens, and find no reason to modify my previous opinion, except in one in particular. The male and female types of *C. hirsutum* belong to different species.... The female type must be taken as the type of the species, the male… being really *O. nigeriensis* (Theo.) [currently a synonym of *Ae*. (*Aed*.) *fowleri* (de Charmoy, 1908)]."

Other described life stages of the nominate form *hirsutus*, a widespread African species, include the adult male (Edwards 1911b), pupa (Ingram & Macfie 1919), male genitalia (Edwards 1941), larva (Hopkins 1952), larval mandible and maxilla (Pao & Knight 1970) and the adult female and male genitalia (Jupp 1996).

Edwards (1941) described subspecies *adenensis* as a variety of *hirsutus* from two sites in the West Aden Protectorate [southwestern Yemen], as revealed by Mattingly (1956): Jebel Jihaf, 7100 ft., ix.1937, 2 females, and Dhala, 4800 ft., 14.ix.1937, 1 male and 7 females. "Since the critical factor, if any, is likely to be altitude I have marked one of the ♀ from Jebel Jihaf as the hololectotype and the ♂ from Dhala as allolectotype." David Pecor (pers. comm.) investigated the localities and noted that the West Aden Protectorate was renamed as part of the independent nation of Yemen, and the locality names were perhaps misspelled when translated from Arabic. Instead they are probably Jabal Jihaf [Jabal is "mountain" in Arabic] (GeoNames ID 74169, coordinates 13.7607 44.67656, altitude 2,402 m) and Dhale, (GeoNames ID 80384, coordinates 13.69572, 44.73137, altitude 1,517 m). The two sites are approximately 9 km apart. Edwards's (1941) description of *adenensis* follows: "Structurally identical with the typical form, and also resembling it in the white-scaled distal part of costa, but differs in colouring of abdomen; the pale basal bands of the tergites [terga] are yellowish rather than white and all the tergites have apical median patches of yellowish scales, usually occupying an extensive area; in some extremely pale specimens the abdominal scales are almost all yellowish, with only a few black ones across the middle of each tergite."

Mattingly & Knight (1956) stated that the male genitalia [of *adenensis*] "are indistinguishable from those of the type form." In their keys they noted: "Wing [of *adenensis*] with relatively few pale scales which are mainly confined to the basal half". They then compared the larva of *adenensis* to *Ae*. (*Aed*.) *natronius* Edwards, 1932b: "Antenna more strongly spiculate; pecten teeth of more normal type; head seta 6 normally single, rarely double, much longer and usually stouter than 5". The illustration in the original description showing the presence of white scaling on the costa of the wing contradicts Mattingly & Knight (1956), who reported the presence of a few pale scales, those confined to the proximal half of the costa. The head of the larva of *hirsutus* illustrated by Hopkins (1952), who did not mention *adenensis*, shows seta 5-C multi-branched and 6-C single, with the latter about twice the length of the former. Unfortunately, Mattingly & Knight (1956) did not note whether 6-C was branched or not.

The inconsistent description of white scales being present or absent apically on the costa in both *hirsutus* and *adenensis* can only be solved by re-examination of the types and study of variation in these taxa. The only character that separates these two, for now, is the pattern of scaling on the abdomen of *adenensis*, which has median, apical patches of yellowish scales that are absent in *hirsutus*. No description of variation in *hirsutus* across its range in Africa includes median apical abdominal pale scales that would suggest *adenensis* represents a morphological variant of the type form. However, the type form has not been well studied morphologically. The type locality of *adenensis*, near the eastern border of the distribution of *hirsutus*, is at a fairly high altitude compared to most mosquito species and appears to us to possibly reside in an extremely dry environment, though indications of green in valleys can be seen from satellite photos. Until further study can be undertaken, we believe *adenensis* is sufficiently different from *hirsutus* to be afforded species status: ***Aedes* (*Aedimorphus*) *adenensis* Edwards, 1941**. *Aedes adenensis* is currently listed as a species in the Encyclopedia of life.

***Aedes* (*Aedimorphus*) *tricholabis* Edwards**

subspecies ***bwamba*** van Someren, 1950—original combination: *Aedes* (*Aedimorphus*) *tricholabis* ssp. *bwamba*. Distribution: Benin, Kenya, Nigeria, Uganda (Wilkerson *et al*. 2021).

subspecies ***tricholabis*** Edwards, 1941—original combination: *Aedes* (*Aedimorphus*) *tricholabis*. Distribution: Benin, Burkina Faso, Central African Republic, Côte d'Ivoire, Kenya, Mali, Nigeria (Wilkerson *et al*. 2021).

This taxon is an example of the scant taxonomic work carried out on mosquitoes in Africa on all but the most important vectors of human and animal pathogens. *Aedes tricholabis* was described from the adult female, male and male genitalia, but not the larval or pupal stages. Subspecies *bwamba* was described, in addition to the larva and pupa, from the adult male and female, which were distinguished from *tricholabis* based on a single, but we think significant, character. Because the larval and pupal stages of *tricholabis* are not known, descriptions of the immature stages of *bwamba* have served to represent *tricholabis* (see below). The dearth of specimens needed to carry out direct comparisons of all life stages is surprising given that *tricholabis sensu lato* has been found to harbor Dengue, Sindbis and other viruses (*e.g.* Ochieng *et al*. 2013; Munyao *et al*. 2020; Musa *et al*. 2020). In a sample of published studies, we found that most authors cited Edwards (1941) as the authority for identifications, and therefore subspecies *bwamba,* not yet described in 1941, was subsequently ignored in post-1950 studies.

Aedes tricholabis was described from two males and five females collected in Gede (or Gedi), located north of Mombasa, Kenya. Townsend (1990) found two females and the lectotype male (designated by Mattingly 1956) in the collection of the Natural History Museum, London. Edwards distinguished *tricholabis* in a key using the following characters: Scutellum with narrow scales only; decumbent scales of vertex all narrow; femora and tibiae not striped; hindtarsus entirely dark; head in female with a distinct patch of dark decumbent scales on vertex (this patch absent in males); abdominal terga usually with complete basal pale bands; postspiracular scales all broad and flat; hindfemur pale beneath almost to apex; hindungues (as hindtarsal claws) simple. The description also states that all scutellar scales are narrow and yellowish, and, in addition to pale basal bands on all terga, there are also dark apical bands on the sterna. The adult male, as noted above, does not have a patch of dark decumbent scales on the vertex, which led Edwards to question if the males and females were the same species, because there were no associated larval and pupal exuviae to prove otherwise. To our knowledge, this query has not been answered. The most remarkable distinguishing feature of *tricholabis* (and subspecies *bwamba*), however, is a gonostylus, which on the ventral surface ("outer edge") is "provided with a row of long soft hairs [setae], most of which are branched, the one nearest the base having most branches." The egg, larva and pupa have not been described and only the male genitalia have been illustrated.

Subspecies *bwamba* was described from the male holotype, six male paratypes, and five larval and nine pupal exuviae from Bwamba Province, Toro District, in western Uganda. Townsend (1990) found the holotype and four paratypes in the collection of the Natural History Museum, London. Van Someren (1950) provided detailed descriptions of the adult male, male genitalia, and larval and pupal stages. Only the male genitalia and pupa were illustrated. Van Someren stated: "The male terminalia of this species do not differ from the figure of *A*. (*A*.) *tricholabis*...". The description of the male of *bwamba* does not appear to us to differ from *tricholabis,* including the lack of a patch of dark decumbent scales on the vertex. However, the scutellum is "clothed with broad creamy white scales on all lobes." This is in contrast to the scutellar scales being all narrow and yellowish in *tricholabis*. The larval stage of subspecies *bwamba* is apparently quite distinctive, as relayed in a personal communication to van Someren: "Dr. Haddow (personal communication) states that the larvae are very pale and transparent in life, with the eye spots very large and black. Usually the swimming is done with the mouth brushes, but when they are disturbed, body swimming movements occur. They are markedly restless, often looping the loop under water and have a habit of browsing. …The larval skins are very fragile, with all the setae pale and transparent and easily detached." The larval stage of *tricholabis* is not known, precluding a comparison with subspecies *bwamba*.

Hopkins (1952) used van Someren's description of the larva of subspecies *bwamba* to represent the type form and Pao & Knight (1970) described the larval mandible and maxilla of subspecies *bwamba* to represent *tricholabis sensu lato*. No explanation was given of how the taxonomic determination was made. Similarly, Cordellier & Geoffroy (1976) represented *tricholabis sensu lato* as both a species and as a species with a subspecies, without explanation.

The distributions of these nominal taxa, therefore, have not been documented, other than for the type localities and for surveys that used Edwards (1941) as an identification resource. Service (1960), however, added to the description of the larva of subspecies *bwamba* from Lokoja, Nigeria (7° 47′ 48″ N, 6° 44′ 25″ E). This site is far from the type locality of *bwamba* in Uganda and gives possible insight into the broad distribution of at least subspecies *bwamba*. Service (1960) also "fully endorsed" Haddow's statement that "the larvae in life are pale and transparent with large dark contrasting eyes."

We do not note consensus regarding the identity and distributions of the nominotypical form or subspecies *bwamba*. The only clear and significant distinction is that *tricholabis* adults have all scutellar scales narrow and yellowish whereas adults of *bwamba* have all scutellar scales broad and creamy white. We consider this a significant difference that stands out in a confused understanding of these taxa, which we think justifies elevation of *bwamba* to species status: ***Aedes* (*Aedimorphus*) *bwamba* van Someren, 1950**. *Aedes bwamba* is currently listed as a species in the Encyclopedia of Life.

Aedes (*Aedimorphus*) *vexans* (Meigen)

subspecies ***arabiensis*** (Patton, 1905)—original combination: *Culex arabiensis* (subspecific status by White 1975). Distribution: Gambia, Mauritania, Mauritius, Nigeria, Saudi Arabia, Somalia, South Africa, South Sudan, Sudan, Tanzania, Yemen (Wilkerson *et al*. 2021).

subspecies ***nipponii*** (Theobald, 1907)—original combination: *Culicada nipponii* (subspecific status by Bohart & Ingram 1946b). Distribution: Georgia, Japan, Mongolia, People's Republic of China, Russia, South Korea (Wilkerson *et al*. 2021).

subspecies ***nocturnus*** (Theobald, 1903a)—original combination: *Culex nocturnus* (subspecific status by Bohart & Ingram 1946b). Distribution: Australia, Cook Islands (Polynesia), Fiji, Indonesia, Kiribati, Malaysia, Mariana Islands, Marshall Islands, New Caledonia, Palau, Papua New Guinea, Samoa, Solomon Islands, Timor, Tonga, Tuvalu, Vanuatu (Wilkerson *et al*. 2021).

subspecies ***vexans*** (Meigen, 1830)—original combination: *Culex vexans*. Distribution [*sensu lato*]: Afghanistan, Albania, Algeria, Armenia, Australia, Austria, Azerbaijan, Bangladesh, Belarus, Belgium, Belize, Bosnia and Herzegovina, Bulgaria, Cambodia, Canada, Corsica, Crimean Peninsula, Croatia, Czech Republic, Denmark, Estonia, Fiji, Finland, France, Former Yugoslav Republic of Macedonia, Gambia, Georgia, Germany, Greece, Guam, Guatemala, Honduras, Hong Kong, Hungary, India, Indonesia Iran, Iraq, Italy Japan, Jordan, Kazakhstan, Kiribati, Kosovo, Laos, Latvia, Liberia, Libya, Lithuania, Macedonia, Malaysia, Malta, Mariana Islands, Mauritania, Mexico, Micronesia, Moldova, Mongolia, Montenegro, Morocco, Myanmar, Nepal, Netherlands, New Caledonia, New Zealand, Norway, Pakistan, Papua New Guinea, People's Republic of China, Philippines, Poland, Portugal, Romania, Russia, Samoa, Saudi Arabia, Serbia, Singapore, Slovakia, Slovenia, Solomon Islands, South Africa, South Korea, Spain, Sri Lanka, Sweden, Switzerland, Taiwan, Tajikistan, Thailand, Tonga, Turkey, Turkmenistan, Tuvalu, Ukraine, United Kingdom, United States, Uzbekistan, Vanuatu, Vietnam, Yemen (Wilkerson *et al*. 2021).

Aedes vexans sensu lato, occurs worldwide except for South America. Since *Ae*. *vexans sensu lato* is a common, medically important species, it has attracted worldwide interest. In summary, we think that two of the nominal subspecies have characteristics that adequately separate them from typical *vexans*: subspecies *nipponii* (Japan and the eastern Palaearctic) and subspecies *arabiensis* (northeastern Africa and Arabia [South Africa?]). However, the third subspecies, *nocturnus* (Central Pacific and Australasia) has generated taxonomic inconsistency since there are no clear differences to distinguish it. There are regional keys to identify the four nominal subspecies from co-occurring species of *Aedes*, but there are no keys to separate the subspecies from each other. A partial exception is Reinert (1973), who compared a worldwide concept of *vexans vexans* with the allopatric *vexans nipponii.*

Nominotypical *vexans*

To compare the nominal forms, we first define nominotypical *vexans* using a recent description from Europe, the continent of the type locality, Berlin, Germany. The nominotypical subspecies was described from a single female. The type specimen is in the Muséum National d'Histoire Naturelle, Paris, France. There are descriptions for what has been called *vexans* from many parts of the world, but it is sensible to use a recent description from Europe (Becker *et al*. 2020). The caveat is that the provenance of specimens and/or literature used for this description are not documented. It will nevertheless serve as a basis for comparison with characters of subspecies and descriptions of *vexans* from other parts of the world. The following is paraphrased from key characters (diagnoses) followed by more complete descriptions, a format often used by F. W. Theobald.

Adult female. Tarsomeres with pale rings only; proboscis distinctly longer than forefemur; scutellum with narrow, curved, yellowish or pale scales; pale basal bands of tarsomeres very narrow, usually not exceeding 0.25 length of tarsomeres; abdominal terga with basal white bands constricted medially, giving them a bilobed appearance.

Tibiae dark-scaled dorsally, pale-scaled ventrally; narrow basal bands present on foretarsomeres 2 and 3, midtarsomeres 1–4 and on all hindtarsomeres. Proboscis and maxillary palpus dark-scaled, palpus with some apical white scales; head covered with narrow curved pale and dark decumbent scales and numerous dark brown erect forked scales which extend anteriorly to interocular space. Scutal integument dark brown, covered with narrow curved dark scales and narrow pale scales forming indistinct patches on anterior submedian, prescutellar and dorsocentral areas; acrostichal and dorsocentral setae well developed; postspiracular area with large patch of narrow curved or moderately broad pale scales; upper and lower mesokatepisternal scale-patches present. Wing veins covered with moderately broad dark scales and isolated pale scales at bases of costa and subcosta. Abdominal terga with basal white bands, distally dark-scaled; basal bands on terga III–VI distinctly narrowed medially, giving a bilobed appearance; sternum VIII with distinct apical V-shaped notch.

Adult male. Maxillary palpus about as long as proboscis; gonostylus attached at apex of gonocoxite, simple, not divided; gonostylus distinctly expanded apically; claspette elongate, well separated from base of gonocoxite; gonostylus gradually expanded toward apex; gonostylar claw articulated subapically, straight. Tergum IX strongly bilobed with 6–11 setae on each lobe. Gonocoxite long and moderately broad with scattered scales on lateral and ventral surfaces; basal and apical lobes absent; gonostylus widens toward apex; gonostylar claw straight, inserted on a small subapical tubercle; claspette moderately broad basally, apex slightly expanded and rounded, with crown of numerous spine-like setae, some curved apically; claspette filament absent; paraproct with pointed apex; aedeagus strongly sclerotized with lateral plates connected at base.

Larva. Integument not covered with obvious spicules. Antenna less than half length of head, with numerous scattered spicules; seta 1-A 5–10 branched, inserted proximal to middle of antenna. Labral brush with median setae apically serrate (in contrast to unmodified setae in *Ae*. *rossicus* and *Ae*. *cinereus*). Setae 5–7-C arranged in a triangular pattern, 5-C posterior to 6,7-C; 5-C 1–4-branched, 6-C 1- or 2-branched, 7-C 7–9 branched. Comb with 7–13 scales arranged in 1 or 2 irregular rows; scales with long median spicules and small spicules at base. Siphon index 2.3–3.0; pecten with 13–18 spines, apical 2 or 3 spines larger and unevenly spaced; basal spines with 1–3 lateral denticles; seta 1-S inserted beyond middle of siphon, with 3–8 short branches, length about half width of siphon at setal insertion. Saddle large but incomplete; seta 1-X with 1 or 2 branches; seta 4-X with 3 or 4 precratal setae; anal papillae distinctly longer than saddle.

The notion that *vexans* is a single species across Europe and North America was recently questioned in two studies. Krtinić *et al.* (2013) used allozyme data to analyze two European populations (Serbia and Germany) and one North American population (California, USA). They found unambiguous differences between European and North American *vexans*. "We observed that populations of *Am*. [as genus *Aedimorphus*] *vexans* from the Palearctic (Germany and Serbia) and from the Nearctic (USA) formed two genetically distinct populations that had no genetic exchange." In other words, they are genetically separate species. Also, they cited Becker *et al*. (2020), who wrote that unlike invasive species such as *Aedes albopictus*, which oviposits above the water line, *vexans* lays eggs onto moist soil, which argues against it being an invasive species in North America. Since a single North American population was sampled, these results require verification. Lilja *et al.* (2018), using the mitochondrial *COI* gene and two nuclear genes found two sympatric genetically isolated *vexans* clades in Sweden and elsewhere in northern Europe. Considering *COI* data only, including sequences in GenBank from other parts of the world, they found four distinct groupings: "Group 1 *vexans* variant," *Ae*. *vexans nipponii*, *Ae*. *vexans* North America and *Ae. vexans* Europe. Given a lack of morphological vouchers for study and weak branch support in some cases, Lilja *et al.* (2018) did not attempt to interpret the taxonomic meaning of their findings, recommending further work. These two studies generate many uncertainties, but they suggest that North American *vexans* could be a different species and that an unrecognized cryptic species occurs in Europe.

Synonyms of *Aedes* (*Aedimorphus*) *vexans* (Meigen, 1830) (Wilkerson *et al*. 2021): *Culex parvus* Macquart, 1834 (type locality: Bordeaux [Gironde], France); *Culex articulatus* Rondani, 1872 (type locality: Italy); *Culex malariae* Grassi, 1898 (type locality: Italy); *Culex sylvestris* Theobald, 1901a (type locality: various, all in Canada) [*montcalmi* Blanchard, 1905 is incorrectly listed as a replacement name for *sylvestris* in Wilkerson *et al*. 2021, see Townsend (1990) for more information]; *Culicada minuta* Theobald, 1907 (type locality: India); *Aedes eurochrus* Howard, Dyar & Knab, 1917 (type locality: Popcum, British Columbia, Canada).

Subspecies *nipponii*

Subspecies *nipponii* was described from a single "perfect ♀" from Karnizana, Japan [Karuizawa, Nagano Prefecture]. Theobald (1907) wrote: "proboscis with scattered golden scales, with black apex, palpi mottled." "Abdomen with the basal segment testaceous, with a median patch of creamy scales and rather short pale golden hairs; the second and third segments with basal uniform creamy bands; on the fourth, fifth and sixth the bands spread out laterally, forming marked lateral areas; the sixth and seventh have yellow apical scales, and the second to the fifth have median pale scales which form a broken median line; venter pale scaled." A distinguishing character is the median pale abdominal scales.

Reinert (1973) did a comprehensive study of *vexans vexans* and *vexans nipponii* as part of a study of the subgenus *Aedimorphus* in Southeast Asia. He treated *vexans vexans* as a single variable worldwide species. He characterized subspecies *nipponii* in the adult female as follows: "Abdomen with terga III, IV each with an incomplete apical median longitudinal white stripe which may or may not connect with basal bands; lower subspiracular scale patch connects, or nearly so, with postspiracular scale patch." In the pupa, the two were very similar but could be separated from other related species by having the "Ventral posterior margin of II [tergum II] with spicules mesally." In the larval stage, he contrasted *vexans vexans* in Southeast Asia with subspecies *nipponii* by the presence of a granulose frontoclypeus in the former not present in the latter. This granularity is rarely seen in the rest of the range, *sensu* Reinert (1973), of the putative subspecies *vexans*. To us, it could also indicate a separate species in Southeast Asia.

Tanaka *et al.* (1979) stated that only *vexans nipponii* occurs in Japan, Korea and the eastern Palearctic, and thus they did not provide a complete comparison of it and *vexans vexans*. As described by Theobald (1907) and Reinert (1973), Tanaka distinguished *nipponii* by noting that "Subspecies *nipponii* is chiefly characterized by the presence of pale median patches on the anterior abdominal terga of the adults." The larva of subspecies *nipponii* is like the larva of typical *vexans* but setae 5–7-C are distinctly aciculate, as are setae 1,3,5-VIII.

Because of its Palearctic distribution and distinct morphological characters, we believe subspecies *nipponii* should be afforded species status: ***Aedes* (*Aedimorphus*) *nipponii* (Theobald, 1907)**. Synonyms: None. *Aedes nipponii* needs to be added in the list of *Aedes* species recognized in the Encyclopedia of Life.

Subspecies *arabiensis*

Patton (1905) described subspecies *arabiensis* from Ulub Camp and Crater, West Aden Protectorate [Yemen] from an unspecified number of adult males, adult females and larvae. No type specimen was designated and type material is presumed to be lost or never existed. White (1975), when he removed *arabiensis* from synonymy (synonymy by Hamon *et al.* 1966) with *vexans* and elevated it to a subspecies of *vexans*, reported finding a male and two females of *arabiensis* from Aden, "topotypic *arabiensis* material", in the collection of the Natural History Museum, London, but did not designate a neotype.

Patton's (1905) original description of *arabiensis* is vague and roughly follows the description of *vexans* by Becker *et al*. (2020) paraphrased above. Confusingly, Patton stated: Thorax "with a dark line down the center and two at the sides. Abdomen brown with apical black bands. …Male genitalia, basal lobes narrow... apical segment thin and somewhat club shaped." The apical black abdominal bands probably refer to contrast with the basal pale bands in all other taxa related to *vexans*. Edwards (1921d) apparently listed it as a synonym, perhaps "in part", in a treatment of *vexans*: "(?) *Culex arabiensis*, Patton (adult, not larva) [alternatively, this could mean he thought the larva was a different species]." Edwards (1925) listed it with the "*vexans* series" as "*A*. *vexans*, Mg. (= ? *arabiensis*, Patton.)." A year later, Edwards (1926b) explicitly listed *arabiensis* as a synonym of *vexans*, but then in 1941 he placed it as a species of the *vexans* group.

Edwards (1941) stated that *arabiensis* was "Distinguished from other Ethiopian species of the subgenus [*Aedimorphus*] by the combination of the following features: basally-ringed tarsal segments, dark-scaled wings, broadly banded abdomen, and pale posterior surface of middle tibiae. *A*. *arabiensis* is very closely related to the Palearctic *A*. *vexans* Mg., from which it differs in having the male palpi rather shorter; abdominal bands in both sexes broader and not emarginate in the middle; middle tibia dark above (in all European and Central Asian females of *A*. *vexans* examined the middle tibia is conspicuously pale above as well as posteriorly)." Further, abdominal "tergites [terga] 2–6 with broad creamy-white basal bands, 2–7 with lateral whitish patches extending most of their length, 6 and 7 with narrow pale apical bands; sternites almost entirely pale scaled."

Lewis (1945) added that the larva has seta A [7-C] with 7 or 8 branches, seta B [6-C] single and seta C [5-C] single or double. "Comb a patch or irregular row of 8–12 sharp-pointed spines with small basal denticles. Siphon with index about 2.5... pecten reaching slightly beyond middle… of the last 1–3 teeth [spines] usually 2 larger and widely spaced.... Gills [anal papillae] subequal, lanceolate, much longer than saddle." The relatively long pointed anal papillae are a particularly obvious characteristic.

Hopkins (1952) expanded the description of Lewis (1945) and provided an illustration. "The only other *Aëdes* larvae with the comb composed of a small number of spines... head-setae B and C [6- and 5-C] single and the last 2–3 pecten spines wider-spaced are *cumminsi*, *fowleri* and *durbanensis*. From the first two of these the larva of *arabiensis* is easily separated... by the shape of the 'gills' [anal papillae]."

Carpenter & LaCasse (1955), without comment, listed *nocturnus*, *arabiensis* and *nipponii* as synonyms of *vexans*. Perhaps those authors were unaware of or disagreed with the recognition of *nocturnus* and *nipponii* as subspecies of *vexans* by Bohart & Ingram (1946b).

The story became less clear to us with Muspratt's (1955) description of *vexans* from Transvaal, South Africa, and its comparison with *vexans* from England and the USA (Washington State). Muspratt pointed out some differences, such as "the tibiae of the former [South Africa] are practically all dark except for the narrow basal pale bands and apical spots, whereas the tibiae of the latter [England; USA] are extensively pale posteriorly..." [as described for *arabiensis* from Yemen]. Also, "on the South African form the basal pale bands of the abdominal tergites [terga] are not narrowed in the middle, thus being as described for *arabiensis*...". Jupp (1996) illustrated and keyed, from South Africa, as *vexans*, a taxon with narrow basal emarginate abdominal tergal bands and with the sterna not all pale but with dark markings. This suggests two species in South Africa, and we think neither is *arabiensis*, which is distributed in northeastern Africa and Arabia.

Mattingly & Knight (1956) treated *arabiensis* from Arabia as a species but wrote: "This is very closely related to the holarctic [*sic*], Oriental and Australasia *Aë. vexans* Meigen, of which it is possibly no more than a subspecies…".

Hamon *et al*. (1966) considered all observed differences as only variation. Regarding this, White (1975) wrote: "Having not seen the types of either *arabiensis* or *sudanensis* [a synonym of *arabiensis*], the former having been lost, Hamon et al [*sic*] (1966:373) formally synonymised both with *vexans* s. str." As noted above, White (1975) removed *arabiensis* from synonymy with *vexans* and elevated it to subspecific rank, and affirmed that *sudanensis* Theobald, 1911b was a junior synonym of *arabiensis*. He also listed the known distribution of *vexans arabiensis* as Aden, Gambia, Mauritania, Nigeria, Saudi Arabia, Somalia, South Africa (Transvaal) [we think doubtful] and Sudan. Since that time, *vexans arabiensis* has been identified in a number of studies, and has been implicated as a possible vector of the Rift Valley Fever virus in northeastern Africa and Arabia (Miller *et al*. 2002; Mondet *et al*. 2005; Fall *et al*. 2011; Clements 2012; Krtinić *et al.* 2013; Francuski *et al*. 2016; Mohamed *et al*. 2017; Azari-Hamidian *et al*. 2019).

Mohamed *et al*. (2017), using the keys in Edwards (1941) and Hopkins (1952), found *vexans arabiensis* to be very common in collections made in the Republic of Sudan. Of special note was the presence of two larval types ("X" and "Z"), both of which keyed to *vexans arabiensis* in Hopkins (1952). Since no larvae were reared to the adult stage, it is not known which might be true *arabiensis*. Nor is it known if the adult females collected during the study belonged to more than one species.

Given the distinctive morphological characters of the adult female and larval stage of subspecies *arabiensis*, we think it should be formally afforded species status: ***Aedes* (*Aedimorphus*) *arabiensis* (Patton, 1905)**. Synonym: *Culex sudanensis* Theobald, 1911b. *Aedes arabiensis* is currently listed as a species in the Encyclopedia of Life.

Subspecies *nocturnus*

Descriptions of subspecies *nocturnus* are very similar to descriptions of *vexans*, which has led to many different opinions concerning its status. It was described by Theobald (1903a) from "several ♀'s" from "Ba in Fiji". Townsend (1990) found two syntype females in the collection of the Natural History Museum, London. Theobald (1903a) described the species as having the "Thorax deep brown, covered densely with narrow-curved, bright brown and golden scales, scarcely showing any definite ornamentation; proboscis with a minute black tip and base, remainder ochraceous." The legs are as in the description of *vexans* above. "Abdomen deep brown with basal white bands curved in the middle…. ♀. Head brown, with narrow curved pale golden scales on the crown, with black upright forked scales, flat black scales at the sides with a median white patch…. Abdomen …sixth and seventh segments with narrow apical yellow bands, no basal pale band or mark to the last; laterally are median white spots…. Legs …tibiae deep brown, paler ventrally…. *Observations....* The abdominal ornamentation is very characteristic; the species cannot well be mistaken for any other. The proboscis is really very broadly pale banded." Theobald included descriptions of all life stages except the egg, none of which provided distinguishing characters.

The following publications concerning the nominal taxon *nocturnus* are arranged by taxonomic status. A few authors gave expanded rationale for their judgements (Bohart & Ingram 1946b; Belkin 1962; Reinert 1973; Lee *et al*. 1982), which were summarized by Lee *et al*. (1982), as shown below. This is not intended to be an exhaustive listing (* = with some sort of illustration).

As a synonym of *vexans*. Dyar (1920, 1921a); Senior-White (1923); Freeborn (1926); Edwards (1924); Edwards (1932a); Natvig (1948); Senevet & Andarelli (1954) [who followed Edwards 1932a]; Carpenter & LaCasse (1955) [subspecies *arabiensis*? and *nipponii* also listed as synonyms of *vexans*]; Reinert (1973); Knight & Stone (1977) [who we assume followed Reinert 1973]; Reinert *et al*. (2004).

As a synonym of *Aedes* (*Ochlerotatus*) *vigilax* (Skuse, 1889). Cooling (1924).

As a subspecies of *vexans*. *Bohart & Ingram (1946b); *Yamaguti & LaCasse (1950); Knight & Hull (1951); *Knight & Hull (1953); Laird (1955); Bohart (1957); Stone *et al*. (1959); Iyengar (1960); Stone (1961b); Lien (1962); *Joyce & Nakagawa (1963); *Holway & Bridges (1970); Basio (1971); *Baisas (1974); Tanaka *et al.* (1979); Harbach (2018); Wilkerson *et al*. (2021).

As species *nocturnus*. *Theobald (1903a); Edwards (1912a), in genus *Ochlerotatus* but "Doubtfully distinct from the preceding [*vigilax* Skuse, 1889]"; *Penn (1949), as *vexans* but possibly represents subspecies *nocturnus*; *Belkin (1962); Peters & Christian (1963), included as both a species and apparently inadvertently as a subspecies of *vexans*; Stone (1963); Belkin (1965); Stephan (1966); Standfast (1967); Maffi (1977).

Lee *et al*. (1982), as species *nocturnus*, stated the following in a footnote.

> Although F.W. Edwards (1924) synonymised *nocturnus* with *vexans* it was later considered a variety or subspecies of *vexans* by regional authors, commencing with Bohart & Ingram (1946).
>
> Belkin (1962) provisionally raised *nocturnus* to specific rank, mainly on the basis of branching of larval head hairs [setae]. He recognised that the taxonomic status of *nocturnus* was uncertain, clarification awaiting study of the *vexans* complex.
>
> Reinert (1973) sank *nocturnus* as a synonym of *vexans vexans* "in the absence of sufficient biological, behavioural and genetical data on the Pacific Island populations of *vexans*, and since specimens of these populations fall within the variable range of the morphological characters of other populations within the distribution of the species".
>
> For the time being we have chosen to retain *nocturnus* as a species partly because the synonymising of *nocturnus* under *vexans* gives *vexans* an extraordinarily wide distribution far greater than that achieved by any other non-domestic species.

We agree with the summary and conclusions of Lee *et al*. (1982) and thus hereby return *nocturnus* to its original species status: ***Aedes* (*Aedimorphus*) *nocturnus* (Theobald, 1903a)**. Synonyms: *Culicada eruthrosops* Theobald, 1910; *Culex nocturnus* var. *niger* Theobald, 1913b. *Aedes nocturnus* is currently listed as a species in the Encyclopedia of Life.

Aedes (*Bifidistylus*) *boneti* Gil Collado

subspecies ***boneti*** Gil Collado, 1936—original combination: *Aedes* (*Aedimorphus*) *boneti*. Distribution: Known only from the type locality, Isla de Bioko (Fernando Po), Equatorial Guinea (Gil Collado 1936).

subspecies ***kumbae*** Chwatt, 1948—original combination: *Aedes* (*Aedimorphus*) *boneti* s.sp. *kumbae*. Distribution: Republic of Cameroon (Chwatt 1948).

The nominotypical subspecies was described from a single male from Rebola, Bioko Island, Equatorial Guinea. The island has an area of 2,017 km^2 and is 32 km from the coast of Cameroon (https://en.wikipedia.org/wiki/Bioko; accessed 7 April 2022). Gil Collado credited F. W. Edwards for identifying the species as new, stating: "I must tender my thanks to J. W. Edwards [*sic*], who... examined the material... verifying my findings and alerting me to a new species of *Aedimorphus*, represented by a specimen it had been impossible for me to identify due to its somewhat deficient state of preservation [translated from the Spanish]." The male holotype is in the Museum, Madrid University School of Agriculture, Madrid, Spain. We used a published translation of the description from the Spanish along with the original article for this treatment. The description is detailed and accompanied by a drawing of a dorsal view of the head and appendages (antenna, maxillary palpus, proboscis) and a hindleg. The forelegs are not described, leaving the impression that they are missing. Damage to the specimen noted by the author included: “The scutellum has very wide whitish scales in its middle lobe, those from the sides [lateral lobes] having been removed... Anterior pronotum [antepronotum] has two groups of 5 to 6 bristles [setae]; the posterior [postpronotum], some 4, though in our specimen, they are somewhat destroyed…. Supra-alar scales are dark and numerous; those from the dorso-central area of our specimen have been torn off….” Our assumption is that characteristics of the cuticle (setae, scales, pollinosity, etc.) might be modified enough to render an accurate description problematical. Re-examination of the holotype is needed to be certain. Gil Collado also noted: “This species presents traits which closest approximate *lamborni* Edw. [the only other species now included in the subgenus *Bifidistylus*], in whose group they must be included because of their tarsal rings; however, in spite of the fact that the specimen’s [as in translation] hypopygium [genitalia] was destroyed in preparation, the coxa [gonocoxite] does not seem as pronounced as in that species...”. Gil Collado then compared *boneti* with *lamborni* Edwards, 1923a. To our knowledge the holotype of *boneti* is the only known specimen of this species. However, given the intense study of *Anopheles* and malaria control on Bioko (*e.g*. Cook *et al*. 2018), it is not surprising that species of other genera might have been overlooked, with the exception of the relatively recent invasive *Aedes albopictus* (Skuse, 1895) (Toto *et al*. 2003), and pest species of *Culex* (*e.g*. Fuseini *et al.* 2019). Gil Collado (1936) documented about 30 mosquito species on Bioko. All but *Anopheles lloreti* Gil Collado, 1936 are also found on mainland Africa. The type of *An*. *lloreti* is perhaps the only specimen of this species as well.

An attribute that to us stands out as unique is paired spots of erect black scales on the vertex of the head. “Head with a broad vertical zone of narrow, reclining, white scales, among which numerous dark standing scales appear; on each side there is a rounded blotch of dark scales, which in turn, has a lateral region of white, narrow, reclining scales, and in the same posterior angle of the eyes there is a small dark spot.” These spots are not noted in *Ae. lamborni*, but they are present in subspecies *kumbae*.

Subspecies *kumbae* was described from Kumba, British Cameroons [Republic of Cameroon] by Chwatt (1948). The type localities of *kumbae* and the type form are 117 km apart (determined by David Pecor on 04/07/2022, https://arcg.is/CqOTz1) and, as stated above, the island and mainland are separated by 32 km of ocean. The description and illustrations of *kumbae* are detailed and based on a series of specimens: 10 larvae, three pupal exuviae and two adult males with dissected genitalia mounted with the associated pupal exuviae. Of these, Townsend (1990) found two males and six larvae in the Natural History Museum, London. Chwatt (1948) apparently relied on the description of the male of *boneti* to compare subspecies *kumbae* with *boneti* since there is no indication that he examined the holotype of *boneti*. Hopkins (1952) included *boneti* in a key but reproduced the description and larval illustration of subspecies *kumbae* to represent *boneti*.

For purposes of comparison, therefore, we only have the descriptions of the adult male of each nominal form. The following are comments and characters that Chwatt (1948) used to justify giving *kumbae* subspecies status: “In Edwards’s (1941) key to the Ethiopian species of *Aëdes* the two male adults [the two specimens used to describe subspecies *kumbae*] would run down to *A. boneti* Gil Collado, described in 1936 from a single damaged male captured on the Island of Fernando Po. The similarity between the two adults described above and the original description of *A. boneti* is considerable. Nevertheless, there are several notable differences—mainly the more extensive, rather differently shaped, dark scaling of the head, the pale (instead of golden) colour of the investiture of the mesonotum, the presence of prescutellar rows of scales, the scaling of the abdominal sternites [sterna], the presence of small pale apical spots on the dorsal surface of the femora, the presence of basal white spots on the costa, and the markings of the last hind tarsal segments.” We itemized the above characters and extracted text from the original descriptions of *kumbae* and *boneti*, *i.e.* from Gil Collado (1948) and Chwatt (1936), respectively, as follow.

“...the more extensive, rather differently shaped, dark scaling of the head...”.

—*kumbae*: “Occiput with two, dark, dorsolateral, conspicuous, oval or comma-shaped spots, formed by dark-brown upright forked scales. The remainder of the upright scales pale. Prominent dark-brown bare vertical area along the median suture [coronal suture].” [large dark spots illustrated]

—*boneti*: “Head with a broad vertica1 zone of narrow, reclining, white scales, among which numerous dark standing scales appear; on each side there is a rounded blotch of dark scales, which in turn, has a lateral region of white, narrow, reclining scales, and in the same posterior angle of the eyes there is a small dark spot.” [dorsolateral and lateral dark spots evident in the illustration]

We do not interpret these two descriptions to be substantially different, in addition the illustrations of the heads are quite similar, especially the two large dark spots of erect scales.

“...the pale (instead of golden) colour of the investiture of the mesonotum [scutum]...”.

—*kumbae*: "Mesonotum covered with a mixture of narrow, curved, dark-brown and pale scales...".
—*boneti*: "Mesonotum, except for its anterior edge, has sparse gold scales mixed with wider black scales."
Pale scales versus sparse gold scales could be explained by differences in lighting used for the observations.

"...the presence of prescutellar rows of scales... ".
—*kumbae*: "...dark-brown and pale scales, the latter broader on the anterior and anterolateral borders [of the scutum] and broad and flat around the prescutellar bare area."
—*boneti*: "In the middle region, in front of the scutellum, there are some white scales."
Neither description mentions rows of scales in front of the scutellum or provides a clear distinction between the two.

"...the scaling of the abdominal sternites [sterna]...".
—*kumbae*: "Sternites covered almost entirely with broad flat pale scales."
—*boneti*: Not noted.
No applicable difference.

"...the presence of small pale apical spots on the dorsal surface of the femora...".
—*kumbae*: "Fore femora dark, with a paler basal ventral surface and a few white scales at the distal end of the dorsal surface; middle femora similar, with a rather more extensive pale ventral area; hind femora dark on the dorsal side, except for a white distal spot, mainly pale on the ventral side...".
—*boneti*: Forefemur not noted. "Legs II [midlegs]: femora with their anterior and dorsal surfaces dark, and the posterior surface completely pale at the base, this coloration narrowing progressively toward the apex, where there is only a single white ventral line…". "Legs III [hindlegs] with predominantly white femora, and a narrow black dorsal strip, while the anterior face is peppered with abundant dark scales."
The apical pale femoral spot in *kumbae* is described only for the hindfemur. The illustration of the hindleg of *boneti* does not show an apical spot. We think this remains ambiguous pending comparison of the holotypes of the two nominal forms.

"...the presence of basal white spots on the Costa... ".
—*kumbae*: "Wings with scales dark and a small basal patch of pale scales on the lower and anterior surface of the costa."
—*boneti*: "The wing scales are dark, and even blackish over C and R_1."
A few pale scales at the base of the costa can be variable.

"...and the markings of the last hind tarsal segments [which markings not stated]."
—*kumbae*: "hind tarsi... first segment [tarsomere 1] dark, with an apical white band, second with one basal and one apical white band, the latter about twice the length of the former, third with one apical and one basal narrow band. The fourth tarsus [tarsomere 4] shows some variation: in one specimen it has a dark median band, while in the other the dark scales form only a narrow longitudinal line on the apical half of the lower surface. In both specimens the fifth tarsus [tarsomere 5] is white but has a similar dark line on the lower surface."
—*boneti*: "The metatarsi [hindtarsomeres 1] are black, with bristles of the same color, and a white spot at their apices which is a little longer than their width. The 2nd article [tarsomere 2] has a narrow pale basal zone, and another at its apex which is two and a half times its thickness; the 3rd with an apical ring the same as the 2nd and one at the base which is a little greater than its diameter. The 4th is white with a middle dark zone of one fourth its total length, and the 5th, completely white." [roughly matches the illustration of the hindleg]
No defining differences are given.

Chwatt (1948) wrote: "This *Aedimorphus* is described here under the provisional name of *A. boneti* s.sp. *kumbae*. Should the still unknown larva of *A. boneti* prove to be different from the one described above, *A. boneti* s.sp. *kumbae* will have to be treated as a new species, *A.* (*Aedimorphus*) *kumbae*." Our interpretation is that when *kumbae* was described, no significant characters were given to distinguish the two nominal taxa, and we therefore treat *kumbae* is a synonym of *boneti* until proven otherwise: ***kumbae* Chwatt, 1948, junior subjective synonym**

of *Aedes* (*Bifidistylus*) *boneti* Gil Collado, 1936. Should the larvae be found, the larva of *kumbae* possesses some potentially unique characteristics for diagnosis, such as an array of variously shaped spines on the siphon and a dense patch of comb scales. The nominal subspecies *kumbae*, which is listed as a species in the Encyclopedia of Life, must be removed from the list of valid species of *Aedes*.

Aedes (*Collessius*) *elsiae* (Barraud)

subspecies ***elsiae*** (Barraud, 1923a)—original combination: *Finlaya elsiae*. Distribution: Cambodia, India, Malaysia, Nepal, People's Republic of China, Taiwan, Thailand, Vietnam (Wilkerson *et al*. 2021).

subspecies ***vicarius*** Lien, 1968—original combination: *Aedes* (*Finlaya*) *elsiae vicarius*. Distribution: Taiwan (Lien 1968).

The nominotypical subspecies was described from male and female cotypes (Barraud 1923a) and other conspecifics from Shillong, Assam, India. Using exuviae from the cotypes and additional specimens to document variation, Barraud (1923c) described the larva with illustrations of the siphon and antenna. Barraud (1934) then described in more detail the adults (both sexes) and larva, with illustrations of the larval head, thorax and siphon. Darsie (2010) described the pupa of *elsiae* (as a species of *Ochlerotatus* Lynch Arribálzaga, 1891a) from sites in Nepal relatively close (about 400 km) to the type locality of *elsiae* in northern India. Townsend (1990) reported 19 syntypes of *elsiae* in the collection of the Natural History Museum, London, but not the cotypes or larval exuviae.

Subspecies *vicarius* was described and illustrated in all life stages, except the egg, from Chuchi, Chiai Hsien, Taiwan, but was also documented from many other localities in the original description. It is apparently found only on Taiwan. It and *elsiae* are similar in many respects in the adult and larval stages. In the larval stage, the two nominal forms have setae 1-M and 1-T very stout and borne on prominent tubercles, and seta 1-S stout and aciculate. The unusual character of these stout thoracic setae is also found in *Aedes* (*Collessius*) *shortti* (Barraud, 1923a) and *Ae*. (*Col*.) *macfarlanei* (Edwards, 1914). The larval cuticle of subspecies *vicarius* is, however, densely covered with spicules, a significant difference from *elsiae*. Lien (1968) summarized the differences between *elsiae* and *vicarius* in the original description: "The mosquito [*vicarius*], in most respects, shows a close resemblance to *Aedes elsiae* and is therefore described here as a new subspecies of *Aedes elsiae*. It differs from type species chiefly as follows: The venter of adults mainly dark brown instead of 'mainly yellowish'; a patch of broad dark scales sandwiched by two patches of broad white scales on upper and middle aspects of *ppn* [postpronotum] instead of 'narrow yellow and broad white scales on lower border of *ppn*'; antennal hair [seta] 1-A of larva inserted at about basal third of shaft and bifid instead of 'at about middle' and 'with 3–5 branches'; thoracic and abdominal integument densely spiculate. The male terminalia is [*sic*] almost indistinguishable from that of type species." We instead judge these differences to clearly indicate separate species. We do not accept the reasoning that since the two forms are similar that they should be subspecies.

The pupal stage of *elsiae* was not available to Lien (1968) when he published a detailed illustration of the pupa of *vicarius*. The description and illustration of the pupa of *elsiae* by Darsie (2010) allowed direct comparison of the pupae of the two nominal forms. Darsie (2010) wrote: "From the illustration it can be separated from the subspecies *elsiae* pupa as follows: in *Oc*. *e*. *vicarius* seta 1-II has 4 branches and *Oc*. *e*. *elsiae* has 10–16 branches; seta 9-VII has 4 branches in the former and 8–10 branches in the latter." We compared the illustrations of the two nominal forms and confirm the differences noted by Darsie. However, we also note many other obvious differences, such as nearly universal differences in the length and number of branches of setae (shorter and fewer in *vicarius*) and a very differently shaped paddle (~1.25 times longer than wide in *vicarius*; nearly round in *elsiae*). It is always possible that this is attributable to an undetected species complex, misidentification or a mix-up of specimens or illustrations, but the differences in the larval stage and adults remain to support our conclusions.

Given the significant morphological differences and the geographic isolation of subspecies *vicarius*, we hereby recognize its status as a species: ***Aedes* (*Collessius*) *vicarius* Lien, 1968**. *Aedes vicarius* is currently listed as a species in the Encyclopedia of Life.

Aedes (*Col*.) *elsiae* has one synonym: *Aedes* (*Finlaya*) *simulatus* Barraud, 1931. It was described from a single female from Assam, Haflong, Cachar Hills, India and was listed as a synonym, without comment, in Barraud (1934). There are no synonyms of *Ae.* (*Col*.) *vicarius*.

Aedes (*Mucidus*) *aurantius* (Theobald)

subspecies ***aurantius*** (Theobald, 1907)—original combination: *Pardomyia aurantia*. Distribution: Australia (Queensland), Indonesia (Western New Guinea [formerly Irian Jaya]), Malaysia, Papua New Guinea (Lee *et al*. 1984).

subspecies ***chrysogaster*** (Taylor, 1927)—original combination: *Mucidus chrysogaster* (subspecific status by Knight *et al*. 1944). Distribution: Australia, Irian Jaya [Western Papua New Guinea, Indonesia], Papua New Guinea (Lee *et al.* 1984).

The two nominal taxa are members of *Aedes* subgenus *Mucidus*, Group B Pardomyia (Edwards 1932a; Tyson 1970; subgenus *Pardomyia* of Reinert *et al*. 2004), which also includes *Ae. quadripunctis* (Ludlow, 1910) (in Theobald 1910) (Philippines) and *Ae*. *nigrescens* (Edwards, 1929) (in Paine & Edwards 1929) (= *painei* Knight, 1948) (Papua New Guinea, Solomon Islands). Species in the Pardomyia Group share some variable characters, which have led researchers to relate them to the nominotypical species. *Aedes quadripunctis* was considered a subspecies of *aurantius* by Basio (1971) and later returned to species status by Tsukamoto *et al.* (1985), and *Ae. nigrescens* was originally described as a variety of *Pardomyia aurantia* but elevated to species (as *painei*) by Knight & Hull (1951).

The nominotypical subspecies was described from an unknown number of adult females collected in the city of Kuching, Sarawak, Malaysia (Island of Borneo). Type specimens are in the Natural History Museum, London (Townsend 1990). Characters given in the original description of *aurantius* have been used in keys and/or descriptions (Knight *et al*. 1944; Knight 1947; Mattingly 1961; Tyson 1970; Lee *et al.* 1984), as indicated in the following extract from the original description (Theobald 1907).

> ♀. Head pale brown, densely clothed with bright golden yellow narrow-curved scales, particularly dense around the borders of the eyes, numerous rich ochraceous to golden yellow long upright forked scales, becoming a little darker at the sides... the whole head presents a general golden yellow appearance.
>
> Thorax bright brown, with a prominent band of brilliant golden yellow narrow-curved scales running across it behind the head [the extent of this band is not noted], the remainder clothed with deep black narrow-curved scales of almost sooty appearance....
>
> Abdomen golden brown, the two basal segments [terga] clothed with almost entirely deep violet black scales, the third with some median spots of bright golden yellow scales, the remainder having gradually more golden yellow scales mixed with the violet black until the segments [terga] become brilliant metallic golden yellow; venter mostly golden yellow....
>
> …femora and tibiae spotted with rich golden and violet-black… in the hind legs the base of the first tarsal [tarsomere 2], second tarsal, and to some extent the third tarsal, with a narrow yellow band, most pronounced on the first tarsal, the last hind tarsal pure white [hindtarsomere 5 not noted].…

Theobald also noted that "It varies to some extent in regard to the amount of golden scales on the abdomen and the spotting of the legs."

Subspecies *chrysogaster* was described from Berner Creek, near Innisfail, in northeastern Queensland, Australia, just south of Cairns. A female holotype and a female paratype served for the description. Illustrations were promised for a future publication but we are not aware of it having been done. The types are in the School of Public Health and Tropical Medicine, University of Sydney, Sydney, New South Wales, Australia. The following characters from Taylor (1927) roughly parallel characters given above for the female of *aurantius*.

> ♀. *Head* covered with golden narrow-curved and dark upright forked scales, the latter very numerous; a dense median row of sickle-shaped golden ones in the middle; the narrow-curved golden scales round the eyes are very prominent, widening out laterally... palpi about one-quarter the length of the proboscis, densely covered with golden scales, except about the apical quarter, which is clothed with black scales... proboscis covered with golden scales with irregular patches of black ones.... Antennae with basal lobes pale testaceous, with a few small flat golden scales on inner surface.... *Thorax*: scutum chocolate-coloured, covered with mixed golden and chocolate-brown, narrow-curved scales; there is a moderately broad median transverse band of golden scales reaching right across the scutum, reaching this but not passing it is a broad (about a quarter the width of the scutum) stripe of golden scales; the golden scales are very pronounced on the anterior margin of the scutum... prothoracic lobes prominent, black, clothed with golden narrow-curved scales… pleurae blackish brown, with pale golden flat scales in the middle.... *Abdomen*: first segment

> dark chocolate-brown covered with black flat scales… also a narrow, median, basal patch of pale golden, loosely applied, flat scales... segments 2 to 4, inclusive... each with two small, submedian, basal, golden spots and golden, median, lateral patches, largest on the fourth; third segment with a small subapical, golden spot toward the edge on either side; fourth flecked with scattered golden scales; segments 5 to the apex black-scaled, profusely mottled with golden scales... venter clothed with golden scales except the apex, which is dark-scaled. *Legs*: femora of fore legs... heavily spotted with golden scales, with a basal golden band, knees golden; tibiae... profusely spotted with golden scales, apex golden; first tarsal joint with basal golden banding, apex narrowly golden, remainder mottled black and golden; second to fourth joints black-scaled with moderately broad basal banding, fifth golden with a few scattered dark scales; femora, tibiae and tarsi of mid legs similar to those of the fore legs... the fifth tarsals are entirely golden; femora and tibiae of hind legs similar to those of the fore and mid legs; first tarsals black-scaled, not mottled, with a basal golden band, second tarsal black with basal golden banding, third and fourth tarsals black with creamy-white basal banding, fifth tarsal creamy-white....

Except for the adult females there are no comprehensive comparisons of the other life stages of the two nominal taxa. Edwards & Given (1928) partially described and illustrated the pupal and larval stages of *aurantius* (as *Pardomyia aurantia*) from Singapore. They noted a long pupal trumpet and rounded paddles lacking fringe; and a larva with mostly single setae and mandibles (illustrated) modified for grasping prey. In contradiction, in a key, Tyson (1970) wrote: "Paddle [of *aurantius*] with the lateral margin densely and conspicuously spiculate." Penn (1949) published a description and illustration of the pupa of subspecies *chrysogaster*, but apparently did not have specimens of subspecies *aurantius*, and did not find sufficient characters in Edwards & Given (1928) to contrast the two subspecies. Mattingly (1970) described the eggs of subspecies *aurantius* from Selangor, Malaysia, but we are not aware of a description of the eggs of subspecies *chrysogaster*.

Tyson (1970) separated the two nominal taxa by geographic area: *chrysogaster* in the Australasian Region and *aurantius* in the Oriental Region. He provided a key for separating females of *aurantius*, *chrysogaster* and *painei* (= *nigrescens*), but stated in a footnote that the males of the *aurantius* complex (these three nominal taxa) are "indistinguishable."

Without comment, Knight *et al.* (1944) included *chrysogaster* as a subspecies of *aurantius* in a key to *Aedes* in the Australasian Region. They used the following characters to separate *aurantius chrysogaster* from *aurantius nigrescens* and *aurantius aurantius*:

chrysogaster—"Tarsal segments [tarsomeres] basally banded with golden scales (V of mid legs all golden), segments III and IV of hind legs with white basal bands, segment V of hind legs entirely creamy-white; abdominal segment I with narrow median patch of golden scales".

aurantius and *nigrescens*—"Tarsal segments of fore and mid legs unbanded, brown, segments I, II and often III of hind legs basally yellow banded, segment V entirely white" Characters to distinguish *aurantius* from *nigrescens* included: "Abdominal tergites [terga] I and II almost entirely black, III with some median spots of golden scales, IV to VII with gradually more golden scales until the last segments are brilliant golden".

Oddly, the key character of a basal white band on tarsomere IV of the hindleg of *chrysogaster* is not mentioned for *aurantius*.

Knight (1948) wrote a note about his efforts to corroborate the distinctness of subspecies *chrysogaster*: "Personal communications from Dr. W. V. King... and Mr. D. J. Lee... both of whom have examined the types, have disclosed that this subspecies (at least the type specimens) differs from either [both?] *aurantius aurantius* (Theobald) or [and?] *a. painei* Knight [= *nigrescens*] in possessing a narrow basal white band on the fourth hind tarsal segment [hindtarsomere 4]. Also, Mr. Lee reported that the scutal scaling of the holotype is strictly as described by Taylor, but that the differentiation of the pattern in the paratype is less obvious."

Mattingly (1961), in his treatment of Indomalayan *Aedes*, including the subgenus *Mucidus,* redescribed all stages of subspecies *aurantius* using specimens from throughout its range, and for females he noted: "Scutum covered mainly with narrow, dark brown scales, golden scales confined to anterior border and shoulders [this is also as later described and illustrated by Tyson 1970]…. Hind tarsus with first two segments pale at base, 3rd and 4th narrowly pale at base or entirely dark, 5th conspicuously pale, contrasting sharply with the dark apex of the 4th segment." And in the key to females: "Abdomen with tergites [terga] IV–VII largely or wholly golden scaled". He did not discuss or describe *chrysogaster* except to contrast it with *aurantius* in a key to females: "Scutum with more numerous golden scales; fourth hind tarsal with narrow basal white band". He did not compare subspecies *chrysogaster* to other life stages of *aurantius*.

Lee *et al.* (1984) distinguished adult females of the two nominal forms in a key (reformatted here to conform to journal style).

2(1) Scutum dark scaled [sharply] contrasting with prominent transverse area of narrow yellow scales on anterior margin and with a few yellow scales around prescutellar area, above wing root and (rarely) behind fossa; ppn [postpronotum] with narrow yellow scales on upper one third to one half. . . . . .*aurantius aurantius*
Scutum with more extensive yellow and/or golden-reflecting scaling; anterior yellow scaled margin not sharply contrasting. 3

3(2) Ppn [postpronotum] with narrow yellow scales on upper one quarter to one half; scutum with yellow scaling variable but usually including a more or less distinct transverse band at mid length. . . . . *aurantius chrysogaster*
Ppn with small patch of narrow yellow scales on upper one fifth; scutum dorsally with areas of golden-reflecting (rather than yellow) scales, not forming a band at mid length. . . . . *painei*

In the above key, the description of the pattern of golden ornamentation on the scutum of *chrysogaster* is rather vague: "yellow scaling variable but usually including a more or less distinct transverse band at mid length". Taylor's (1927) description (see above) is more detailed but since it lacks an illustration it is rather difficult to visualize, and does not seem to follow closely the characteristics of the holotype. In notes recorded by Stone and Knight for their 1977 catalog, we found an unpublished sketch of the holotype of *chrysogaster*, presumably drawn by Stone, which we interpret as follows: Anterior promontory with a pair of small chocolate-brown spots, annotated by the illustrator as "(bare?)"; scutal fossa with "chocolate brown scales", outlined anteriorly, laterally and posteriorly with "prominent golden scales"; dorsocentral area golden-scaled, anterior dorsocentral area "largely golden with some chocolate brown intermingled" and the posterior dorsocentral area "mainly golden, some brown"; antealar and supraalar areas "golden", antealar area bordered anteriorly by a bare dark brown line, presumably along the prescutal suture.

There are two distinct scutal patterns outlined above. The nominotypical form has an anterior golden band, and *chrysogaster* has a variously described broad transverse band. There are also apparent differences in characteristics of the legs and abdomen, which we do not consider here but which could be of significance in separating the two nominal taxa, or could be indicators of a species complex.

Lee *et al*. (1984) included distributional notes which we believe are based on identifications by E. N. Marks that indicate sympatry of the two nominal forms: "*Ae aurantius aurantius* is known from Malaya, Indonesia and Borneo and in the Australasian Region has been recorded a number of times from West Irian and Papua and from 2 locations in Queensland (Innisfail and Lockhart R. Mission); the type locality of *Ae aurantius chrysogaster* is Innisfail, Qd. and it has also been recorded from West Irian, New Guinea and Papua...."

In summary, 1) Knight *et al*. (1944) provided no justification for regarding *chrysogaster* as a subspecies of *aurantius*, which has since been unjustifiably followed by others; 2) we believe the divergent patterns of golden scutal scales alone are sufficient to distinguish species; 3) *aurantius* and *chrysogaster* are sympatric and identifiable with no apparent difficulty in the area of overlap. For these reasons, we hereby reinstate *chrysogaster* to its original species status: ***Aedes* (*Mucidus*) *chrysogaster* (Taylor, 1927)**. *Aedes chrysogaster* is currently listed as a species in the Encyclopedia of Life.

Aedes aurantius has a single synonym: *Ekrinomyia aureostriata* Leicester (1908) from Klang, near Kuala Lumpur [Selangor], Malaya [Malaysia], synonymy with *aurantius* by Edwards (1913b), who stated "In Dr. Leicester's collection in the British Museum are 3 ♂ and 4 ♀ cotypes of *E. aureostriata*; the females agree exactly with the type of *P. aurantia*." *Aedes* (*Muc.*) *chrysogaster* is without synonyms.

Aedes (*Neomelaniconion*) *lineatopennis* (Ludlow)

subspecies ***aureus*** Gutsevich, 1955—original combination: *Aedes* (?*Aedes*) *aureus* (subspecific status by Danilov 1977). Distribution: Russia, Russian Federation (Wilkerson *et al*. 2021).

subspecies ***lineatopennis*** (Ludlow, 1905)—original combination: *Taeniorhynchus lineatopennis*. Distribution: Australia, Bangladesh, Borneo (island), Cambodia, India, Indonesia, Laos, Malaysia, Nepal, Pakistan, People's Republic of China, Philippines, Russia, South Korea, Sri Lanka, Thailand, Timor, Vietnam (Wilkerson *et al*. 2021).

The taxonomic study of Huang (1985) provides a prelude to the treatment of these nominal taxa. Multiple identifications of *lineatopennis* in Africa have complicated the definition of this species. Huang, based on detailed morphological comparison of African specimens with type specimens and other material collected in the Philippines, determined that records of *lineatopennis* in Africa pertained to a previously unrecognized species, which she described and named *Ae*. *mcintoshi*. Since Huang excluded *lineatopennis* from Africa, all references to *lineatopennis* in Africa require re-evaluation (*e.g.* Ingram & de Meillon 1927; Edwards 1941; Gutsevich 1973).

The nominotypical subspecies was described from two adult females captured at Camp Gregg, Bayambang, Pangasinan, Luzon, Philippines. Knight & Hull (1953) designated a lectotype, which was later validated by Stone & Knight (1956a). Its most distinctive features include the head with median golden scales, scutum dark brown with broad golden lateral stripes, legs unmarked, abdominal terga with pale basal bands and wings with pale scales on some veins. A condensed version of the original description (Ludlow 1905) follows.

> *Taeniorhynchus lineatopennis*, n. sp.—♀. Head dark brown, with brassy yellow curved scales on median portion and extending from occiput to vertex... dark brown flat lateral scales, and a few forked scales... antennae dark brown... palpi... proboscis... clypeus dark brown....
>
> Thorax: prothoracic lobes dark brown... no scales; mesonotum dark brown, the median portion covered with dark brown curved scales bordered by a heavy band of brassy yellow curved scales, extending cephalad from one wing joint (inverted “U”) across to the other, a very distinct and easily-recognized marking. …pleura brown and clothed only with a few brown hairs [setae]; scutellum dark brown, with brassy yellow curved scales....
>
> Abdomen dark brown, with broad basal bands of “dirty white” scales hardly extending the full width of the terga; the first segment is dark, and the second has merely a median light spot, while on the ultimate segment the band is quite narrow; venter dark.
>
> Legs are brown throughout; coxae and trochanters and ventral side of femora somewhat lighter than the rest, a light spot near the apex of fore femora on dorsal side, *i. e.*, the ventral colour runs up... more distal joints are darker, ranging from purplish to fawn colour....
>
> Wings clear, clothed with brown and light typical *Taeniorhynchus* scales. The costa is dark throughout, the subcosta and first longitudinal [vein R_1] are mostly light scaled from the base of the wing to about the junction of the subcosta, and the stem of the fifth long vein [vein CuA] is also light, with some light scales on the lower fork. …halteres have a light stem and dark knob.

Knight & Hull (1953) described the male genitalia and larva, Tanaka (2003) described the pupa and Choochote *et al*. (2001) described the egg of subspecies *lineatopennis*. Gutsevich (1955) described *aureus* from Kraskino, Russia, which is an urban locality in the Khasansky District of Primorsky Krai, located on the shore of Posyet Bay, 282 km southwest of Vladivostok, near the border with North Korea. If or where a type series was deposited is not known. An unpublished (1973) translation by B. F. Eldridge of the original Russian description follows.

> *Aedes* (*Aedes*?) *aureus* Gutzevich, sp. n.
>
> Distinguishing features: Intense golden scales on lateral part of mesonotum. Large clearly outlined golden spot on occiput, presence of light scales on wings, irregularly shaped light spot on abdominal tergites [terga], entirely dark proboscis and tarsi.
>
> Female: Scales behind eye brown, abutting [eyes abutting? abutting eyes?]. Occiput with large spots of upright golden scales and hairs [setae]. Proboscis and palpi with unicolored brown scales; sometimes with middle third of proboscis having a single light scale. Proboscis as long as front femur. Length of antennae about 1/5 of length of proboscis. Antennae brown. Mesonotum with a longitudinal expanding [posteriorly?] stripe of chocolate-cinnamon scales. Lateral part of mesonotum with golden scales. Body of thorax devoid significantly of accumulated scales; the last forming a small spot on sternopleuron and mesepimeron. Bristles [Setae] (their arrangement and quantity play a part in the classification of the Oriental species of the subgenus *Aedes*): Proepimeral 6–8, parastigmatic [postspiracular] 5–7, upper mesepimeral 7–9, lower mesepimeral 3–5. Wing: costal vein covered with dark scales, subcosta mostly clear, cream-colored; base of radial, medial, and cubital vein with light scales, which vary among particular wings; anal vein with dark scales. Legs usually with dark scales; light longitudinal streak on posterior surface of femur, tibia, and first segment of tarsus. Tarsi without light rings. Claws equal on the anterior and middle tarsi and with teeth, the

> posterior tarsi without teeth. Abdomen from above usually with brown scales. Lighter yellowish-gray concentrated mainly in the middle and the anterior edge of the tergites, formed as indistinct spots. Abdominal hairs long, golden. Cerci very short. Length of body with proboscis 7–8 mm.
>
> Material (13 females) collected by K.P. Chaginem north of the Kraskino Primorskovo region in August 1947.

Gutsevich (1973), after comparison of *aureus* with *lineatopennis* from South Africa [= *Ae*. *mcintoshi* Huang, 1985], determined that *aureus* belonged in *Aedes* subgenus *Neomelanoconion,* thus removing the initial doubt expressed in the original description.

Danilov (1977) [summarized from a translation of the Russian] compared four *aureus* females from near the type locality with a female of *lineatopennis* from an undetermined [by us] locality in China (from the "IMP & TM collection"). To separate *lineatopennis* from *aureus*, Danilov determined that since there was a wide range of variation in the key character of the extent of basal pale scaling on the abdominal terga of putative *aureus* specimens, and also a wide range in the number of setae on the frontal stripe, that the characters were unreliable. He cited the wide distribution of *lineatopennis*, Afrotropical to South Korea, to conclude that *aureus* was simply a variant on the peripheral distribution of *lineatopennis*. He then decided, without explanation, that this distribution merited subspecies status for *aureus*. Of probable diagnostic significance, Danilov noted that *aureus* was much larger than *lineatopennis*.

The larva and male genitalia of *aureus* were later described and illustrated by Shestakov (1980) from specimens collected near the type locality. To further our understanding of his description, we generated a rough translation of his paper using Google Translate. Most informative to us, however, are his illustrations of the head and terminal segments of the larva and the male genitalia. We compared Shestakov's illustrations of the larva with the larva of *lineatopennis* illustrated by Mattingly (1961) and Knight & Hull (1953), and his illustrations of the male genitalia with the male genitalia of *lineatopennis* illustrated by Huang (1985). In the larval stage, the antenna of *aureus* has large spines on the inner surface but in *lineatopennis* the large spines are distributed over all surfaces. The siphon of *aureus* is short (index about 1.5) and widened medially whereas in *lineatopennis* it is longer (index about 2.5) with the widening more basal. The anal papillae of *aureus* are about 1.5 times the length of the saddle, gradually narrowing, while in *lineatopennis* they are about 2.5 times the length of the saddle, slender and tapered to a point. In the male genitalia, the stout subapical spines of the gonocoxite appear to be shorter and more numerous in *aureus* (the *aureus* illustration is a bit stylized so it is difficult to confidently compare them). Huang (1985) used differences in the nature of these spines to distinguish *Ae*. *mcintoshi* from *lineatopennis*. Also, tergum IX of *aureus* is somewhat rounded, while in *lineatopennis* it is slightly emarginate.

The siphon of the *lineatopennis* larva illustrated by Lee (1999) and the siphon of *aureus* illustrated by Shestakov (1980) are both short and mesally expanded. Also, both nominal taxa exhibit peak activity in August and September (Shestakov 1980; Hwang *et al.* 2020). Since both are found in temperate climates in the same geographic region, we suspect that they are conspecific and the correct name for the form found in Korea is probably *aureus*, not *lineatopennis*. The name *lineatopennis* appears in all recent keys for the identification of mosquitoes that occur in the Republic of Korea (South Korea) (Lee & Egan 1985; Lee & Zorca 1987; Lee 1999; Ree 2003). The nominal taxon *aureus* has only been treated as a species by Gutsevich (1955, 1971, 1973, 1974) and Danilov (1977), and has only been designated and treated as a subspecies of *lineatopennis* by Danilov (1977).

The nominal taxon *lineatopennis* apparently has a wide tropical distribution that extends from India to Australia. The nominal taxon *aureus* is only known from temperate areas ranging from the Korean peninsula to western Russia and probably China. In view of distinct ecological and morphological differences, we hereby restore subspecies *aureus* to species status: ***Aedes*** **(*Neomelanoconion*)** ***aureus*** **Gutsevich, 1955**. *Aedes aureus* is currently listed as a species in the Encyclopedia of Life. Synonyms: None.

Aedes (*Neomelanoconion*) *lineatopennis* (Ludlow, 1905) has one synonym: *Pseudohowardina linealis* Taylor, 1913. Synonymy by Taylor (1916).

Aedes (*Ochlerotatus*) *canadensis* (Theobald)

subspecies ***canadensis*** (Theobald, 1901c)—original combination: *Culex canadensis*. Distribution: Canada, Dominican Republic, Mexico, United States (Alaska and continental) (Wilkerson *et al.* 2021).

subspecies ***mathesoni*** Middlekauff, 1944—original combination: *Aedes* (*Ochlerotatus*) *mathesoni* (subspecific status by Rings & Hill 1948). Distribution: Southeast United States (Alabama, Florida, Georgia, South Carolina) (Rings & Hill 1948).

The nominotypical subspecies was described from specimens collected near Toronto, Canada. Theobald (1901c) stated: "A very distinct species, in which the legs are very characteristically marked, the last tarsal joint [tarsomere 5] of the hind legs being entirely dull white and the banding of the legs involving both sides of the joints. The dusky scaled abdomen, with the creamy-white basal lateral patches, is also very characteristic." Additionally we note: Maxillary palpus with apical half of palpomere 2 pale; scutum dull purplish brown to deep chestnut brown, covered with varying patterns of curved golden-brown scales; wing all dark; and venter of abdomen covered with pale yellowish scales. In the Natural History Museum, London, Townsend (1990) found: "Lectotype male, designated by Belkin, 1968b: 4 – Canada: Ontario, near Toronto, Trout Creek. Paralectotypes (14) – Canada: 1 male, 13 female." "Belkin misread the type locality as 'Front Creek', and overlooked some of the paralectotypes." Other pertinent descriptions include: Adult female, larva and male genitalia (Carpenter & LaCasse 1955); larva and male genitalia (Ross 1947); pupa (Darsie 1951); and egg (Craig 1956; Craig & Horsfall 1958; Ross & Horsfall 1965; Kalpage & Brust 1968; Horsfall *et al*. 1970). Notably, *canadensis* is cold adapted, emerging very early in the spring (reviewed by Horsfall 1972).

Notable characters of the larva include: Setae 1-A and 5–7-C multi-branched, 5–7-C not in a straight line, 6-C inserted far forward of 5-C; seta 1-M small and short, not reaching bases of prothoracic setae; comb with many scales in a patch, individual scales pointed and fringed with rather slender subequal spinules; siphon index 3.0–4.0, pecten with 13–24 evenly spaced spines on basal two-fifths of siphon, siphonal tuft (seta 1-S) usually 3–8-branched, inserted beyond pecten; saddle incomplete, extending about 0.67 down side of segment, ventral brush (seta 4-X) large, usually with 2 precratal setae; anal papillae tapered, about 1.5 times as long as saddle (Carpenter & LaCasse 1955; Harrison *et al.* 2016).

Subspecies *mathesoni* was described, as a species, by Middlekauff (1944) from specimens collected in south-central Florida (Kissimmee) in late summer and autumn [early season occurrence not noted]. Middlekauff recognized *mathesoni* as quite similar to *canadensis*: "This species [*mathesoni*] is most closely related to *Aedes canadensis* (Theob.), but that species [*canadensis*] lacks the nearly black scales of the mesonotum and the white areas on the legs are more extensive. The male genitalia of *canadensis* differ only slightly, the spines of the ninth tergites [terga] being less regularly placed and more abundant, and the tenth sternites [paraprocts] being somewhat curved and acutely [*sic*] apically." "Holotype, allotype and one paratype [are] in the collection of the United States National Museum."

Rings & Hill (1946) described the larva of *mathesoni* using reared-associated specimens from Georgia (Camp Gordon) and from northeastern Florida (Camp Blanding). They found the larvae of *canadensis* and *mathesoni* "to be remarkably similar, the only apparent difference being in the degree of branching in the head hairs [setae] and antennal tufts [seta 1-A]." In general, mean branch counts for setae 5- and 6-C were lower in specimens from further north (*canadensis*) than southern specimens. They counted setal branches of 89 *canadensis* in places ranging from British Columbia to Florida and 33 *mathesoni* from Georgia and Florida: Seta 5-C, mean number of branches 6.77 (4–10) (*canadensis*), 9.8 (6–14) (*mathesoni*); seta 6-C 5.06 (range not given) (*canadensis*), 7.1 (4–9) (*mathesoni*). Rings & Hill compared specimens of *mathesoni* from Georgia and Florida and found the same tendency: "... individuals collected in the more southern portions of the geographical range showed relatively more branching than those from the north." Seta 5-C, mean 8.9 (Georgia), 10.7 (Florida); seta 6-C, 7.0 (Georgia), 7.2 (Florida). We think these numbers are suggestive of clinal variation. Rings & Hill concluded: "...there is a very close phylogenetic relationship between the two forms and that these forms do not possess differences of specific rank."

Rings & Hill (1948) documented and illustrated the scutal patterns of *canadensis* and *mathesoni* and noted that there were many "intergrades". They stated: "The data here presented are interpreted by the authors as evidence that *mathesoni* is a melanistic, geographical variation of *A. canadensis*." They illustrated intergrades showing the extent of pale scaling on the hindtarsomeres and mapped the geographical extent of intergradation and showed a broad area of intergrades. Those north and south of this zone were easily identified as either *canadensis* or *mathesoni*, respectively. Darker coloration seen on the legs was explained as directly related to higher temperatures at decreasing latitudes. They found little or no differences (intergrades) in the larvae or male genitalia of the two forms. The notion that *mathesoni* was a subspecies of *canadensis* was introduced in this paper; however, their unattributed definition of subspecies allows for sympatry (which for us precludes subspecific status). They concluded: "The phylogenetic rank of subspecies is generally applied to a part of a species showing geographical variations which intergrade with a subspecies occupying different though usually adjacent and overlapping parts of the general range of the species." They, however, continued to use the subspecies rank as a convention for pointing out observed variability.

Bickley (1981) furthered the observations of Rings & Hill (1946, 1948) in an analysis of adults and larvae of more than 1,400 specimens in the United States National Museum (Smithsonian Institution, National Museum of Natural History (USNM), Washington, D.C.). He concluded: "From the survey described here, involving specimens from 43 North American states and provinces, it may be concluded that the geographical range of *Ae. canadensis mathesoni* does not extend northward from southern Georgia and South Carolina. Only 1 character, the narrow pale rings on the hindtarsomeres, is available as a means of recognizing this rare subspecies, the validity of which is certainly complicated by the existence of intergrades."

Harrison *et al.* (2016) also used the pale bands of the hindtarsomeres to separate *canadensis canadensis* from *canadensis mathesoni*, but they could not separate them in the larval stage. They stated (Note 14): "The two subspecies of *Ae. canadensis* are separated in the adult female key, but are not separated in the larval key. Those subspecies, *Ae. canadensis canadensis* and *Ae. canadensis mathesoni* represent a real taxonomic enigma that begs to be resolved with more study and the use of modern techniques." An explanation for this enigma may lie in the abundant examples of mosquito morphological and physiological variation influenced by the environment, for example: Factors affecting larval setal branching (Colless 1956; Mattingly 1975); altitude and latitude influencing diapause and the size of anal papillae in *Wyeomyia smithii* (Coquillett, 1901) (Bradshaw & Lounibos 1977); season and temperature affecting melanism in species of the genus *Anopheles* (Harrison 1980); and the effect of temperature on morphological attributes of *Anopheles merus* (Dönitz, 1902) (Le Sueur & Sharp 1991).

Ongoing sampling of mosquitoes at several locations in North America is being carried out by the National Ecological Observatory Network (NEON). Their sampling is based on light trapping of adult females, which are then identified morphologically. A subsample is kept as morphological and DNA vouchers, with single legs used for sequencing of the barcoding region of the mtDNA *COI* gene. The NEON database (https://biorepo.neonscience.org/portal/collections/list.php?usethes=1&taxa=80835) has 571 records for *canadensis canadensis* (also written simply as *canadensis*) and *canadensis mathesoni*. The database includes a limited number of sympatric records of nominotypical *canadensis* with *canadensis mathesoni* in the area of historical "intergrades," *i.e.* Florida Disney Wilderness Preserve near Kissimmee and near Gainesville, Florida, which is relatively close to Camp Blanding. The Barcode of Life Data System (BOLD: boldsystems.org) includes a single entry for *canadensis mathesoni* (http://www.boldsystems.org/index.php/Taxbrowser_Taxonpage?taxon=Aedes%20canadensis) that corresponds to a specimen collected by NEON (specimen number MOSN4427-20), which allowed us to visualize, using tools available in BOLD, its genetic distance from more than 300 other nominal *canadensis* in the database. This specimen clustered very closely with all others at a distance of < 1.0%, well within accepted *COI* barcode criteria for an individual species. This is a single data point, from a single gene, from unpublished data, but it suggests that further focused collecting and sequencing will probably reveal that *canadensis* and *mathesoni* are conspecific, at least using the *COI* gene.

We do not think there is any indication of genetic divergence, only easily explicable clinal variation. Plus, the two nominal taxa are apparently sympatric and, although weak, the single molecular indicator shows they are genetically very similar. We therefore think that subspecies *mathesoni* is a synonym of *Aedes* (*Ochlerotatus*) *canadensis*, which we formally assert here: ***mathesoni* Middlekauff, 1944, junior subjective synonym of *Aedes* (*Ochlerotatus*) *canadensis* (Theobald, 1901c)**. Future work may prove we have not interpreted the literature correctly, but until then *mathesoni* belongs as a synonym. An alternate hypothesis, that there is a northern species and a southern species with a zone of hybridization, is valid. We do not see signs of that, but it should not be totally discounted. The nominal subspecies *mathesoni*, which is listed as a species in the Encyclopedia of Life, must be removed from the list of valid species of *Aedes*.

There is one other synonym of *Ae. canadensis*, *Culex nivitarsis* Coquillett, 1904, synonymized by Howard *et al.* (1917), who wrote: "Coquillett described *Culex nivitarsis* from two specimens and none have been since collected. Dr. C. S. Ludlow suggested to us that these specimens were only aberrations of *A. canadensis*, and we have adopted this view."

Aedes (*Ochlerotatus*) *caspius* (Pallas)

subspecies ***caspius*** (Pallas, 1771)—original combination: *Culex caspius*. Distribution: Afghanistan, Albania, Algeria, Armenia, Austria, Azerbaijan, Bahrain, Belarus, Belgium, Bosnia and Herzegovina, Bulgaria, Croatia, Cyprus, Czech Republic, Denmark, Djibouti, Egypt, Estonia, Finland, France, FYRO Macedonia, Georgia, Germany, Greece, Hungary, Iran, Iraq, Ireland, Israel (Gaza Strip and West Bank), Italy, Kosovo, Japan, Jordan, Kazakhstan, Latvia, Lebanon, Libya, Lithuania, Malta, Mauritania, Moldova, Mongolia, Montenegro, Morocco, Netherlands, Norway, Pakistan, Palestine, People's Republic of China, Poland, Portugal, Qatar, Romania, Russia, Saudi Arabia, Serbia, Slovakia, Slovenia, Spain (includes Balearic & Canary Islands), Sri Lanka, South Sudan, Sudan, Sweden, Switzerland, Tajikistan, Tunisia, Turkey, Turkmenistan, Ukraine, United Arab Emirates, United Kingdom, Uzbekistan, Yemen (Robert *et al*. 2019; Wilkerson *et al.* 2021, incorrectly listed from Canada and the United States).

subspecies ***hargreavesi*** (Edwards, 1920)—original combination: *Ochlerotatus caspius* var. *hargreavesi* (subspecific status by Harbach & Howard 2007). Distribution: Taranto, Italy [Puglia region] (Edwards 1920).

subspecies ***meirai*** Ribeiro, da Cunha Ramos, Capela & Pires, 1980—original combination: *Aedes* (*Ochlerotatus*) *caspius meirai*. Distribution: Cabo Verde [Cape Verde] (Republic of Cabo Verde) (Ribeiro *et al*. 1980).

The nominotypical subspecies was described from specimens collected in marshes near the Caspian Sea (Pallas 1771). No type specimens are known but Edwards (1920) wrote that the species was first collected from the northern Caspian Sea in the marshes near the city of Guriev [Guryev], present day Atyrau, capital of the Atyrau Region, Kazakhstan. However, Edwards did not give a source for his information. Given that *caspius* is a complex of at least two species (see below), a neotype and complete description from topotypic specimens are certainly needed.

Nominal *caspius* can be a very abundant pest. It is distributed throughout Europe, around the Mediterranean, the Middle East, Mongolia (Minàř 1976), China (Becker *et al*. 2020) and the northern sub-Saharan countries of Chad (Ndiaye *et al*. 2021), Mauritania (Mint Lekweiry *et al*. 2015) and Cabo Verde (subspecies *meirai*). Specimens from Mauritania "showed 100% homology [rDNA ITS2] with published *Ae*. (*Ochlerotatus*) *caspius* sequences from Italy." Nominal *caspius* is halophytic, found in dryer climates, but it is also adapted to freshwater habitats. Predictive spatial modelling by Wint *et al*. (2020), based on specimens and literature, reflects the above distribution, which would be expected since it is based on combined data that includes cryptic species.

The following are characters commonly used to identify the nominotypical form (after Becker *et al.* 2020 and Wilkerson *et al.* 2021).

Adult female. Hindtarsomeres 1–4 with basal and apical pale bands, hindtarsomere 5 entirely pale-scaled; wing speckled with more or less evenly mixed dark and pale scales, costa predominantly dark-scaled; abdominal coloration highly variable, terga usually with median longitudinal pale stripe, tergum VII sometimes nearly all pale, or entire abdomen pale-scaled (variability documented in Toma *et al*. 2017) [associated with hotter, drier areas]; scutum fawn-colored [light yellowish tan], with a pair of narrow dorsocentral pale yellowish stripes [usually referred to as white] reaching to posterior margin of the scutum.

Male genitalia. Gonocoxite with undivided basal mesal lobe (BML) [basal lobe of authors] gradually arising from the gonocoxite, bearing two closely approximated spine-like setae, larger seta hook-shaped and strongly curved apically (tip usually extending backwards to almost the middle of the seta).

Larva. Body surface without spicules; antenna uniformly spiculate, seta 1-A 3–12-branched; 18–28 comb scales in triangular patch, scales pointed (median apical spine distinctly longer than the others, at least on some scales); siphon index 1.8–2.6, elements of seta 1-S with 5–10 branches, inserted beyond middle of the siphon, with about 20 evenly spaced pecten spines reaching to about mid-length of the siphon, base of siphon with acus; segment X (anal segment) with incomplete saddle, and ventral brush (seta 4-X) with 12–17 cratal and 2 or 3 precratal setae; anal papillae lanceolate, 0.3–0.9 length of the saddle.

Edwards (1920) sought to define the nominate subspecies to separate it from closely related species, such as *Ae*. (*Och*.) *dorsalis* (Meigen, 1830) and *Ae*. (*Och*.) *leucomelas* (Meigen, 1804) [as *salinellus* Edwards, 1921b]. He described variation in a "Large series of this species [*caspius*]... recently... received at the British Museum from Italy, Macedonia, Palestine, Egypt and Mesopotamia, which show every gradation in the variation in the colour of the abdominal scales.... The thoracic coloration varies less; the two white longitudinal lines are nearly always present, though sometimes very narrow in two specimens from Italy, and in the type of *G. longisquamosa* [current synonym of the nominate subspecies], they are absent, the mesonotum then being uniformly fawn-coloured." Edwards (1920) then named subspecies *hargreavesi* [as a variety of *caspius*] stating: "Among a series sent from Taranto, Italy (*E. Hargreaves*), are six females which have the whole of the central area of the mesonotum covered with whitish scales though in regard to abdominal markings they agree with moderately dark specimens of the species [*caspius*]. Nothing approaching this variation has been seen from elsewhere and it therefore seems justifiable to distinguish them under a separate name." However, it is a bit puzzling that he also mentioned the pale lines as being absent in the type of *G. longisquamosa*. Harbach & Howard (2007) later elevated variety *hargreavesi* to subspecific status in accordance with Article 45.6.4 of the *International Code of Zoological Nomenclature*.

The type locality of *hargreavesi*, Taranto, is a coastal city in southern Italy in the region forming the heel of Italy's "boot". We are not aware of further collections in that part of Italy and *hargreavesi* is usually only mentioned in lists. This leaves us without confirmation/refutation of its validity using other life stages and DNA. Townsend (1990) reported the presence of four syntypes in the collection of the Natural History Museum, London, which allows the possibility of DNA analysis.

Edwards (1921d), in a revision of Palearctic mosquitoes, wrote that the basal lobe in the closely related *Ae. dorsalis* was "very prominent", as opposed to "much less prominent" in *caspius*. The distinction is evident in an accompanying illustration.

In Egypt, Kirkpatrick (1925) noted in a key that the basal lobe of *caspius* had two spines and that the appendage of the claspette was not keeled. This is in contrast to *Ae. detritus* (Haliday, 1833), which has a single spine and the claspette is keeled in the middle. Among specimens that Kirkpatrick otherwise considered to be *caspius*, he found two larval varieties. One with "Siphon about 2.3–2.6 times as long as broad; anal gills [anal papillae] longer than broad, two or three hair tufts [setae] outside barred area [grid] of ventral brush [precratal setae]. *Aedes* (*Ochlerotatus*) *caspius*." The other with "Siphon about 1.9–2.0 times as long as broad; anal gills very small and round; ventral brush with four or five tufts outside barred area. *A. caspius*, larval variety."

Kirkpatrick (1925) described and illustrated the basal mesal lobe of *caspius* thusly: "Basal lobe rather large, triangular, with an almost straight spine [seta] rising from near its apex, and a longer stouter spine with a strongly curved tip rising at about one third of the distance from the apex; the basal lobe also bears a row of short straight bristles [setae]." A large triangular lobe and the row of short "bristles" are unlike what others had observed for *caspius*.

Barraud (1934) likewise described and illustrated an apparently different basal mesal lobe: "coxite [gonocoxite] with pronounced basal [mesal] lobe carrying a strong bristly spine [seta] with hooked tip, one short spine, and a small number of flattened straight, bristles [setae]". Flattened straight setae are not mentioned elsewhere in the literature.

Marshall (1938), in *The British Mosquitoes*, described and illustrated all life stages (except the egg) in detail, seemingly in agreement with the general concept of *caspius* given above. Regarding the basal mesal lobe, he stated: "The basal [mesal] lobe of *A. caspius* carries a dense mass of bristles [setae], as well as two stout, conspicuous spines [setae]; the spine lying nearer to the base of the coxite [gonocoxite] being considerably longer than its companion, and having a markedly recurved extremity. As will be noted later, the hypopygium [genitalia] of *A. caspius* would be practically indistinguishable from that of *A. dorsalis* were it not for the fact that the basal lobe of the latter species is noticeably constricted at the base". Clavero (1946) and Natvig (1948) also described similar characteristics of *caspius* from other European countries.

Senevet *et al*. (1949) reported putative *caspius* specimens from three sites in French North Africa: Quargla, capital city of Quargla Province in the Sahara in southern Algeria; Salah, an oasis town in central Algeria, and Gabès, capital city of the Gabès Governorate, located on the coast of the Gulf of Gabès in what is now Tunisia. The Quargla specimens were different from typical *caspius* and different from specimens from the other two North African sites. "The scutum is absolutely devoid of the classically described white lines. It is completely and uniformly covered with tan [pale brown] scales. The basal mesal lobe is like the classical descriptions and drawings of Edwards [1921d], of Kirkpatrick [1925], of Barraud [1934], etc., and stands out only slightly, at a slight angle, covered with numerous setae. One of them is very large and bent into an 'S' shape or hooked, inserted on the apical half or two thirds of the lobe. There is another less developed seta, half the length of the large one, borne anteriorly on the lobe. The lobe therefore agrees well with the illustration of Edwards" (translated from the French). Senevet *et al*. (1949) did not describe exactly how the basal lobe differs, but the illustration suggests a rounded lobe with a much longer primary seta. The lobes of tergum IX of males from Quargla are different from the others as well. They are twice as long as wide, straight and slightly curved inwards. The illustrations given of the ninth tergal lobes from the three sites appear different in shape and in the number and nature of the setae. The claspette is also different from others, not exhibiting a narrowing on the base of the claspette, having a large tubercle between the base and filament, and having a seta basally.

The *caspius* reported by Minàř (1976) from Mongolia was compared to the closely related *Ae. dorsalis*. Of note is the depiction of the basal mesal lobes of both species as slightly projecting but of slightly different shapes, but not rounded.

The above variation was brought into sharper focus by Cianchi *et al*. (1980), who, using allozyme electrophoresis, found two distinct sympatric entities, *caspius* species "A" and *caspius* species "B". Since then there have been multiple indications of a complex of species. Darsie & Samanidou-Voyadjoglou (1997) separated two larval forms of *caspius sensu lato* in Greece. Schaffner (1998) suggested that only species "A" of Cianchi *et al*. was identified in France, so far only along the Atlantic coastline. Knio *et al*. (2005) wrote that "*Ochlerotatus caspius* appeared to be a complex of species. Morphological differences... between the population in the South of Lebanon from the Kasmieh River and the rest of the populations. ...Kasmieh River matched the typical description of *Oc*. *caspius*... in having... two submedial lines of whitish scales running along the length of the scutum. ...The rest of the specimens differed in having a scutum covered with scales golden-brown in color, which was similar to the description of *Ochlerotatus* (*Ochlerotatus*) *mariae* [scutum mainly golden brown-scaled, without definite longitudinal stripes].... Therefore, they seem to be a species near *caspius* and thus remain to be classified under *Oc*. *caspius*, which seems to be a species complex." Wassim *et al*. (2013) stated that "They [the two forms of *caspius*] have been identified as an autogenous [*sic*, anautogenous] form which requires a blood meal for egg development, need open space to breed (eurygamous) and abound in fresh water pools in agricultural areas, while the autogenous form is able to mate in confined spaces (stenogamous) and inhabits brackish and salty water breeding sites in coastal and inland desert areas...". Soliman *et al*. (2014), in a study of egg morphology, found that the "Fine structure micrographic work of eggs of the Egyptian *Ae*. *caspius* provides new morphological evidence that both autogenous and unautogenous [*sic*] forms are certainly different and suggests that those forms are two distinct species." Doosti *et al*. (2017) found strong evidence using mtDNA *COI* and *COII* gene sequences that indicated two species in *caspius sensu lato*. Detailed distributions of these two putative species have not yet been determined. Neither is it clear if *caspius* "A" or *caspius* "B" found in the Middle East corresponds to forms in Europe. The assumption seems to be that "A" and "B" are in Europe and that "A" is *caspius sensu stricto*.

In contrast, Porretta *et al*. (2011), using *COI* and *COII* gene sequences, studied the population genetics of 12 *caspius* populations from southern Europe and four from the western Mediterranean. They found no genetic structuring, which would be expected if habitats of this species had not been fragmented during the last ice age. They did not acknowledge the existence of *caspius* "A" or "B", subspecies *hargreavesi* from Italy or subspecies *meirai* from Cabo Verde.

The existence of a species complex is not only suggested but proven with the characterization of *caspius* "A" and "B", and other species probably exist in the complex. It is problematic to guess the status of subspecies *hargreavesi* since it has not been reported again from near its type locality and no other life stages have been studied. However, with the caveat that normal variation could be responsible for the pale scuta that Edwards observed, the character, supposedly representative of *caspius* "B", by Knio *et al.* (2005) (see above). We tentatively predict that subspecies *hargreavesi* corresponds to *caspius* "B" of Cianchi *et al.* (1980). For this reason we formally elevate it here to species status: ***Aedes* (*Ochlerotatus*) *hargreavesi* (Edwards, 1920)**. *Aedes hargreavesi* is not currently included as a species in the Encyclopedia of Life and should be added to the list of species of the genus.

Ribeiro *et al.* (1980) described subspecies *meirai* from islands in the Republic of Cabo Verde (also called Cape Verde). Cape Verde is located 570 km from the westernmost point of Africa, the Cape Verde Peninsula, Dakar, Senegal, after which it is named. It is in the Macaronesia ecoregion, along with the Azores, the Canary Islands, Madeira and the Savage Isles. Cabo Verde is about the same distance west from the Cape Verde Peninsula as it is from where *caspius* was found on continental Africa in Mauritania (Mint Lekweiry *et al.* 2015).

Aedes caspius sensu lato was first recorded from Cabo Verde by de Meira (1952). Ribeiro *et al.* (1980) wrote: "...a detailed analysis of the Cabo-Verdian *Aedes caspius* revealed the existence of some morphological differences which, combined with other factors, namely the practically complete geographical isolation of the Cabo Verde population, assumed taxonomic significance at the subspecific level. ...the comparisons [with the new subspecies] were based on samples of *caspius s.1.* from the south of Portugal (Algarve and Alentejo)" (translated from the Portuguese). Further they wrote: "Diagnosis. Not all individuals of the new subspecies are distinguishable from the nominate subspecies…. [new paragraph] The distinction of the two subspecies of *Ae*. *caspius* is based on the presence or absence of an accessory spine [seta] on the basal [mesal] lobe of the coxite [gonocoxite], on the terminalia [genitalia] of males, duplicating the postero-external spine [seta] (fig. 59) [figure number from the original publication]. Absent in the nominal subspecies (49 specimens examined from Portugal), this spine was present, at least on one side, in 12 of the 36 males from the island of Boa Vista examined for this character (six of which, including the holotype and 2 ♂ paratypes, have accessory spines on both sides)" (translated from the Portuguese).

Ribeiro *et al.* (1980) also did counts of select features in comparison with their specimens from Portugal. Pupa:

Setae 1-III,IV and 10-CT. Larva: Comb scales, pecten spines, antenna length to width ratio and seta 1-A. We noted significant overlap in all of these.

We do not believe that a single apparently anomalous character, present in only one third of the males of *caspius* from Cabo Verde, in comparison with a small sample from a single locality in the extensive range of the nominal form, is sufficient evidence to demonstrate genetic divergence. For this reason, we regard subspecies *meirai* as a synonym of the nominal form: ***meirai*** **Ribeiro, da Cunha Ramos, Capela & Pires, 1980, junior subjective synonym of *Aedes* (*Ochlerotatus*) *caspius* (Pallas, 1771)**. Consequently, "*Aedes meirai*" should be removed from the list of species of *Aedes* in the Encyclopedia of Life.

There is a parallel example which reinforces our decision. There are six other mosquito species in Cape Verde that are also present on mainland Africa, one of which is *Anopheles* (*Cellia*) *arabiensis* Patton, 1905. A year before the description of subspecies *meirai*, the same authors (Ribeiro *et al.* 1979) proposed a new subspecies, *An*. *quadriannulatus davidsoni* Ribeiro, da Cunha Ramos, Pires & Capela, 1979*,* based on many overlapping characters with other members of the Gambiae Complex known at the time. Cambournac *et al*. (1982) disagreed and asserted that the species in Cabo Verde was *An*. *arabiensis*, and the populations in Cape Verde were not different from those on the mainland. The implied synonymy of *davidsoni* with *arabiensis* is currently accepted.

Eleven synonyms of the nominotypical form are listed in Wilkerson *et al.* (2021). Until species in the Caspius Complex are characterized, we retain, in addition to *meirai*, 11 synonyms of *Ae*. *caspius*: *Culex punctatus* Meigen, 1804 (Aden); *Culex siculus* Robineau-Desvoidy, 1827 (Sicily); *Culex maculiventris* Macquart, 1846 (Algeria); *Culex penicillaris* Rondani, 1872 (Italy, potentially a synonym of *Ae. hargreavesi*); *Grabhamia longisquamosa* Theobald, 1905b (Tunisia); *Grabhamia subtilis* Sergent & Sergent, 1905 (Algeria); *Mansonia arabica* Giles, 1906 (Bahrain); *Taeniorhynchus africanus* Neveu-Lemaire, 1906 (Egypt); *Grabhamia willcocksii* Theobald, 1907 (Egypt); *Culex arabicus* Becker, 1910 (Yemen); *Aedes* (*Ochlerotatus*) *epsilonn* Séguy, 1924 (Algeria). There are no synonyms for *Ae. hargreavesi* (Edwards, 1920).

Aedes (*Ochlerotatus*) *fulvus* (Wiedemann)

subspecies ***fulvus*** (Wiedemann, 1828)—original combination: *Culex fulvus*. Distribution: Argentina, Belize, Bolivia, Brazil, Colombia, Costa Rica, Cuba, Ecuador, French Guiana, Guatemala, Guyana, Mexico, Panama, Peru, Suriname, Trinidad and Tobago, Venezuela (Wilkerson *et al.* 2021, South Korea listed in error).

subspecies ***pallens*** Ross, 1943—original combination: *Aedes* (*Ochlerotatus*) *fulvus pallens*. Distribution: United States (continental) (Wilkerson *et al*. 2021).

Distributions listed in Wilkerson *et al*. (2021) for *fulvus sensu stricto* from the continental United States and for *pallens* from Cuba and Mexico could not be documented and should be omitted.

The nominal forms are members of the Chrysoconops Group of Wilkerson *et al*. (2015)—genus *Chrysoconops* Goeldi, 1905; Group C, *fulvus*-group of Edwards (1932a); *Ochlerotatus* subgenus *Chrysoconops* of Reinert *et al*. (2008, 2009). In addition to the two nominal taxa, the group also includes *bimaculatus* (Coquillett, 1902b); *jorgi* Carpintero & Leguizamón, 2000; *pennai* Antunes & Lane, 1938; and *stigmaticus* Edwards, 1922.

Wiedemann (1828) described the nominotypical subspecies from "Brazil". The holotype female was seen by Belkin (1968) in the collection of the Senckenberg Naturmuseum Frankfurt, Germany. Belkin *et al*. (1971) later restricted the type locality to Salvador, Bahia, Brazil.

Goeldi (1905) described the egg of *fulvus* (as *Taeniorhynchus fulvus*) from a female captured in Murutucú, near Belém, Brazil. He was, however, unable to rear immature stages for study. Goeldi provided a description of the adult from separate observations: "Among our mosquitoes it is one of the largest species. It is characterized, in addition to its distinct size, by the beautiful general yellow coloration, color of gold, that extends over all [body] parts, including a good part of the anterior margin of the wings, contrasting here on the wing with the distal margin having a dark spot, while the rest shines giving a beautiful iridescent effect. Also ostensibly distinctive are the dark middle articulations of all six pairs [*sic*] of legs, the tarsi, the tip of the proboscis and the tip of the palps [maxillary palpi]. The back of the thorax [scutum] and the posterior margins of the abdominal rings [bands] exhibit some areas of a slightly different tint, darker than the beautiful general golden yellow [translated from the Portuguese]."

In his description of subspecies *pallens*, Ross (1943) contrasted the subspecies with *fulvus*, and with the very similar *Ae. bimaculatus*. For reference, Ross included detailed illustrations of the male genitalia and larvae of *fulvus* *pallens* and *bimaculatus*. He wrote: "This paper presents evidence to show that two distinct species of *Aedes* occurring in the United States are both at present identified as Coquillett's *bimaculatus*. The true *bimaculatus*, described from Brownsville, Texas, and ranging from central Texas to El Salvador, is very distinct from the '*bimaculatus*' collected throughout the southeastern United States which is here described as a new subspecies of the Neotropical *fulvus* (Wiedemann). Vargas's *rozeboomi*, recently described from Campeche, Mexico, is shown to be a synonym of the true *bimaculatus*." After describing the "true *bimaculatus*", Ross compared the species with *fulvus* as follows: "The male terminalia [genitalia] characters of *bimaculatus* are very distinctive and set the species well apart from *fulvus* [*sensu lato*]. The larval differences between *bimaculatus* and *fulvus pallens*, on the other hand, are relatively slight. Adults of both sexes of these species may be separated as follows: *fulvus* [*sensu lato*] has apical triangular areas of black scales on all abdominal tergites [terga], thoracic pleura with at least one black integumental spot (*fulvus pallens*) or two longitudinal black stripes (*fulvus fulvus*); *bimaculatus*, with scarcely any black scales on tergites except toward base of abdomen, thoracic pleura yellow—no integumental maculation".

Before describing *fulvus fulvus*, Ross (1943) stated: "The writer has before him the *fulvus* material in the U. S. National Museum from many localities in Central and South America. Representatives from Panama [not Brazil] are described...". The following are pertinent excerpts from his description of the male: "Thorax with mesonotal [scutal] integument lemon-yellow except for the subbasal spots [posterolateral spots]; each spot is transversely divided medially by a yellow area, the spots are brownish-black with blending margins.... Pleural integument lemon-yellow with two longitudinal brownish-black bands, one extending caudad from side of anterior promontory of mesonotum to prealar sclerite [prealar area], the lower band crossing middle of sternopleural sclerite [mesokatepisternum] and covering lower half of mesepimeron. ...*Male terminalia* [genitalia] without significant differences from that described later for *fulvus pallens* (fig. 1) [figure number from original]."

Following his description of "*fulvus pallens*, new subspecies", Ross noted: "Because of the lack of apparent terminalia differences between the United States series and that from Panama, and because the more superficial characters such as color and vestiture are relatively slight, though constant, the United States series is placed as a subspecies of *fulvus*. *Pallens* can be separated at once from typical *fulvus* by the almost complete absence of pleural maculation of the thorax and by the greater development of the mesothoracic [posterolateral scutal] spots."

We could not find any evidence of sympatry or intermediate forms of the two subspecies—*pallens* is found only in the southeastern United States and *fulvus* is distributed from southern Mexico and the Caribbean (Cuba) to Brazil, but does not occur in the United States.

We disagree that lack of male genitalia differences is a reason to ignore significant diagnostic characters and quite disparate distributions. Because of these factors, we believe that *fulvus* and *pallens* are separate species. We therefore afford species status to ***Aedes* (*Ochlerotatus*) *pallens* Ross, 1943**. *Aedes pallens* is currently listed as a species in the Encyclopedia of Life.

Aedes pallens has one synonym, *Culex flavicosta* Walker, 1856. Edwards (1932a) was apparently the first to treat *flavicosta* as a synonym of *fulvus*. Alan Stone saw the type specimen, and in an unpublished taxonomic catalog research note (1955) he wrote: "British Museum: A ♀ type labeled Amaz. [Amazon] in BM, lacking head. The triangular apical areas of dark scales on the abdomen are scarcely visible, but it's [*sic*] synonymy with fulvus [*sic*] is probably correct." The holotype was also examined by Belkin *et al.* (1971) in the Natural History Museum, London, who, instead of "Amazon Region," restricted the type locality to "Manaus (Amazonas)". Townsend (1990) also examined the holotype and noted "head missing", but he did not note that Belkin had restricted the type locality.

While it is clear to us that *pallens* should be accorded species status, variation can be found in adult characters of *fulvus* in Central and South America and the Caribbean. This variation, and the highly unlikely occurrence of any mosquito species naturally occurring in very different zoogeographic areas, make the existence of a species complex likely. In addition, we are not aware of studies of specimens from the generalized Amazonian type localities, nor the restricted type localities, of *fulvus* or the synonym *flavicosta*. A few examples of morphological variation follow.

Gutsevich & Garcia-Avila (1969) described *Ae. fulvus* from Cuba. Their description is not entirely clear but, in part: "The lateral surface of the thorax is also of two colors: upper half dark brown; lower half yellowish. A spot of broad silvery scales on the upper part of the sternopleuron [mesokatepisternum] and on the upper mesepimeron.... The specimens we have collected occupy an intermediate position between the southern and North American forms [between *fulvus fulvus* and *fulvus pallens*] [translated from the Spanish]." The thoracic pleura being dark above and yellowish below has not been described for any other taxon related to *fulvus*. The broad silvery scales usually have not been emphasized but are of possible significance in the Chrysoconops Group. These scales were also noted by Carpenter & LaCasse (1955) for *fulvus pallens* and by Ross (1943) for *fulvus fulvus*.

Rodriquez-Martinez *et al.* (2020) documented the sympatry of *bimaculatus* and *fulvus* in southern Mexican states bordering the Gulf of Mexico and Guatemala. To identify *fulvus*: "I distinguish this species from the preceding [*stigmaticus*, which was shown by them not to occur in Mexico] by the dark bands of the pleura, by the gold-colored scales in the region of the subcosta, and by the initial dark apical part [of the wing] at the point where the subcosta ends on the costal vein [translated from the Spanish]." Martini (1935) also mentioned the apically dark wings of *fulvus*: "A series of example specimens from South America has, without exception, the characteristic of a dark spot at the end of the wings [translated from the Spanish]." We found wide variability in the descriptions of the extent of yellow scales and dark apical areas of the wings in this group of species. The division of the posterolateral dark scutal spots, a character used by Ross (1943) as characteristic of *fulvus*, is not mentioned by Rodriguez-Martinez *et al.* (2020), but an undivided dark scutal spot is clearly shown in a photograph (their fig. 1b). The dark pleural lines, also characteristic of *fulvus* according to Ross (1943), are present in a photograph of Rodriguez-Martinez *et al.* (2020: fig. 1d), but the authors of both publications only pointed out that there is a dark spot in the hypostigmal area, but did not discuss the two obvious dark pleural bands.

In keys to the mosquitoes of Guatemala (Clark-Gil & Darsie 1983), the characters used to identify adult females of *fulvus* were "Scutal integument yellow with posterolateral dark marks" and "Thoracic pleuron with dark hypostigmal spot [not two dark bands]; abdominal terga yellow-scaled basally, dark-scaled apically."

***Aedes* (*Ochlerotatus*) *impiger* (Walker)**

subspecies ***daisetsuzanus*** Tanaka, Mizusawa & Saugstad, 1979—original combination: *Aedes* (*Ochlerotatus*) *impiger daisetsuzanus*. Distribution: Hokkaido Japan (Hokkaido Island) (Tanaka *et al*. 1979).

subspecies ***impiger*** (Walker, 1848)—original combination: *Culex impiger*. Distribution: Canada, Finland, Norway, Russia (Northwestern Region), Sweden, United States (Alaska, continental) (Wilkerson *et al*. 2021, incorrectly listed from Japan), tundra of Russia (Gutsevich 1971, 1974).

The nominotypical subspecies was described from "Martin's Falls", Ontario, Canada, located at 51.30 N, 86.20 W. This locality was listed for many of Walker's species as St. Martin's Falls, Albany River, Hudson's Bay, but was corrected to "Martin's Falls" by Handfield & Handfield (2020). The exact type locality is therefore unknown since the place name only represents the shipping origin. Belkin (1968) found "Two ♀… apparently part of type series" in the collection of the Natural History Museum, London, one of which he designated as the lectotype. Other entries in Wilkerson *et al.* (2021) with the anomalous "St. Martin's Falls" include *Culex implacabilis* Walker, 1848, synonym of *Aedes* (*Ochlerotatus*) *punctor* (Kirby, 1837), and *Culiseta* (*Culiseta*) *impatiens* (Walker, 1848).

The adult female, male genitalia and larva of the nominotypical subspecies were described in detail by Carpenter & LaCasse (1955), Gutsevich *et al.* (1971, 1974) and Becker *et al*. (2020). Ecologically, it is a univoltine early season species, which "is found in the treeless arctic regions of Alaska, Canada, Scandanavia [*sic*] and Siberia. Its range is known to extend southward to Utah and Colorado at the higher elevations.... The larvae... are found in clear pools of water formed by melting snow at high elevations in mountains where alpine arctic conditions prevail" (Carpenter & LaCasse 1955). In Russia, Gutsevich *et al*. (1971, 1974) recorded it from "...the Kola Peninsula, in the Arkhangelsk Region, Nenets National District, Taimyr, mouth of the Kolyma, and the Novosibirskie Islands. It usually occurs together with *A. nigripes*. *A. impiger* predominates in Noril'sk…".

Distinguishing characters (after Becker *et al.* 2020).

Adult female. Small species with brownish gray integument, scutum with conspicuous long black setae. Proboscis and maxillary palpus black-scaled; proboscis distinctly longer than forefemur. Vertex with spot of dark-brown scales; occiput covered with erect black setae and white scales. Antenna black, pedicel with some scattered white scales. Scutum with dense long black setae, median stripe of narrow bronze scales and lateral stripe of narrow white scales; scutellum with narrow white scales. Postpronotum with a few bronze scales, otherwise broad white scales; postpronotal setae scattered on entire postpronotum; postprocoxal, subspiracular and postspiracular scale-patches present, hypostigmal scale-patch absent; postspiracular setae 10 or fewer; upper mesokatepisternal scale-patch not reaching anterior margin; mesepimeron with large white scale-patch. Coxae white-scaled; femora and tibiae dark with scattered white scales, tibiae with conspicuous black setae; tarsomeres dark-scaled. Wing veins usually entirely dark-scaled, a few pale scales sometimes present at the base of the costa and radius. Abdominal terga with broad basal white bands. Cerci long, tapering.

Male genitalia. Tergum IX lobes rounded. Gonocoxite with short setae predominating on inner side; basal mesal lobe well developed with a spine-like seta distinctly stouter than others; apical lobe of gonocoxite small, weakly developed. Gonostylus slender, somewhat broadened in middle. Claspette filament about as long as stem, with a unilateral wing; aedeagus elongate.

Larva. Body surface without spicules. Antenna very short, spiculate. Head wider than long. Setae 5,6-C always single, 7-C 3-branched. Comb scales 10–14 (6–16), each scale with long median apical spine and several short spicules at base. Siphon index 2.8–3.0; pecten spines close together, evenly spaced, each spine with one long lateral denticle; seta 1-S inserted slightly below middle of siphon, with 4–6 long branches. Saddle covers approximately half of segment X; ventral brush (seta 4-X) with 2 precratal setae; anal papillae at least 1.3 length of saddle.

Tanaka *et al.* (1979) described subspecies *daisetsuzanus* from specimens collected at an elevation of 2,300 to 3,100 m above sea level, from "Yukomambetsu, in Mt. Daisetsu [a volcanic mountain range], Hokkaido", Japan's second largest island and northernmost prefecture. Tanaka *et al.* (1979) provided a complete description of the adult female, male genitalia and larva, and Tanaka (1999) provided a complete description of the pupa. Subspecies *daisetsuzanus* is adapted to similar extremely cold conditions as the nominotypical form. Tanaka *et al.* (1979) stated that "*Ae. (Och.) impiger daisetsuzanus* and *Ae. (Och.) hakusanensis* [Yamaguti & Tamaboko, 1954] appear to be relics of the Glacial epoch, now restricted to high mountains." *Aedes hakusanensis* is found further south on Honshu Island. In a footnote, Tanaka *et al*. (1979) stated that "The nominal subspecies, *Aedes* (*Ochlerotatus*) *impiger impiger* (Walker, 1848) does not occur in this region."

Unusual to both nominal taxa, not mentioned elsewhere in the literature, the larval maxilla is highly modified and described by Tanaka *et al*. (1979) in great detail, their summary follows. "The characteristic larval maxilla is especially remarkable. All other Japanese species of *Ochlerotatus* studied have maxillae typical for browsers; their maxillae in general are moderately sclerotized; the mesostipes [galeastipes] slightly longer than wide, peach-shaped, with a narrow somewhat detached mesal area (lacinial sclerite - Gardner *et al.* 1973), bearing spine-like spicules along the mesal margin; the maxillary brush apical and moderately long; the stipital sensoria [seta 1-Mx] and lacinial seta 5-Mx [seta 2-Mx] located usually somewhat distad of middle; the palpostipes [maxillary palpus] much shorter than the mesostipes. The strongly sclerotized maxilla in general, very broad square mesostipes with a broad mesal detached area, somewhat ventrally located maxillary brush, distally removed stipital sensoria and lacinial seta 5-Mx, and very large palpostipes of *impiger daisetsuzanus* resemble the maxilla of predaceous *Toxorhynchites*. The maxilla of *impiger daisetsuzanus* may possibly be regarded as an intermediate type between browsers and predatory species. However, the mandible of *impiger daisetsuzanus* is not modified." "The Japanese subspecies *daisetsuzanus* is identical with North American *impiger* in the male genitalia and most of the larval characteristics including the modified maxilla...".

This leaves little doubt as to the close phylogenetic relationship of the two nominal taxa. Some differences, however, were pointed out by Tanaka *et al.* (1979) and Tanaka (1999), which are summarized in Table 1. These differences were enough for the authors to suggest species status for *daisetsuzanus*, but because of the few specimens available, they chose to rank it as a subspecies.

Hokkaido Island was partially covered by ice at the last glacial maximum (Sawagaki *et al*. 2004). We assume that populations of the nominal taxon *impiger* were isolated at that time and have been diverging genetically since [perhaps for 18,000–20,000 years]. For this reason, since Tanaka *et al*. (1979) did not encounter the nominal form in the "Japanese Archipelago" and there are morphological differences which we believe will be sustained with examination of a larger number of specimens, we formally afford species status to ***Aedes* (*Ochlerotatus*) *daisetsuzanus* Tanaka, Mizusawa & Saugstad, 1979**. *Aedes daisetsuzanus* is currently listed as a species in the Encyclopedia of Life.

The nominotypical form has two synonyms: *Aedes* (*Ochlerotatus*) *nearcticus* Dyar, 1919b and *Aedes* (*Ochlerotatus*) *parvulus* Edwards, 1921d. We retain both as synonyms of *Ae. impiger*.

TABLE 1. Differences between the subspecies of *Aedes impiger*.

Life stage	Character	*daisetsuzanus*	*impiger*
Adult female (Tanaka *et al.* 1979)	Thoracic setae	Less setose	More setose
	Scutal setae	Relatively short	Relatively long
	Postpronotal setae	5–12 in irregular row or double row close to posterior margin	13–20
Adult male (Tanaka *et al.* 1979)	Pleural setae	Whitish to yellowish brown	Dark brown to nearly black (North America)
Larva (Tanaka *et al.* 1979)	Seta 11-II	1,2 branches	*2–5 branches
	Seta 4-III	4–6 branches	*2–4 branches
	Seta 1-IV	Single, subequal to seta 1-V	*1–3 branches, shorter and more slender than seta 1-V
	Seta 6-IV	2,3 branches	*single
	Seta 8-VI	1–3 branches	*3–7 branches
	Seta 8-VII	5–8 branches	*3–6 branches
	Anal papillae x length of saddle	1.1–11.4	*2.1–3.0
Pupa (Tanaka 1999)	Seta 10-C	†3–8(5) branches	‡2 branches
	Seta 5-II	†2–5(3) branches	‡single
	Seta 5-III	†2–8 branches	‡single
	Seta 7-V	†3–5(3) branches	‡2 branches
	Seta 7-VI	Single	‡2 branches
	Seta 8-VII	†2–6(3) branches	‡Single
	Paddle index	1.50–1.98 (x = 1.69)	‡1.33

*Two specimens from Alaska.

†Range (mode).

‡Danks & Corbet (1973: fig. 4) (referenced in Tanaka 1999).

Aedes (*Ochlerotatus*) *lasaensis* (Meng)

subspecies ***gyirongensis*** Ma, 1982—original combination: *Aedes* (*Ochlerotatus*) *lasaensis gyirongensis*. Distribution: China (Xizang Autonomous Region) (Ma 1982).

subspecies ***lasaensis*** Meng, 1962—original combination: *Aedes* (*Ochlerotatus*) *lasaensis*. Distribution: China (Xizang Autonomous Region) (Meng 1962).

Aedes lasaensis and subspecies *gyirongensis* were described from localities in the Xizang Autonomous Region (Tibet) of China. The former was described from males and females reared from larvae taken from a "marsh in the vicinity of Lasa [Lhasa]"; the latter was described from males and females collected in Gyirong, which is a county bordering Nepal (Gyirong is also the name of a town in the country). Both localities lie within the Himalayas, Lhasa at an altitude of 3,656 m and Gyirong town at an altitude of 2,700 m. Gyirong town lies approximately 585 km west-southwest of Lhasa city.

Meng (1962) described the adults and fourth-instar larva of *Ae. lasaensis* and distinguished the species from *Ae. punctor* (Kirby, 1837). Ma (1982) briefly described the adults of subspecies *gyirongensis* and illustrated the male genitalia. Since the original descriptions, the two forms have only been treated by Lu *et al.* (1997), who described the adults of the two forms and the larva of *lasaensis* (the larva of *gyirongensis* remains unknown). Lu *et al.* provided illustrations of the male genitalia and larva (head, thorax and terminal abdominal segments) of *lasaensis* and reproduced Ma's illustrations (slightly modified) of the ninth tergal lobes and gonocoxite of *gyirongensis*. The morphological distinctions provided in the descriptions and illustrations of these authors are summarized in Table 2.

TABLE 2. Differences between adults of the subspecies of *Aedes lasaensis*.

Anatomical feature		***gyirongensis***	***lasaensis***
Females—wing	Radius, dark scales at base	More numerous	Normal
	Cubitus (base?)	White scales more numerous than dark scales	White scales not more numerous than dark scales
Males—genitalia	Ninth tergal lobes	Each lobe with 3–7 simple and forked spine-like setae	Each lobe with 6 or 7 simple spine-like setae
	Gonocoxite—scales	Relatively numerous, spatulate	Relatively few, truncate
	Gonostylus	Slender, gently curved distally	Stout proximally, sharply curved distally
	Basal mesal lobe (BML)	Quadrate in dorsal view, setae longer	Somewhat trapezoidal in dorsal view (slightly narrower at base), setae relatively short
	Parabasal setae, insertions	Opposite mid-basal margin of BML, larger hooked seta inserted laterad of smaller seta	At distal basal margin of BML, larger hooked seta inserted proximad of smaller seta
	Line of needle-like setae at level of lower edge of BML	Present	Absent
	Dorsomesal apical lobe, setae	More numerous, longer	Sparse, short
	Claspette, stem	With prominent preapical mesal protuberance	Slightly and evenly tapered to base of filament

Aedes lasaensis is a member of the Punctor Subgroup (Knight 1951) of the Communis Group (Edwards 1932a) of species within the subgenus *Ochlerotatus*. In contrast with some other species of the Punctor Subgroup in which the male genitalia are indistinguishable, *e.g. Ae. aboriginis* Dyar, 1917a, *Ae. hexodontus* Dyar, 1916 and *Ae. punctor* in Canada (Wood *et al*. 1979), the distinguishing features of the male genitalia listed in Table 2, especially those of the gonocoxite and shape of the claspette stem, clearly indicate that *lasaensis* and *gyirongensis* are separate species, which are likely to occur in sympatry in areas of Tibet. We expect that morphological details of the larval stage, once known for both forms, in concert with DNA sequence data, will verify our decision here to formally recognize *gyirongensis* as a distinct species: ***Aedes* (*Ochlerotatus*) *gyirongensis* Ma, 1982**. *Aedes gyirongensis* is currently listed as a species in the Encyclopedia of Life.

Aedes (*Ochlerotatus*) *pulcritarsis* (Rondani)

subspecies ***asiaticus*** Edwards, 1926b—original combination: *Aedes* (*Ochlerotatus*) *pulchritarsis* [*sic*] var. *asiaticus* (subspecific status by Monchadskii 1951). Distribution: Bangladesh, India, Nepal, Pakistan, People's Republic of China, Sri Lanka (Wilkerson *et al*. 2021).

subspecies ***pulcritarsis*** (Rondani, 1872)—original combination: *Culex pulcritarsis*. Distribution: Albania, Afghanistan, Azerbaijan, Bulgaria, Crimean Peninsula, Croatia, Cyprus, Czech Republic, France (includes Corsica), Georgia, Greece, Hungary, India, Iran, Israel (Gaza Strip and West Bank), Italy (includes Sicily), Kazakhstan, Kosovo, Lebanon, Macedonia, Moldova, Morocco, Pakistan, Portugal, Romania, Russia (Southern Districts), Serbia, Slovakia, Spain (includes Balearic Islands), Tunisia, Turkey, Ukraine, Uzbekistan (Wilkerson *et al*. 2021).

The taxonomic history of *Aedes pulcritarsis* involves eight nominal forms: *Culex pulcritarsis* Rondani, 1872; *Culex leucacanthus* Loew, 1873; *Aedes berlandi* Séguy, 1921; *Aedes praeteritus* Séguy, 1923; *Finlaya versicolor* Barraud, 1924; *Aedes pulchritarsis* [*sic*] var. *asiaticus* Edwards, 1926b; *Aedes pulchritarsis* [*sic*] var. *stegomyina* Stackelberg & Monchadskii, 1926 (in Montchadsky 1926); and *Aedes simici* Baranoff, 1927.

In his treatment of the subgenus *Ochlerotatus*, Edwards (1932a) listed *leucacanthus* and *simici* as synonyms of *pulcritarsis* (as *pulchritarsis*), recognized *asiaticus*, *berlandi*, *praeteritus* and *versicolor* as varieties of *pulcritarsis*, and listed *stegomyina* as a synonym of variety *asiaticus*. Monchadskii (1951) raised *asiaticus* to subspecific status, recognized *stegomyina* and *versicolor* as its synonyms, and retained *berlandi*, *praeteritus* and *simici* as synonyms of *pulcritarsis*. *Aedes berlandi* was restored to specific status by Rioux & Arnold (1955), with *praeteritus* as a synonym. Much later, Danilov (1978) removed *versicolor* from synonymy with *asiaticus* and recognized it as a valid species of the subgenus *Finlaya*. *Aedes versicolor* is currently regarded as a species of *Aedes* without subgeneric placement (Reinert *et al*. 2009; Harbach 2018; Wilkerson *et al*. 2021). As a result of these taxonomic actions, *Ae. pulcritarsis* is currently recognized as consisting of two subspecies, the nominotypical subspecies with two synonyms (*leucacanthus* and *simici*) and subspecies *asiaticus* with a single synonym (*stegomyina*).

Aedes pulcritarsis was apparently described from a single damaged female collected at an undisclosed locality in Italy (Rondani 1872; Theobald 1901c). Edwards (1926b) briefly described subspecies *asiaticus* from an undisclosed number of adult mosquitoes without explicitly mentioning where they were collected. The holotype female in the Natural History Museum, London was collected in "Pakistan: Chitral, Drosh" (Townsend 1990). Drosh is a city located at an elevation of 1,359 m in the Chitral District of Khyber Pakhtunkhwa Province.

Seventy-six mtDNA *COI* sequences derived from specimens identified as *Ae. pulcritarsis* are available in GenBank. Three are from specimens collected in Austria, one is apparently from a specimen collected in Greece and the remaining 72 (also available in the BOLD database) are from specimens collected in Pakistan. The similarities between all of the sequences is greater than 97.8%, mostly greater than 99%.

All of the *COI* sequences obtained from specimens collected in Pakistan were submitted by Ashfaq *et al*. (2014). The authors indicated that the specimens were collected at altitudes of 111–2,376 m in urban and rural areas of Punjab and Khyber Pakhtunkhwa Provinces in central-eastern and northwestern regions of the country, respectively, and identified retrospectively as *Ae. pulcritarsis* "through barcodes". It is also interesting to note that the specimens from Austria which Bakran-Lebl *et al*. (2022) used to generate *COI* sequences were identified to species using the morphological keys of Gunay *et al*. (2018) and Becker *et al*. (2020), with the identifications subsequently confirmed by comparison "to sequences available in GenBank® and BOLD." Obviously, the only sequences available in the databases for comparison at the time were those deposited by Ashfaq *et al*. (2014). Even though the holotype of *asiaticus* was collected at an altitude intermediate between the altitudes where Ashfaq *et al*. (2014) collected their alleged specimens of *Ae. pulcritarsis* (see above), we do not think that the genetic data are sufficient to unambiguously indicate the former is a synonym of the latter. Although the currently available barcode sequences appear to indicate that the same species is present in Austria, Greece and Pakistan, the existence of a complex of species, which may not be distinguished by barcodes, cannot be ruled out.

Edwards (1934) (in Barraud 1934) stated, with reference to *Ae. pulcritarsis* (as *pulchritarsis*) that "The species is usually scarce and still but little known, but appears to be subject to considerable local variation. Two different varieties [*asiaticus* and *versicolor*] or possibly distinct species, occur within the Indian area and are described below." As noted above, *versicolor* is now recognized as a species of the subgenus *Finlaya*. Edwards gave a brief description of the female of *asiaticus* and included a description of the larva based on the descriptions of Montchadsky (1926) and Montschadsky (1930). His descriptions of the females of *pulcritarsis* (as *pulchritarsis*) and *asiaticus* are not entirely comparable. The comparable characters are listed in Table 3.

Contrary to Edwards, Gutsevich *et al*. (1971, 1974) indicated that the ornamentation of the legs is more variable in subspecies *pulcritarsis* (as *pulchritarsis*): "Femora and tibiae dark anteriorly, with small spots of dark scales or with scattered light scales, often also completely dark anteriorly, with white apex." They reported that subspecies *asiaticus* "differs mainly in the coloration of the mesonotum. Head with white and black scales which form spots. Mesonotum with blackish brown or dark brown sales, with a longitudinal median stripe of white scales and white transverse stripes, stripes on the mesonotum sometimes formed by yellowish scales which are indistinct against the background; lateral margins of mesonotum with white scales." Oddly, Gutsevich *et al*. did not mention the head scaling of subspecies *pulcritarsis*; however, for comparison, Edwards described the head of this subspecies as having "a median line of long and rather wide white lanceolate scales on vertex, continued forwards between eyes and around eye-margins; white upright scales in centre of nape [occiput]; a large patch of black scales on either side of middle line of vertex." It is uncertain but the median line of white scales and lateral patches of black scales described by Edwards probably correspond with the white and black spots described by Gutsevich *et al*. (1971, 1974).

TABLE 3. Comparable differences between the adult females of the subspecies of *Aedes pulcritarsis* observed by Edwards (in Barraud 1934).

Females	***asiaticus***	***pulcritarsis***
Thorax	"Mesonotum mainly dark brown, with a double median line of white scales on anterior ½, narrowly bordered externally with yellow scales; on each side of the posterior end of this stripe a rather large patch of whitish scales."	"Mesonotum with a variable amount of golden scales toward front in middle; pale scales along margins and over wing-roots, remainder dark brown."
Legs	Apparently differing as follows: "Femora and tibiae with fairly numerous scattered white scales; hindfemur (except for this speckling) dark on nearly the whole outer surface."	…"mostly black, with conspicuous white knee-spots and shite rings on tarsi marrow on front and middle pairs, broader on hand pair; 5th tarsal segment of all legs white."
Abdomen	"White basal bands on tergites [terga] II–VI complete, that on VI very narrow."	…"black, with white basal bands on tergites II–VI, sternites [sterna] similarly coloured."

The most recent treatment of *Ae. pulcritarsis*, the nominate form in Europe, is that of Becker *et al*. (2020). Those authors merely stated that the female is "Very similar to the females of *Ae. berlandi*. A slight difference exists in the scutal colouration pattern. Whereas the scutum of *Ae. berlandi* is distinctly contrasted by dark and pale golden scales, *Ae. pulcritarsis* exhibits a weaker pattern of pale and dark scales on the scutum and looks rather uniformly golden brownish coloured. However, the median and lateral stripes may be somewhat lighter than the submedian spots." There is no mention of the median line of white scales on the anterior half of the scutum that is present in subspecies *asiaticus*.

As far as we know, the male genitalia and larva of subspecies *pulcritarsis* were first described and illustrated by Martini (1930). Montchadsky (1926) described and illustrated the four larval instars of subspecies *asiaticus* (as var. *stegomyina*). Martini included a brief description of var. *stegomyina* and reproduced the terminal abdominal segments of the second and third-instar larvae (his fig. 359) that were illustrated for this variety in Montchadsky (1926: figs 4 and 3, respectively). The head and terminal abdominal segments of *pulcritarsis sensu stricto* were illustrated by Martini (1930). The only other illustration of the larva of *pulcritarsis sensu stricto* known to us is the drawing of the terminal abdominal segments found in Becker *et al*. (2020: fig. 10.69), which, except for the larger anal papillae, agrees with the illustration of Martini (1930). Monchadskii (1951) and Gutsevich *et al*. reproduced Montchadsky's (1926) illustrations of the head and terminal abdominal segments of var. *stegomyina* for their descriptions of subspecies *asiaticus*. It is interesting to note that the largest seta of the basal mesal lobe of the male genitalia illustrated for *pulcritarsis* by Martini (1930: fig. 358) differs significantly from the largest seta of the basal mesal lobe illustrated for *pulcritarsis* by Gutsevich *et al*. (1971, 1974: fig. 111) and Becker *et al*. (2020: fig. 10.68).

Even though the adults and larvae of *asiaticus* and *pulcritarsis* have not been described in detail, and the pupae are unknown, the known morphological differences listed in Table 4 provide a clear indication that the two forms are quite distinct.

TABLE 4. Morphological differences between the subspecies of *Aedes pulcritarsis*.

Anatomical feature		***asiaticus***	***pulcritarsis***
Larvae	Comb scales	Bluntly pointed	Sharply pointed
	Pecten	16–18 spines	17–24 spines
	Siphon	Long, index 4.0–5.0, slightly tapered	Short, index 3.0–3.5, more strongly tapered
	Anal papillae	≈ length of seta 2-X	≈ 2x length of seta 2-X
Male	Basal mesal lobe	Largest seta stout, curved distally	Largest seta slender with hooked tip
Female	Scutum	With anterior median white stripe	Stripe absent
	Abdominal tergum VI	Basal pale band normal	Basal pale band very narrow

The distributions of the two subspecies listed in Wilkerson *et al*. (2021) require some adjustments. Firstly, India and Pakistan should be removed from the distribution of subspecies *pulcritarsis* for the reason explained for other taxa treated herein. Secondly, Tajikistan, Turkmenistan and Uzbekistan (includes the type locality of *stegomyina*) should be added to the distribution of subspecies *asiaticus* (see Gutsevich *et al*. 1971, 1974). By association, the distribution of *asiaticus* should include Afghanistan and probably most of Iran and Kazakhstan. Afghanistan and Uzbekistan should be removed from the distribution of subspecies *pulcritarsis*, and Iran (far northwest) and Kazakhstan (far western region) questionably retained. In agreement with Gutsevich *et al*. (1971, 1974) and Becker *et al*. (2020), the distribution of *pulcritarsis sensu stricto* extends eastward from the Mediterranean region to southwestern Russia and Caucasia; the distribution of *asiaticus* lies east and southeast of those areas, essentially from areas northeast to southeast of the Caspian Sea.

We suspect that integrated morphological and molecular studies conducted on specimens collected throughout the ranges of the two forms are likely to show that *Ae. pulcritarsis* is a complex of species. For that reason, based on currently available morphological and distributional information, we believe a prudent course of action is to recognize *asiaticus* as a separate species until proven otherwise: ***Aedes* (*Ochlerotatus*) *asiaticus* Edwards, 1926b**. *Aedes asiaticus* is currently listed as a species in the Encyclopedia of Life.

There is no doubt that var. *stegomyina* Stackelberg & Monchadskii, 1926 is synonymous with *Ae. asiaticus* based on its morphology and type locality. As the type localities of *leucacanthus* Loew, 1873 (Kasan in southwestern Russia) and *simici* Baranoff, 1927 (Macedonia) lie within the distribution of *Ae. pulcritarsis*, we accept that they should be retained as synonyms of this species.

***Aedes* (*Ochlerotatus*) *spencerii* (Theobald)**

subspecies ***idahoensis*** (Theobald, 1903a)—original combination: *Grabhamia spencerii* var. *idahoensis* (subspecific status by Nielsen & Rees 1959). Distribution: Canada, United States (continental) (Wilkerson *et al*. 2021).

subspecies ***spencerii*** (Theobald, 1901c)—original combination: *Culex spencerii*. Distribution: Canada, Mexico, United States (continental) (Wilkerson *et al*. 2021).

Aedes spencerii was described, originally as a species of *Culex*, from four adult females collected in Manitoba Province of Canada, two from Stony Mountain, the type locality based on lectotype selection by Belkin (1968), and two from St. Boniface (Theobald 1901c). Theobald provided a color illustration of the adult female in dorsal aspect (Theobald 1901a [plates]): fig. 104, pl. XXVI), which shows the pattern of dark tergal scaling typical of subspecies *spencerii*: "Abdomen covered with creamy and white scales, with large, black-scaled patches on each side of the middle line" (Theobald 1901c).

Subspecies *idahoensis* was originally described as a variety of *spencerii* based on an unspecified number of females collected at Market Lake, Idaho, United States (Theobald 1903a); however, Townson (1990) reported the presence of two syntype females in the collection of the Natural History Museum, London. Theobald indicated that *idahoensis* only differed from the typical form in "abdominal ornamentation", which he described as "Abdominal basal bands almost white, broad apical bands yellowish-white to white, very narrow, almost obliterated on some segments; the abdomen not pale at the sides, so that only broad basal and narrow apical pale areas are shown, the two apical segments are mostly pale scaled, and there are scattered pale scales on the others." In contrast, *idahoensis* has traditionally been characterized as having dark-scaled abdominal terga with white transverse basal bands (see references listed below).

Seven *COI* sequences for *Ae. spencerii* are registered in GenBank, three from Saskatchewan Province, Canada (KR444402, 596 bp; KR443924, 551 bp; and KR440309, 596 bp); two from Manitoba Province, Canada (KF535006, 658 bp and KF535007, 658 bp); one from Utah State, USA (JX260472, 213 bp); and one from Colorado, USA (JX259672, 658 bp). BLAST comparison of sequences revealed that two of the sequences from Saskatchewan (KR444402 and KR440309) and the sequence from Colorado (JX259672) are identical, and the 551 bp of the third sequence from Saskatchewan (KR443924) is 99.82% similar to the corresponding segments of those three sequences. Additionally, a 589-bp sequence from Saskatchewan identified as "*Aedes* sp. BOLD-2016" is 98.13% similar. The sequence from Utah (JX260472, 213 bp) was too short to obtain a meaningful comparison, and the two sequences from Manitoba were apparently obtained from misidentified specimens: KF535006 is identical with 11 *COI* sequences of *Ae. dorsalis* and KF535007 is 99.39% similar to a *COI* sequence from Alberta (KP047935) identified as "Culicidae sp. BOLD:AAD7982". No DNA sequences are available for specimens identified as subspecies *idahoensis*.

Ward (1984, 1992) and Wilkerson *et al*. (2021) were apparently not aware that Wood *et al*. (1979) had synonymized *idahoensis* with *spencerii*, with the following explanation: "The status of *idahoensis* has not been satisfactorily resolved. A few females in the Canadian National Collection have the characteristic abdominal pattern of *idahoensis*, but there are no males or larvae in the collection. According to Carpenter and LaCasse (1955), larvae of *idahoensis* have comb scales (13–29 instead of 7–13 in *spencerii*), and each scale has a less pronounced apical spine. Males of the two species were not separated. Nielsen and Rees (1959) found 'almost every degree of variation' between the typical female abdominal pattern of *idahoensis* and that of *spencerii* in Utah, Montana, and Wyoming. Furthermore, they cited three other authors who described similar variations in *spencerii*. They concluded that *idahoensis* was a more southerly subspecies of *spencerii* and that a zone of integration occurred in the three states previously mentioned. Until detailed biological or genetical studies resolve the status of *idahoensis*, we have no choice but to consider it a synonym of *spencerii*."

Darsie & Ward (1981, 2005) continued to recognize the two nominal forms as subspecies, stating in 1981: "Following Nielsen and Rees (338) [number of the article in the list of references cited] we recognize two subspecies under *Ae. spencerii* (Theobald), the typical subspecies which inhabits the central plains of North America, and subspecies *idahoensis* (Theobald), a more westerly and northwesterly form, also reported from southern British Columbia (135)." Based on published records, Darsie & Ward showed that the distributions of the two subspecies overlap in Montana, Nebraska, North Dakota, South Dakota and Wyoming. They indicated that only *idahoensis* was known to occur in Colorado; thus, the *COI* sequence in GenBank (JX259672) of the specimen from Colorado identified as *spencerii sensu stricto* suggests that either both subspecies occur in the state or *idahoensis* is conspecific with the typical form that occurs in Canada. More specimens and study are needed to resolve this question.

It is interesting to note that *idahoensis*, originally described as a variety of *spencerii*, has been regarded as a distinct species (Dyar & Knab 1908; Dyar 1917b; Dyar 1928; Edwards 1932a; Gjullin 1937; Rees 1943; Yamaguti & LaCasse 1951d; Carpenter & LaCasse 1955), a synonym (Pratt 1956; Wood *et al*. 1979) and a subspecies (Nielsen & Rees 1959; Smith 1966; Myers 1967; Darsie & Ward 1981, 2005). In as much as *idahoensis* is apparently morphologically distinct in the adult and larval stages (Carpenter & LaCasse 1955; Darsie & Ward 1981, 2005) in areas southward and westward of an area of overlap or a zone of introgression with *spencerii* in Montana, Nebraska, North Dakota, South Dakota and Wyoming, we believe it is prudent to recognize it as a separate species, pending a comprehensive morphological and genetic analysis of specimens from throughout the distributions of the two forms: ***Aedes* (*Ochlerotatus*) *idahoensis* (Theobald, 1903a)**. *Aedes idahoensis* is currently listed as a species in the Encyclopedia of Life.

***Aedes* (*Ochlerotatus*) *vigilax* (Skuse)**

subspecies ***ludlowae*** (Blanchard, 1905)—original combination: *Culex ludlowi* [*sic*] (subspecific status by Knight & Hull 1951b). Distribution: Philippines (Blanchard 1905).

subspecies ***vansomerenae*** Mattingly, 1955 (in Mattingly & Brown,1955)—original combination: *Aedes* (*Ochlerotatus*) *vigilax* subspecies *vansomerenae*. Distribution: Seychelles (Mattingly & Brown 1955).

subspecies ***vigilax*** (Skuse, 1889)—original combination: *Culex vigilax*. Distribution: Australia, Fiji, Indonesia (Java, Flores, Kalimantan, Sulawesi, Sumatra), Malaysia, New Caledonia, New Hebrides, Papua New Guinea, Solomon Isl., Taiwan, Thailand, Timor, Tonga, Vanuatu, Vietnam (Wilkerson *et al.* 2021, incorrectly listed from the Philippines and the Seychelles).

Summary. *Aedes vigilax sensu lato* is a species complex. A key indicator for us was the report of two molecularly identified species-level taxa that occur throughout coastal Australia, with co-occurrence at the type localities of the nominotypical form (see below). It is not yet known if one or both extend northward into Indonesia and Southeast Asia, or which one should bear the name *vigilax*. Neither do we know for certain the identity of *Ae. vigilax sensu lato* north of Australia. The subspecies *ludlowae* and *vansomerenae* are geographically isolated in the Philippines and Seychelles, respectively, and can be morphologically characterized. Also known are one or two unnamed taxa in New Caledonia and the New Hebrides. Researchers have usually treated the nominotypical form as a single entity for purposes of discussion and identification, which makes definition of other putative OTUs problematical. See Mattingly (1961) for an example of mixing life stages from different geographical areas to define *vigilax*. Also, the extensive biological and disease transmission literature (reviewed by Lee *et al*. 1984) consists of an array of variable attributes, which would be expected when multiple species are lumped together.

The taxa considered here are exclusive members of the Empihals Group of Wilkerson *et al*. (2015), formerly *Ochlerotatus* subgenus *Empihals* Reinert *et al*., 2008. In the comprehensive infrasubgeneric classification of the subgenus *Ochlerotatus*, the taxa are members of the Vigilax Subgroup (Marks 1949; Vigilax Section of Marks 1957; Empihals Group in part of Wilkerson *et al*. 2015) of the Taeniorhynchus Group (Edwards 1932a, in part; Culicelsa Group of Wilkerson *et al*. 2015). The larvae are primarily adapted to coastal brackish-water marshes and mangroves. Keys and descriptions to nominal *vigilax* are included in Belkin 1962 (South Pacific), Tanaka *et al*. 1979 (Ryukyu Archipelago, Japan), Lee *et al.* 1984 (Australasia), Rattanarithikul *et al*. 2010 (Thailand) and Becker *et al*. 2020 (Asia, Australia). Subspecies *vansomerenae* is compared by Le Goff *et al.* (2012) to other species found in the Seychelles, and subspecies *ludlowae* is included in the key of Knight & Hull (1951) to species of *Aedes* in the Philippines.

Based on morphological characters included in the keys and individual descriptions contained in the publications cited above, Wilkerson *et al.* (2021) characterized the adult female and larva of nominal *vigilax*, paraphrased below. The characters of the male genitalia are from (Harbach 2022a).

Adult. Decumbent scales of vertex mostly narrow, erect scales cover most of dorsal surface; basal 0.67 of proboscis with midventral pale scaling. Scutum without distinctive markings, sometimes with pale brown scales along acrostichal line and an entirely white scale-patch just anterior to scutellum. Scale-patches on antepronotum, proepisternum and paratergite, broad whitish scales on postspiracular and prealar areas; subspiracular area without scales; lower mesepimeron without setae. [Postpronotal scale patterns are not noted here but we believe they are diagnostic for four of the taxa discussed below, *i.e. vigilax sensu lato*, *ludlowae*, *vansomerenae* and the "Celebes Form".] Tarsomeres of all legs with distinct white basal bands, hindtarsus with basal pale bands ≥ 0.25 length of tarsomeres. Wing with small areas of white scaling. Abdominal terga with white basal bands of uniform width.

Larva. Seta 4-C short, nearer level of 6-C than 5-C; setae 11,12-C short. Seta 5-P single or double, lateral spine of plate bearing setae 9–12-M,T small and lightly pigmented. Most abdominal setae comparatively short; seta 1-III–V short, branched; seta 6-III branched. Comb scales in 1–3 irregular rows; saddle incomplete; anal papillae shorter than 0.5 length of saddle; seta 3-X single; siphon short, index < 2.0; pecten spines evenly spaced, not inserted beyond seta 1-S.

Male genitalia. "Ninth tergal lobes with flattened setae; gonocoxite with scales, with setose dorsal basomesal lobe, mesal surface membranous; gonostylus attached at apex of gonocoxite, with apical gonostylar claw; claspette a long narrow columnar stem with an *apical seta (claspette filament) [hooked in subspecies *ludlowae* and *vigilax* and not hooked in subspecies *vansomerenae*], *stem ≤ 0.85 length of aedeagus; aedeagus tube-like, widest at mid-length; cercal setae present." [* = diagnostic character for subgenus *Empihals* of Reinert *et al*. 2009]

The nominotypical form was described by Skuse (1889) from specimens collected at four localities in southeastern Australia: Gosford, Kiama and National Park [unclear what this represents], New South Wales; and Brisbane, Queensland. Lee *et al.* (1984) cited Hahn (1962) [not seen by us] for the deposition of female syntypes [number not given] and a type female of *vigilax* in the Macleay Museum of Natural History, University of Sydney, Sydney, Australia. The Macleay Collection is now housed in the Chau Chak Wing Museum on the same campus. Many insects from the Macleay Collection were transferred to the Australian National Insect Collection in Canberra, but *vigilax* does not appear in their inventory of primary types. It is assumed that the type specimens of *vigilax* remain in the Macleay Collection.

Puslednik *et al.* (2012) used comprehensive collection records and multiple DNA sequences from 66 *vigilax* females from Australia and New Caledonia to test the validity of the Carpentaria Barrier, which is one of "a number of important biogeographical barriers [that] have been identified and are thought to have played a pivotal role in speciation events of Australian fauna...". Aside from partially answering in the affirmative, their primary question concerning the influence of past patterns of change having resulted in the Carpentaria Barrier, they stated that "Within *Ae*. *vigilax* we have identified three distinct and divergent lineages that may well represent cryptic species. Sequence divergence between the three distinct lineages of *Ae*. *vigilax* was higher than between other *Aedes* species (Cook *et al*., 2005). Furthermore, total genetic divergence within the *COI* barcoding region was 4.23%, which is higher than the cutoff suggested by proponents of DNA barcoding (Hebert *et al*., 2003)." We think this is clear indication of three species, two of which are sympatric in eastern Australia (Clades II and III of Puslednik *et al.* 2012). Specimens of Clade III were from eastern and western Australia and those of Clades II and III were found in sympatry near the type localities of nominotypical *vigilax*. The third taxon, Clade I, was found in New Caledonia, nearly 1,400 km from the Australian mainland.

The results of Puslednik *et al.* (2012) raise many questions, such as: What are the distributions of Clades II and III outside of Australia? Does Clade II or Clade III correspond to *vigilax sensu stricto*? To which clade(s) do the three current synonyms correspond?—*Culex marinus* Theobald, 1901a (eastern Australia), *Culicelsa pseudovigilax* Theobald, 1907 (eastern Australia) or *Culicelsa uniformis* Strickland, 1911 (western Australia). The type specimens of the three synonyms are in the Natural History Museum, London. In addition, an older name, *Culex albirostris* Macquart, 1850 (eastern Australia), was suppressed by the International Commission on Zoological Nomenclature 1972, Opinion 979, and is available to represent one of the two clades, as long as it is not *vigilax sensu stricto*. The type of *albirostris* is in the Muséum National d'Histoire Naturelle, Paris. And lastly, does Clade I already have a name, or is it undescribed? Answers to these questions could be possible with further molecular analyses.

Subspecies *ludlowae* (replacement name for *Culex annulifera* Ludlow, 1903, not *Culex annuliferus* Blanchard, 1852) was described as a species from the Philippines. Ludlow stated: "The female was described from a lot (28) [a "lot" apparently means "many specimens"], all females, sent... from Mangarin, Mindoro: the males from a lot (234)... from Dagupan, Pangasinan, Luzon." A female lectotype of *annulifera* was designated by Knight & Hull (1951) and is in the National Museum of Natural History, Washington, D.C..

Regarding *ludlowae*, Knight & Hull (1951) stated: "Not known from outside the Philippines." "DISCUSSION: The Philippine form is treated here as a distinct subspecies of *vigilax* (Skuse) on the basis of the scaling of ppn [postpronotum] in the female. In *v. vigilax* this area [postpronotum] is covered with flat-lying slightly elongate broad scales; except for a fringe of narrow dark scales dorsally. The broad scales are dark except for a small ventral posterior patch of pale ones. The type of *v. vigilax* has not been seen by us, but the types of the synonyms *uniformis* Strickland [type locality: Perth, Western Australia] (female) and *marinus* (Theobald) [Queensland] (male, female), which are in the British Museum, have been."

Since *ludlowae* is only found in the Philippines and it has a distinctive postpronotal scale pattern, we believe this is evidence of genetic isolation. Because of these factors (morphology and distribution) we think *ludlowae* merits return to its original species status: ***Aedes* (*Ochlerotatus*) *ludlowae* (Blanchard, 1905)**. *Aedes ludlowae* is not currently included as a species in the Encyclopedia of Life and should be added to the list of species of the genus.

Subspecies *vansomerenae* Mattingly, 1955 (in Mattingly & Brown 1955) was described from "a holotype ♂ and allotype ♀ from Anse Lascar, Silhouette I. ...3 ♂ and 4 ♀ paratypes with the same data as the holotype and 2 ♂ and 1 ♀ paratypes from Dennis I. ...". This differs somewhat from what Townsend (1990) found in the Natural History Museum, London: "Holotype male [Pe on slide] – Seychelles: Silhouette I., Anse Lascar. Paratypes (17) – Seychelles: 5 male, 6 female, 6L." "Pe & Le of some paratypes in alcohol."

Mattingly prefaced his description of *vansomerenae* as follows: "Adults of this subspecies differ from type form *Aë. vigilax* Skuse... and from ssp. *ludlowae* (Blanch.)... in having a greater proportion of the scales on the posterior pronotum [postpronotum] pale, in the presence of strongly developed lateral prolongations of the pale tergal bands on the abdomen of the male and in not having the terminal appendage of the male claspette hooked. The larva differs in usually having more branches in the antennal tuft [seta 1-A], in having more teeth in the mentum [dorsomentum] and, apparently, in having the comb spines [scales] more delicately fringed with less tendency to thickening of the median denticle. The males also differ from the description of ssp. *ludlowae* given by Knight & Hull in having the lateral patches of broad pale scales on the vertex narrowly interrupted by dark scales. A similar condition is, however, shown by a male of ssp. *ludlowae*, from Manila, in the British Museum. The present form differs from Knight & Hull's description of the Philippines subspecies in usually having 6 instead of 3–4 bristles [setae] on each lobe of the male ninth tergite [tergum IX]."

Additionally, in his description: "Posterior pronotum [postpronotum] with a conspicuous patch of broad white or whitish scales posteriorly and ventrally, rather smaller flat blackish scales forming a patch in the middle and narrow golden scales along the upper margin." And for the larva, Mattingly noted that "Mouth brushes [palatal brushes] with serrated teeth of inner bristles [filaments] very strongly developed." This is a character not mentioned in other descriptions of *vigilax sensu lato*.

The above comparisons by Mattingly, along with the at least 5,000 km of distance to the nearest member of the Empihals Group (*sensu* Wilkerson *et al*. 2021), lead us to conclude that *vansomerenae* is a distinct and independently evolving species, and is raised here to specific rank: ***Aedes* (*Ochlerotatus*) *vansomerenae* Mattingly, 1955**. The proximity to Madagascar even suggests that it might be more related to species in that region, rather than to the other species discussed here. *Aedes vansomerenae* is currently listed as a species in the Encyclopedia of Life.

Aedes vigilax has three synonyms, which we retain: *Culex marinus* Theobald, 1901a, *Culicelsa pseudovigilax* Theobald, 1907 and *Culicelsa uniformis* Strickland, 1911.

Aedes **(*Phagomyia*)** ***gubernatoris*** **(Giles)**

subspecies ***gubernatoris*** (Giles, 1901a)—original combination: *Culex gubernatoris*. Distribution: Bangladesh, India, Nepal, People's Republic of China, Sri Lanka (Wilkerson *et al*. 2021, incorrectly listed from Thailand).

subspecies ***kotiensis*** Barraud, 1934—original combination: *Aedes* (*Finlaya*) *gubernatoris* var. *kotiensis* (subspecific status by Harbach & Howard 2007). Distribution: India (Western Himalayas) (Barraud 1934).

Barraud (1934) described and named *kotiensis* as a variety of *gubernatoris* based on larvae that differ in having shorter antennae and lateral palatal brush filaments with "comparatively very large teeth"; however, "adults resulting from these larvae appear to be indistinguishable from the type-form." Information provided by Barraud indicates that the two forms may be allopatric. In the absence of features that distinguish the adults, the perceived larval distinctions may be associated with conditions that influence growth and development in the tree-hole habitats utilized by the larvae. Based on these observations, we believe that subspecies *kotiensis* is a morphological variant of *Aedes gubernatoris*, which we therefore formally recognize as a synonym: ***kotiensis*** **Barraud, 1934, junior subjective synonym of *Aedes* (*Phagomyia*) *gubernatoris* (Giles, 1901a)**. This agrees with the Encyclopedia of Life, which does not list *kotiensis* as a species.

In addition to *kotiensis*, *Ae. gubernatoris* has another synonym, *Lepidotomyia magna* Theobald, 1905a, first recognized by Barraud (1934), which we retain. All three nominal forms have type localities in India.

Aedes **(*Pseudarmigeres*)** ***argenteoventralis*** **(Theobald)**

subspecies ***argenteoventralis*** (Theobald, 1909)—original combination: *Dendromyia argenteoventralis*. Distribution: Cameroon, Central African Republic, Côte d'Ivoire, Ghana, Liberia, Nigeria, Sierra Leone, Togo (Wilkerson *et al*. 2021).

subspecies ***dunni*** Evans, 1928—original combination: *Aedes* (*Armigeres*) *albomarginata* var. *dunni* (subspecific status by White 1975). Distribution: Cameroon, Democratic Republic of the Congo, Nigeria (Wilkerson *et al*. 2021).

Theobald (1909) described and named *Dendromyia argenteoventralis* based on females collected in present-day Ghana, characterized by a moderately broad border of white scales on the anterior margin of the scutum. A form later found in Nigeria and described as *Aedes albomarginata* [*sic*] var. *dunni* by Evans (1928) was considered to be a variety of *Ae. argenteoventralis* by Edwards (1930) (afforded subspecific status by White 1975) that differs from the typical form in having few or no white scales on the anterior margin of the scutum. As noted by Edwards (1930, 1941), the male genitalia of the two forms appear to be identical. Whereas the larva and pupa of *dunni* have been described (Evans 1938; Hopkins 1952; Edwards 1941), these life stages of the typical form are unknown. Based on the known distributions of the two forms, with the typical form recorded from the Central African Republic, which is bordered by Nigeria to the west and the Democratic Republic of the Congo to the south where *dunni* is recorded, it is probable that the two forms occur in sympatry and the amount of white scaling on the anterior margin of the scutum is normal variation within a single species. Consequently, *Aedes albomarginatus* var. *dunni* Evans, 1928 is hereby formally regarded as a synonym: ***dunni*** **Evans, 1928, junior subjective synonym of *Aedes* (*Pseudarmigeres*) *argenteoventralis* (Theobald, 1909)**. This agrees with the Encyclopedia of Life, which does not list *dunni* as a species.

In addition to *dunni* (type locality: Lagos, Nigeria), *Dendromyia affinis* Theobald, 1909 is also a recognized synonym of *Ae. argenteoventralis*. The type locality of *Dendromyia affinis*, Obuasi, Ashanti Region of Ghana, is also the type locality of *Ae. argenteoventralis*.

Aedes (*Pseudarmigeres*) *michaelikati* van Someren

subspecies ***gurneri*** van Someren, 1946a—original combination: *Aedes* (*Dunnius*) *michaelikati gurneri*. Distribution: Democratic Republic of the Congo, Kenya, Tanzania (White 1980; Wilkerson *et al*. 2021).
subspecies ***michaelikati*** van Someren, 1946a—original combination: *Aedes* (*Dunnius*) *michaelikati*. Distribution: Kenya, Tanzania (White 1980).

These nominal taxa are poorly known. The typical form and subspecies *gurneri* were described in the same paper (van Someren 1946a). Available data suggest that the former is restricted to coastal areas (type locality near Mombasa, Kenya) whereas the latter (type locality near Nairobi) has an inland distribution. The two forms are also morphologically distinct—the adults of *gurneri* are darker than those of *michaelikati*, there are no white scales on the maxillary palpi of either sex, abdominal terga V and (usually) VI of females lack basal white bands and the shape and armature of the male gonostylus are different. The larvae of the two forms have not been studied in detail, but they may be distinguished by the shape of seta 1-C, which is blunt-tipped in *michaelikati* and sharply pointed in *gurneri*. Based on apparent allopatry and morphological distinctions, *gurneri* is hereby formally recognized as a separate species: ***Aedes gurneri* (van Someren, 1946a)**. *Aedes gurneri* is currently listed as a species in the Encyclopedia of Life.

Aedes (*Rampamyia*) *notoscriptus* (Skuse)

subspecies ***montanus*** Brug, 1939—original combination: *Aedes* (*Finlaya*) *notoscriptus* var. *montana* [*sic*] (subgeneric status by Stone *et al*. 1959). Distribution: Indonesia (Java) (Brug 1939).
subspecies ***notoscriptus*** (Skuse, 1889)—original combination: *Culex notoscriptus*. Distribution: Australia, Indonesia (Moluccas, Western New Guinea), New Caledonia, New Zealand, Papua New Guinea, Solomon Islands, United States (continental) (Wilkerson *et al*. 2021, Philippines record unverified).

Brug (1939) described *montanus* as a variety of *Aedes notoscriptus* and Stone *et al*. (1959) treated it as a subspecies of *notoscriptus*. The two forms are widely allopatric. The typical form is restricted to the Australasian Region whereas *montanus* is only know from its type locality in western Java, which lies within the Oriental Region. Brug (1939) noted that he was greatly surprised "to find a specimen of *A. notoscriptus* (Skuse) when rearing larvae found in Lembang, Java" because "this species was considered to be truly Australian, not being found further westward than in Saparoea, a small island near Ceram (Moluccas)." The specimen, a male, differs from the typical form in having a much shorter and distally narrowed white stripe on the hindtibia, a longer gonostylus, the claspette with a longer filament and longer setae at the base of the claspette stem, and sternum IX with a different number of setae. Based on its allopatric distribution and morphological distinctions, *montanus* is undoubtedly a distinct species, which is hereby formally elevated to specific status: ***Aedes* (*Rampamyia*) *montanus* Brug, 1939**. *Aedes montanus* is currently listed as a species in the Encyclopedia of Life.

Aedes (*Rusticoidus*) *rusticus* (Rossi)

subspecies ***rusticus*** (Rossi, 1790)—original combination: *Culex rusticus*. Distribution: Albania, Algeria, Austria, Belgium, Bulgaria, Crimean Peninsula, Croatia, Czech Republic, Denmark, Estonia? (see Kirik *et al*. 2022), France, Macedonia, Germany, Greece, Hungary, Ireland, Italy, Latvia, Lithuania, Luxembourg, Montenegro, Morocco, Netherlands, Poland, Portugal, Serbia, Slovakia, Spain, Sweden, Switzerland, Turkey, Ukraine, United Kingdom (Wilkerson *et al*. 2021, excluding Norway, see Mehl 1996).
subspecies ***subtrichurus*** Martini, 1927—original combination: *Aedes subtrichurus* (varietal status by Edwards 1932a; subspecific status by Harbach & Howard 2007). Distribution: Turkey (Martini 1927).

Martini (1927) originally described *subtrichurus* as a distinct species of *Aedes*, but later (Martini 1931a) considered it to be a variety of *Ae. diversus* (Theobald, 1901c). It became a variety of *Ae. rusticus* when *diversus* was synonymized with that species (Edwards 1932a). Harbach & Howard (2007) recognized *subtrichurus* as a subspecies of *Ae. rusticus* because it was originally proposed as the valid name of a species, per Article 45.6.4.1 of the *International Code of Zoological Nomenclature*. Martini (1927) described *Ae. subtrichurus* based on specimens from the eastern end of the Gulf of Izmit (spelled as Ismid), located at the easternmost edge of the Sea of Marmara. Because this is the only record of *subtrichurus*, the locality lies within the wide distribution of *Ae. rusticus* and it is based merely on minor morphological differences, *Aedes subtrichurus* Martini, 1927 is hereby formally regarded as a synonym: ***subtrichurus* Martini, 1927, junior subjective synonym of *Aedes* (*Rusticoidus*) *rusticus* (Rossi, 1790)**. Consequently, "*Aedes subtrichurus*" should be removed from the list of species of *Aedes* in the Encyclopedia of Life.

With the synonymy of *subtrichurus*, *Ae. rusticus* now includes seven junior synonyms. The previously recognized synonyms include *Culex maculatus* Meigen, 1804, *Cx. musicus* Leach, 1825, *Cx. pungens* Robineau-Desvoidy, 1827, *Cx. quadratimaculatus* Macquart, 1834, *Cx. diversus* Theobald, 1901c and *Cx. nemorosus* var. *luteovittata* Theobald, 1901c, all of which have type localities in Europe.

Aedes (*Stegomyia*) *aegypti* (Linnaeus)

subspecies ***aegypti*** (Linnaeus, 1762)—original combination: *Culex aegypti*. Distribution: Worldwide tropics and subtropics (Mattingly 1957b; Huang 2004; Powell *et al.* 2018; Soghigian *et al.* 2020) [see postscript note regarding current nomenclature].

subspecies ***formosus*** (Walker, 1848)—original combination: *Culex formosus* (subspecific status by Mattingly 1957b). Distribution: Sub-Saharan Africa (Mattingly 1957b; Huang 2004; Powell *et al.* 2018; Soghigian *et al.* 2020).

It is apropos here to reiterate what we advocated in the Introduction, *i.e.* we follow the definitions of species and subspecies of de Queiroz (1998, 1999, 2005a, 2005b, 2007, 2020, 2021). Herewith, a brief taxonomic conspectus of *Ae*. *aegypti aegypti* and *Ae*. *aegypti formosus* is provided, followed by some examples of how *formosus* fits as an incompletely separated lineage.

Aedes aegypti aegypti and *Ae*. *aegypti formosus* are members of the Aegypti Group (Huang 2004), which also includes *Ae*. *mascarensis* (MacGregor, 1924), type locality Mauritius, an island nation in the Indian Ocean located about 800 km east of Madagascar, and *Ae*. *pia* Le Goff & Robert, 2013 (in Le Goff *et al*. 2013), type locality Mayotte, officially the Department of Mayotte, an Overseas Department of France in the Comoro Archipelago in the Indian Ocean located between Madagascar and Mozambique.

Using three molecular datasets, Soghigian *et al.* (2020) "found that: (a) the Aegypti Group diverged 16 MYA (95% HPD: 7–28 MYA) from its nearest African/Asian ancestor; (b) SWIO [Southwest Indian Ocean] populations of *Ae*. *aegypti* are basal to continental African populations; (c) after diverging 7 MYA (95% HPD: 4–15 MYA) from its nearest formally described relative (*Ae*. *mascarensis*), *Ae*. *aegypti* moved to continental Africa less than 85,000 years ago, where it recently (<1,000 years ago) split into two recognized subspecies, *Ae*. *aegypti formosus* and a human commensal, *Ae*. *aegypti aegypti*...". The latter invaded the New World about 500 years ago via ships involved in the slave trade, and from there it invaded Asia about 150 years ago (Gloria-Soria *et al*. 2016). Soghigian *et al.* also noted that "*Ae*. *pia* is clearly the most distantly related and thus serves as an outgroup in [their] later analyses." They also refer to *Ae*. *aegypti* in Madagascar as '*aegypti*' Madagascar due to its large genetic distance from global *aegypti sensu stricto* and *Ae*. *mascarensis* from Mauritius.

Mattingly (1957b) considered three forms of *aegypti sensu lato*.

> 1. *A. aegypti* sens. str., the type form [worldwide tropics]. This form is variable in depth of colour but always either distinctly paler and browner (at least in the female) than the blackish African subspecies which is next described, or with pale scaling on the first abdominal tergite [terga], or both. In the type form extensions of pale scaling, if any, are limited either to bleaching of the two dark areas on the back of the head, or to the presence of pale scaling on the first abdominal tergite, or to both in combination.
>
> 2. *A. aegypti* ssp. *formosus* (Walker) [presumably retrieved from synonymy with *aegypti* in this cited publication]. This is a geographically representative form confined to Africa south of the Sahara, where it is the only form known to occur, except in coastal districts and in one or two areas of limited inland penetration. It is therefore designated as a subspecies. The name *formosus* was the first to be applied to any form occurring in the area (Walker, 1848). The type, a female from Sierra Leone, is in the British Museum. It is in poor condition but there is nothing about either it or Walker's description which would suggest either of the paler forms [the type form, above, and *queenslandensis*, below]. This subspecies differs from the type form in the markedly blackish appearance of the dark areas of the thorax and abdomen and in entirely lacking any bleaching or extension of pale scaling on any part of the body. It never has any pale scales on the first abdominal tergite.

A third form discussed by Mattingly, *A. aegypti* var. *queenslandensis* Theobald, 1901a [as *Stegomyia fasciata* variety] was later synonymized with *aegypti sensu stricto* by Huang (1979) and shown to be genetically indistinguishable from nominotypical *aegypti* in Australia (Rašić *et al*. 2016).

It is hypothesized that nominotypical *aegypti* evolved in sub-Saharan Africa from a forest species utilizing natural containers for larval development, and then diverged into two forms, one remaining adapted to forest habitats (*Aedes aegypti formosus*) and the other adapted to primarily seek human hosts and to utilize artificial containers provided by humans (*Aedes aegypti aegypti*). Significantly, McBride *et al.* (2014) found a genetic change in an odorant receptor responsible for the change to a preference for human blood.

A few examples of differences between *aegypti* and *formosus* follow, many demonstrating incomplete lineage separation. Note that most work comparing *aegypti* and *formosus* in Africa has been carried out in East Africa, while the type locality of *formosus* is in West Africa (Sierra Leone). Also note that despite the medical importance of *aegypti* and *formosus*, morphological studies of all stages have only been carried out on the invasive form in the New World and Asia. No detailed comparisons, other than documentation of adult abdominal markings, have been done for larvae and pupae of African *aegypti* or *formosus*, and therefore there are no comparisons with populations outside of Africa either.

McClelland (1974) scored pale abdominal markings of *Ae*. *aegypti sensu lato* worldwide in relation to biology using an artificial "paleness" scoring scheme. He found continuous intra- and interpopulation variation and determined that identification was not reliable using abdominal markings, *i.e.* there were discernible but no discrete groupings. He pointed out that part of the problem of correlating markings with habitat was imprecise terminology, and gave the example of "The same population of mosquitoes regarded as 'feral' when breeding in a forest would become 'peridomestic' if it persisted after a human settlement arose in the forest and 'urban' if the village grew to a town." He then provided a list of what he considered to be more usable terms. In conclusion he stated: "I would venture further that *A. aegypti* comprises two species or incipient species. The pale or synanthropic species competitively excludes the dark or feral species from habitats where water and man are continuously present. The reverse occurs in habitats where most breeding sites are filled naturally by rainfall."

Scott & McClelland (1975), using starch gel electrophoresis and specimens from eastern Kenya, stated: "The indoor and outdoor ecotypes differed considerably at three loci." In the laboratory, caged indoor and outdoor ecotypes mated freely, but they stated: "We have demonstrated partial reproductive isolation between them; therefore, what we are calling two 'ecotypes' may actually be incipient species, partially isolated by habitat selection."

Paterson *et al.* (1976) concurred with Scott & McClelland (1975), stating that "the data on the alkaline phosphatase and protein loci... are sufficient to eliminate the possibility that we are dealing with a single polymorphic species. In fact, the data for these two loci provide strong evidence for the existence of positive assortative mating in the field, thus supporting the view that they are distinct genetic species."

Moore (1979), based solely on laboratory crossing experiments, determined that data for *aegypti* and *formosus* from Kenya were "consistent with the contention that *Aedes aegypti* is a single polytypic species." We note that laboratory mating experiments with closely related, perhaps currently diverging species, probably do not reflect what is happening in nature.

Tabachnick *et al.* (1979), in a larger study of *aegypti* and *formosus*, also using starch gel electrophoresis and specimens from (eastern) Kenya, were ambiguous in their judgement of the status of the two forms. They stated: "The results suggest that gene flow between the two forms is restricted. None of the loci examined in this study provided evidence for the complete absence of gene flow between forms. We feel that, at present, the two forms can still be thought of as members of the same polytypic species. However, due to the distinct behavioral differences characteristic of each, and the evidence for restricted gene flow, speciation may be a likely eventuality."

Lounibos (1981) studied the larval ecologies of mosquito species at two sites near the Kenyan coast (Rabai Location, Kilifi District and Shimba Hills National Park, Kwale District). *Aedes aegypti* larvae [*sensu lato*] were found in cultivated and ecotonal macrohabitats, predominantly in large tree holes and bamboo. Lounibos also noted that 96% of the *Ae*. *aegypti* collected for his study of tree holes and other natural containers corresponded to the morphologically dark subspecies *formosus*, as characterized by Mattingly (1957b). Most research on the two nominal taxa has been carried out on East African populations. In one study, in contrast to discrete local partitioning of the two forms in Kenya, Sylla *et al.* (2009), working in Senegal in West Africa, found a clear northwest to southeast cline in change in the proportions of individuals fitting the concept of *aegypti* versus *formosus*—in the northwest significantly more *aegypti*, in the southeast many more *formosus*. Vector competence measures also followed this cline but molecular genetic measures did not. The authors, however, pointed out many uncontrolled variables in the relatively small study.

Jupp *et al*. (1991) concluded "that in South Africa, *Ae*. *aegypti* is a single polymorphic species showing a considerable amount of variation in the degree of white scaling on the first two abdominal tergites [terga]. The presence of some rural sylvan non-anthropophilic populations in our country... might, however, indicate incipient speciation."

Brown *et al.* (2011) used polymorphic microsatellite markers to test worldwide populations. They "identified two distinct genetic clusters: one included all domestic populations outside of Africa and the other included both domestic and forest populations within Africa. This suggests that human association in Africa occurred independently from that in domestic populations across the rest of the world. …Interestingly, two forms identified as subspecies *aegypti* and *formosus* were shown to coexist in a few places along the coast of East Africa, including the Rabai district of Kenya... where the former bred inside homes in villages and the latter bred in surrounding forests." Three years later, Brown *et al*. (2014) "used DNA sequences of four nuclear genes and 1504 single nucleotide polymorphism (SNP) markers developed with restriction-site associated DNA (RAD) sequencing to test the hypothesis that *Ae*. *aegypti* originated in Africa, where a domestic form arose and spread throughout the tropical and subtropical world with human trade and movement."

In Sudan, Abuelmaali *et al.* (2021) and Elnour *et al.* (2022) both reported geographically separated populations of *a. formosus* (in the west) and *a. aegypti* (in the east). Elnour *et al.* (2022) wrote that "Analysis supports a scenario in which *Ae*. *aegypti* entered Sudan on at least two independent occasions nearly 70–80 years ago." We think this raises the possibility of interesting scenarios as *aegypti* reinvades localities in Africa. For example, if *a. formosus* evolved into a proto-*a. aegypti* and then into *a. aegypti* (see Powell *et al*. 2018), which then invaded the rest of the world, where is *a. aegypti* in Africa and how is it evolving in relation to the invasive *a. aegypti* in the rest of the world? Powell & Tabachnick (2013) stated that *a. aegypti*, as it occurs in the New World, is not known in West Africa today, except perhaps as a reintroduction into ports (Brown *et al*. 2011).

We think there is abundant evidence concordant with the subspecies concept of de Queiroz (2020) to hereby elevate *formosus* to its original specific status: ***Aedes* (*Stegomyia*) *formosus* (Walker, 1848)**. *Aedes formosus* is currently listed as a species in the Encyclopedia of Life.

The following nominal forms are currently listed as synonyms of *Aedes aegypti* in Wilkerson *et al.* (2021). Many will remain in doubt until existing types are examined to see if any correspond to *Ae. formosus*. Some of these are probably from a now extinct Mediterranean (North African, European) distribution of what was thought to be reintroduced *Ae. aegypti* from the New World (Powell *et al*. 2018). There are also New World synonyms, which are probably *Ae. aegypti*, but verification is needed since it is possible that *Ae. formosus* is present in the New World. Given the unusual biogeography of the Madagascar area, and predictions of undescribed taxa by Soghigian *et al.* (2020), synonyms from Madagascar and Mauritius also require further scrutiny. African synonyms could potentially be *Ae. agypti* or *Ae. formosus*.

Unless otherwise indicated, * = Mediterranean, † = New World, $^{+}$ = Madagascar and Mauritius and $^{\#}$ = Africa in the following list of current synonyms of *Aedes aegypti*: **Culex argenteus* Poiret, 1787; †*Culex fasciatus* Fabricius, 1805; **Culex calopus* Meigen, 1818; †*Culex mosquito* Robineau-Desvoidy, 1827; †*Culex frater* Robineau-Desvoidy, 1827; †*Culex taeniatus* Wiedemann, 1828; **Culex sugens* Wiedemann, 1828; **Culex kounoupi* Brullé, 1833; †*Culex toxorhynchus* Macquart, 1838a; **Culex annulitarsis* Macquart, 1846a; locality not known, *Culex viridifrons* Walker, 1848; †*Culex excitans* Walker, 1848; $^{\#}$*Culex inexorabilis* Walker, 1848 (could be *aegypti* or *formosus*); †*Culex exagitans* Walker, 1856a; $^{+}$*Culex insatiabilis* Bigot, 1959; Australia, *Culex bancrofti* Skuse, 1889; **Culex elegans* Ficalbi, 1890b; India, *Culex rossi* Giles, 1899; Australia, *Stegomyia fasciata* var. *queenslandensis*; Theobald, 1901a; †*Stegomyia fasciata* var. *luciensis* Theobald, 1901a; $^{\#}$*Stegomyia nigeria* Theobald, 1901a (could be *aegypti* or *formosus*); $^{+}$*Stegomyia lamberti* Ventrillon, 1904; Canary Islands, *Stegomyia calopus* var. *canariensis* Pittaluga, 1905; Philippines, *Stegomyia fasciata* ssp. *persistans* Banks, 1906b; Tenerife, Canary Islands, *Culex anguste-alatus* Becker, 1908; Tenerife, Canary Islands, *Culex albopalposus* Becker, 1908; Philippines, *Duttonia alboannulis* Ludlow, 1911b; Australia, *Mimeteomyia pulcherrima* Taylor, 1919; $^{\#}$*Stegomyia fasciata* var. *atritarsis* Edwards, 1920a.

Note. An explanation of the complex nomenclatural history of the nominotypical subspecies is beyond the scope of this treatment. In summary, in the interests of nomenclatural stability, Mattingly *et al.* (1962) petitioned the International Commission on Zoological Nomenclature (ICZN) to fix the name *Aedes* (*Stegomyia*) *aegypti*

(Linnaeus, 1762) with designation of a neotype from Kuala Lumpur, Selangor, Malaya [Malaysia]. The petition was validated in ICZN Opinion 711 (International Commission on Zoological Nomenclature 1964). See Clements & Harbach (2018) for an alternative perspective. Since we now know that the nominotypical form is an invasive species that was restricted to sub-Saharan Africa until only about 500 years ago, we think that the choice of Malaysia for the neotype and type locality, with an even more recent history of invasion than the initial movement to the New World, is problematic.

Aedes (*Stegomyia*) *annandalei* (Theobald)

subspecies ***annandalei*** (Theobald, 1910a)—original combination: *Stegomyia annandalei*. Distribution: Bangladesh, Cambodia, India, Indonesia, Myanmar, Nepal, Papua New Guinea, People's Republic of China, Taiwan, Thailand, Vietnam (Wilkerson *et al*. 2021).

subspecies ***quadricinctus*** (Barraud, 1923b)—original combination: *Stegomyia annandalei* var. *quadricincta* (subspecific status by Harbach & Howard 2007). Distribution: India (Barraud 1923b).

The taxonomic history of *Ae*. *annandalei* involves three nominal forms: *Stegomyia annandalei* Theobald, 1910a, *Aedes horishensis* Yamada, 1921 and *Stegomyia annandalei* var. *quadricincta* Barraud, 1923b. *Aedes horishensis*, described from a single female collected at or near Horisha in present-day Taiwan, was recognized as a subspecies of *annandalei* by Lien (1962). Its taxonomic status thereafter is a matter of confusion. Mattingly (1965) listed it as a synonym of *annandalei*, but also indicated that he considered it to be a variety: "I agree with Lien that the evidence no longer warrants this being treated as a distinct species. However, the apparently low incidence of this type of marking [slight posterior shifting of pale bands on abdominal terga IV–VI] in Taiwan and its simultaneous occurrence in Indonesia, in both cases in areas where normal markings are the rule, seems to me to render his suggestion that it should be treated as a subspecies unacceptable. Since this character reappears in the *Ae. scutellaris* complex and is, therefore of particular interest, I consider that specimens showing it should be distinguished as var. *horishensis* Yamada." Likewise, Huang (1977) also made conflicting statements about the status of *horishensis*. In the abstract of her publication, she stated that "*Aedes horishensis* Yamada is regarded as a variety of *annandalei* Theobald", whereas in her discussion of *annandalei*, she sided with Mattingly in noting that the posterior shifting of the abdominal bands is variable, and stated "Therefore, I consider *horishensis* Yamada to be a synonym of *annandalei*." Despite these contradictions, *horishensis* was listed as a synonym of *annandalei* by Knight & Stone (1977), attributed to Mattingly (1965), Harbach (2018) and Wilkerson *et al*. (2021), attributed to both Mattingly (1965) and Huang (1977). Lu *et al*. (1997) agreed with the synonymy. Based on the findings and actions taken by Mattingly (1965), Huang (1977) and Lu *et al*. (1997), we agree that *horishensis* is probably conspecific with *annandalei* and should continue to be recognized as a synonymous nominal taxon.

Barraud (1923b) described *Stegomyia annandalei* var. *quadricincta* based on "One female from Nongpoh, Assam, July, 1922 (Barraud)." He noted there was "another female specimen from the same place which agrees with the above [description of *quadricincta*] in the markings of the hind tarsi, but the fore and mid legs have only two rings, as in the type form." This is obviously an indication that the two forms were sympatric. Barraud (1934) more explicitly described the distinctive tarsal banding of *quadricinctus* as follows: "Differs from the type-form in having basal white markings to first four tarsal segments on all legs; markings at base of segments 3 and 4 on fore and mid-legs small and not forming complete rings; complete white rings on tarsal segments 1–4 on hind legs, that on 4 occupying nearly whole segment."

Concomitant with the recognition of *Stegomyia* as a subgenus of *Aedes* by Edwards (1932a), the variety described by Barraud (1923b) became known as *Aedes* (*Stegomyia*) *annandalei* var. *quadricinctus*, and was subsequently listed as such in the catalogs of Stone *et al*. (1959) and Knight & Stone (1977). Mattingly (1965) and Huang (1977) both listed *quadricinctus* as a synonym of *annandalei* without explicit mention or discussion of its taxonomic status. Mattingly, however, noted that "Var. *quadricinctus* Barraud… has white rings on the first 4 tarsi [tarsomeres] of all legs. An otherwise similar ♀ from the type locality had only the first 2 segments [tarsomeres] banded on the fore and mid legs. I have not seen this type of variation in any Indomalayan material." Perplexingly, Huang (1977) vaguely (doubtfully?) indicated that the tarsi of *annandalei* may sometimes exhibit the condition described for *quadricinctus*, *i.e.* that tarsomeres 1–4 of all legs have white bands. She described the tarsi of males as having the "fore- and midtarsi with basal white band on tarsomere 1, sometimes midtarsus with a few white scales on basal area of tarsomere 2 as well; hindtarsus with basal white bands on tarsomeres 1,2; **tarsomere 3 dark** [emphasis ours]; tarsomere 4 with basal 0.67 white band to all dark…”. She noted females are essentially the same except that “Foretarsomere 2 sometimes with a few white scales on basal area; midtarsomere 2 with basal white band; hindtarsomere 4 with basal 0.83 white band; sometimes **hindtarsomere 3** [emphasis ours] with a few white scales on basal area as well…”.

The tacit synonymy of *quadricinctus* with *annandalei* published by Huang (1977) was not published in the world catalog of the Culicidae of Knight & Stone (1977) because the cut-off date for additions to the catalog was the end of 1973, but neither was it recorded in the three subsequent catalog supplements (Knight 1978; Ward 1984, Ward 1992). Unaware of the synonymy by Huang (1977), Harbach & Howard (2007) followed Knight & Stone in recognizing *quadricinctus* as a variety, which they deemed to be subspecific under provisions of Article 45.6.4 of the *International Code of Zoological Nomenclature*. Despite knowing that the leg markings of *annandalei* are subject to variation (Barraud 1923b; Mattingly 1965; Huang 1977) and recognizing that “Although it is likely that the name *quadricincta* applies to an infrasubspecific form…”, Harbach & Howard were obligated to reveal that *quadricinctus* “officially has subspecific rank” under provisions of the *Code*. In view of the earlier synonymy by Huang (1977), the change of rank from variety to subspecies was unnecessary and unsupportable.

A number of different DNA sequences are available in GenBank for specimens of *Ae. annandalei* from China and Singapore, but until molecular data become available for specimens of *quadricinctus* from its type locality in India, we must agree with Mattingly (1965) and Huang (1977) that *quadricinctus* is merely a morphological variant and synonym of *Ae. annandalei*. To avoid any doubt, *quadricincta* is hereby formally regarded as a synonymous name: ***quadricincta* Barraud, 1923b, junior subjective synonym of *Aedes* (*Stegomyia*) *annandalei* (Theobald, 1910a)**. Consequently, “*Aedes quadricinctus*” should be removed from the list of species of *Aedes* included in the Encyclopedia of Life.

***Aedes* (*Stegomyia*) *flavopictus* (Yamada)**

subspecies ***downsi*** Bohart & Ingram, 1946a—original combination: *Aedes* (*Stegomyia*) *downsi* (subspecific status by Tanaka *et al*. 1979). Distribution: Amami and Okinawa Islands, Japan (Tanaka *et al*. 1979).

subspecies ***flavopictus*** Yamada, 1921—original combination: *Aedes flavopictus*. Distribution: Guam, India, Japan, Russia, South Korea (Wilkerson *et al*. 2021).

subspecies ***miyarai*** Tanaka, Mizusawa & Saugstad, 1979—original combination: *Aedes* (*Stegomyia*) *flavopictus miyarai*. Distribution: Ishigaki and Iriomote Islands, Ryukyu Archipelago, Japan (Tanaka *et al*. 1979).

Yamada (1921) described *Ae. flavopictus* from specimens collected in Shiba, which was a ward of Tokyo until 1947 when it was merged with two other wards to form present-day Minato Ward. The Shiba area is in the eastern and southern parts of Minato Ward, and Tokyo is located on Honshu Island, which lies within the Palaearctic portion of Japan and has a humid subtropical climate. In contrast, the type localities of subspecies *downsi* and *miyarai* are located on southern islands of the Ryukyu Archipelago, which lie within the Oriental Region. Unlike the northern islands of the archipelago, which have a climate similar to that of Honshu Island, the southern islands have a tropical rainforest climate. The type locality of *downsi* is on Okinawa Island, located approximately 1,140 km south of the main island of Honshu, and that of *miyarai* is on Ishigaki Island, which lies approximately 410 km south of Okinawa Island.

Subspecies *downsi*, originally described as a species by Bohart & Ingram (1946a), was reduced to a subspecies of *flavopictus* by Bohart (1953). Huang (1972) re-instated *downsi* to its original species rank, but it was returned to its previous subspecific rank by Tanaka *et al*. (1979) based on a much more detailed morphological analysis of adults, larvae and pupae. Huang (1979) retained *downsi* as a species, but she was apparently not aware of Tanaka *et al*. (1979). The following observations and rationale for the taxonomic acts of these investigators are extracted from their publications.

Bohart & Ingram (1946a):

> [*Ae. downsi*] is probably most closely related to *flavopictus* Yamada from northern Japan and Korea which according to Yamada’s figure of the male genitalia… has an irregular margin of the ninth tergite [tergum IX] and stout setae on the basal [mesal] lobe of the basistyle [gonocoxite]. This species differs from *flavopictus*, however, in having no spot at the end of the scutal suture, in the more angular and sharply serrate male ninth tergite and the stouter setae of the basal lobe of the male dististyle.

> Bohart (1953):
>
> From a comparison of this material [type series and reared adults of *flavopictus*] with paratypes and other specimens of *downsi*… I am of the opinion that *downsi* represents a subspecies with the following tendencies: (1) restriction of the silver stripe on the front surface of the hind femur to the basal two-thirds or three-fifths of the femur, (2) expansion of the white markings of hind tarsal IV to cover five-sixths to nine-tenths of the segment [hindtarsomere 4], (3) reduction of the tergal pale stripes of the abdomen to weak or incomplete bands especially on III. The gills [anal papillae] are variable in length, often quite short, and always unequal. The fifth pentad hair [seta 5-VIII] almost always has more than 4 branches…. In the typical subspecies from various of the main islands of Japan the fifth pentad is 6 to 20 branched according to Sasa and Kano (1951) and 5 to 17 branched according to LaCasse and Yamaguti (1950).

> Huang (1972):
>
> The similarity between these two forms is so close that one would be inclined to regard *downsi* as a subspecies of *flavopictus*. However, it can be separated from *flavopictus* by the diagnostic characters mentioned in the key. In addition, the immature stages of *downsi* are markedly differentiated from *flavopictus*. The larva of *downsi* has the saddle incomplete, hair [seta] 14-P with 3–4 branches, hair 11-M and 11-T usually single (l–2); in *flavopictus* the saddle is complete, hair 14-P has 5–7 branches, hair 11-M is double and 11-T double or 3-branched. The pupa of *downsi* has hair 9-VI much stouter than 9-V, at least twice as long as 9-V, hair 9-VI usually single and barbed; in *flavopictus* hair 9-VI about same magnitude as 9-V, always single and simple. Based on the morphological difference in all stages of these two forms, I believe that *downsi* should be recognized as a distinct species.

> Tanaka *et al*. (1979):
>
> Huang (1972) elevated it again to a species. Her discussion of *downsi* appears accurate as far as specimens from Okinawa are concerned. However, more local and individual variations occur.
>
> As a result of the above diagnosis on 13 adult characters, the populations of Palaearctic Japan and Korea, Amami, Okinawa and Yaeyama are considered as a single species. The Palaearctic population is the nominate subspecies, *flavopictus*. The Amami and Okinawa populations are identical, conforming to subspecies *downsi*. The southernmost population (Yaeyama) of *flavopictus*, is identical with subspecies *flavopictus* in 2 characters, with subspecies *downsi* in 2 characters, intermediate in 4 characters, different from both in 5 characters, 3 of the lattermost not appearing clinal. This population is assigned to another subspecies, *miyarai*.
>
> The larvae of *f. flavopictus* are characterized by stiff stellate body setae, but the variation is wide…. No definite hairy type was found in… *downsi* and *miyarai*, whose setae have in general fewer branches and are usually weak. … The larvae of *f. downsi* and *f. miyarai* are, contrary to the adult, fairly homogenous, there being only minor differences, e.g., the laterobasal fringe of spicules of the comb scales is usually very weak and basally restricted in *f. downsi*, usually a little stronger and extending up to near middle of the apical spine in *f. miyarai*; the number of the pecten teeth [spines] is 4–12 (19; $x = 6.7$) in *f. downsi*, 7–19 (20; $x = 11.6$) in *f. miyarai*. Subspecies *downsi* and *miyarai* differ from *flavopictus* in the longer seta l-VII (the average length relative to the antenna being 1.63, 1.57 and 1.06 in *downsi* (19), *miyarai* (13) and *flavopictus* (30), respectively) and in that the ventral anal gill [papilla] is usually shorter than the dorsal one, while in 75% of *flavopictus* they were equal. …It is interesting that, in *f. flavopictus*, many setae, such as 14-P, 5-T, 2-I, III–VII, 5-III-V, 9-VI, 13-I, III–V, have double or quadruple the numbers of branches found in the equivalent setae of *f. downsi* and *f. miyarai*. The non-hairy type in *f. downsi* and *f. miyarai* may represent an ancestral form of this species.

In our opinion, the morphological data indicate that the three forms are distinct polythetic taxa that are diagnosed by unique combinations of characters. Polythetic species are common in many groups of mosquitoes, particularly large groups like *Aedes* and *Culex*.

Numerous sequences for the *COI* and *ND5* mitochondrial genes are available in the GenBank depository, including the entire mitochondrial genome for specimens of *flavopictus* from South Korea (NC_050044). Among these are *COI*, ITS1 and ITS2 sequences for *flavopictus* from the Palaearctic region of Japan, *downsi* from the Amami and Okinawa Islands and *miyarai* from Ishigaki and Iriomote Islands in the southern region of the Ryukyu Archipelago. Phylogenetic analysis of the ITS1 and ITS2 sequences (Toma *et al*. 2002) produced a cladogram comprised of three distinct lineages, corresponding to the three subspecies. Despite this, because the three forms have allopatric distributions and “reproductive isolation cannot be tested, except experimentally”, Toma *et al*.

were only willing to acknowledge that "the molecular genetic information we have gathered supports the current classification of the complex based on morphological data."

Drawing conclusions about the status of the subspecies of *flavopictus* has been a problem of uncertainty. However, we believe the available data provide an alternative interpretation: The geographic isolation is analogous with reproductive isolation, the morphological data are seen as an indication of polythetic species, and the ITS1 and ITS2 sequence data support the specific status of the three forms. In light of this, we believe that Bohart (1953), Tanaka *et al.* (1979) and Toma *et al*. (2002) were very circumspect in their decision to treat the three forms as subspecies. As in the case of subspecies of *Culex hayashii*, *Toxorhynchites manicatus* and *Uranotaenia novobscura* treated below, we believe it is appropriate to return *downsi* to its original specific status and to recognize *miyarai* as a separate species: ***Aedes* (*Stegomyia*) *downsi* Bohart & Ingram, 1946a** and ***Aedes* (*Stegomyia*) *miyarai* Tanaka, Mizusawa & Saugstad, 1979**. *Aedes downsi* and *Ae. miyarai* are currently listed as species in the Encyclopedia of Life.

It is important to note that Miyagi & Toma (1976) showed that laboratory cross mating between *flavopictus* from Nagasaki, Kyushu Island (Palaearctic) and *downsi* from Okinawa Island produced hybrid offspring. However, this is meaningless as hybridization between the two forms is unlikely to occur in nature. Besides, the ability to hybridize does not invalidate the existence of separate species, which is amply supported by hybridization studies between members of species complexes, *e.g.* the Dirus Complex (Walton *et al*. 2001) and Gambiae Complex (Besansky *et al*. 1997; Thelwell *et al*. 2000) of the genus *Anopheles*.

***Aedes* (*Stegomyia*) *gardnerii* (Ludlow)**

subspecies ***gardnerii*** (Ludlow, 1905)—original combination: *Stegomyia gardnerii*. Distribution: Bangladesh, Cambodia, Indonesia, Malaysia, Philippines, Singapore, Thailand, Vietnam (Wilkerson *et al*. 2021).

subspecies ***imitator*** (Leicester, 1908)—original combination: *Stegomyia imitator* (subspecific status by Mattingly 1965). Distribution: Bangladesh, Cambodia, India, Malaysia, Nepal, People's Republic of China, Taiwan, Thailand, Vietnam (Wilkerson *et al*. 2021).

Ludlow (1905) described the female and male of *Stegomyia gardnerii* from specimens captured on the Philippine Island of Mindoro (Bulacao), but she also examined specimens from Luzon Island (Angeles, Pampanga). A lectotype male was designated by Knight & Hull (1952), who described the adults in more detail, described the fourth-instar larva and illustrated the male genitalia. Leicester (1908) described *Stegomyia imitator* from two females captured in jungle near Kuala Lumpur, Malaysia. One of the females was selected as the lectotype by Mattingly (1965). Mattingly described and compared the adults (both sexes), pupa and fourth-instar larva of *gardnerii sensu stricto* and subspecies *imitator*, and illustrated the scutal scale-pattern and hindleg of both, the midfemur and entire pupa of *imitator*, the head and terminal abdominal segments of the larva of the type form, and the male genitalia of *imitator*. Huang (1977) provided more detailed descriptions of the male, female, pupa and larva, and illustrated the scutal and pleural scaling of both subspecies. For *gardnerii sensu stricto*, she also illustrated the maxillary palpus and genitalia of the female, the midfemur, male genitalia, entire pupa and entire larva. It is worth noting that in available identification keys (Mattingly 1965; Huang 1977, 1979), the two subspecies are only distinguishable as adults based on the pattern of the scutal scaling. The scutum of the nominate form bears a pair of longitudinal, midlateral stripes of white scales that extend from the anterior margin to the antealar area. The stripes are absent in subspecies *imitator*, which bears a large patch of white scales on the anterior margin that may be divided medially into two anterolateral patches. The two forms are included but are not distinguished in keys for the male genitalia, pupae and larvae.

Huang (1977) seems to have contradicted herself, by saying on the one hand that "Although *imitator* (Leicester) can easily be distinguished from that of *gardnerii* (Ludlow) by the scutal markings", and on the other that "this adult external morphological character (the scutal markings) seems to be geographically variable." We believe she intended to say that due to variation in the scutal pattern of *imitator*, "I have here followed Mattingly (1965) in considering *imitator* as a sub-species of *gardnerii*."

Wilkerson *et al*. (2021) mistakenly combined the country records for *imitator* with those of *gardnerii*. In the case of *gardnerii*, the records for Bangladesh, Cambodia, China, Malaysia, Singapore, Thailand and Vietnam apply to subspecies *imitator*, based on the records of Mattingly (1965), Matsuo *et al*. (1974, Taiwan), Huang (1977), Darsie

& Pradhan (1990, Nepal), Lu *et al*. (1997, China), Jeffery *et al*. (2010, Singapore), Rattanarithikul *et al*. (2010, Thailand), Irish *et al*. (2016, Bangladesh), Bui & Darsie (2008, Vietnam) and Maquart *et al*. (2021, Cambodia). As indicated by Huang (1977), the nominate subspecies "is apparently confined to the Eastern part of Indomalayan area… presently known from the Philippines, Sabah [Malaysia], Sulawesi and Alor Island."

Two partial sequences of the cytochrome c oxidase subunit I (*COI*) gene are registered in GenBank for *Ae. gardnerii*: Accession MW321943 (667 bp), *Ae. gardnerii* from Singapore (Yeo *et al*. 2021) and accession MK654753 (661 bp), *Ae. gardnerii imitator* from Thailand (P. Somboon). A BLAST search revealed that the two sequences are identical. Obviously, the sequence from Singapore is derived from a specimen of subspecies *imitator*, which concurs with the recorded occurrence of this form in the island country (Jeffrey *et al*. 2010).

Although the male genitalia, larva and pupa of *gardnerii sensu stricto* and subspecies *imitator* may be indistinguishable, the fact they exhibit distinct and constant differences in the pattern of white scales on the scutum and have separate distributions is a clear indication that they are probably separate species. We believe this is likely to be proven when *COI* sequences become available for the nominate form. Therefore, it seems prudent to formally reinstate *imitator* to its original specific status: ***Aedes* (*Stegomyia*) *imitator* (Leicester, 1908)**. *Aedes imitator* is currently listed as a species in the Encyclopedia of Life.

Four nominal species originally described as species of *Stegomyia* Theobald, 1901 (in Howard 1901) are regarded as synonyms of *Ae. imitator*: *argenteomaculata* Theobald, 1907 (Narcondam Island; synonymy by Huang 1977); *christianus* Dyar, 1921b (China; synonymy by Mattingly 1965); *minutissima* Theobald, 1910a (India; synonymy by Huang 1977); and *indosinensis* Borel, 1928 (Indochina; synonymy by Huang 1977). These nominal species should remain in synonymy with *Ae. imitator*; however, it is possible that *argenteomaculata* could be a distinct species because it is described from a remote island outside the continental range of *Ae. imitator*.

***Anopheles* (*Anopheles*) *bancroftii* Giles**

subspecies ***bancroftii*** Giles, 1902—original combination: *Anopheles bancroftii*. Distribution: Australia, Papua New Guinea, including the Admiralty Islands in the Bismarck Archipelago (Lee *et al*. 1987).

subspecies ***barbiventris*** Brug, 1938—original combination: *Anopheles bancrofti* [*sic*] var. *barbiventris* (subspecific status by Harbach & Howard 2007). Distribution: Indonesia, Sulawesi (Lee *et al*. 1987).

Giles (1902) described *Anopheles bancroftii*, a widely distributed species in Australia (Lee *et al*. 1987), based on specimens from Burpengary, Queensland. Misidentification of *An. pseudobarbirostris* Ludlow, 1902 as *An. bancroftii* has resulted in erroneous listings of *bancroftii* in the Philippines, Sulawesi (Celebes) and Sri Lanka (Lee *et al*. 1987).

Subspecies *barbiventris* was described from specimens collected in Kalawara, Palou, Gumbasa, Sigi Regency, Central Sulawesi, Indonesia (Gazetteer: GoeNames; Kalawara; populated place; coordinates: -1.1808, 119.9385; D. Pecor pers. comm.). In the description, it was compared to *An. bancrofti* [*sic*] var. *pseudobarbirostris* (now a separate species), *An. tessellatus* Theobald, 1901a and *An. vagus* Dönitz, 1902. Foote & Cook (1959) listed *barbiventris* as being from "Australasia", which includes many countries, but it's only known occurrence is in Sulawesi (Celebes). Harbach & Howard (2007) recognized *barbiventris* as a subspecies of *An. bancroftii* per Article 45.6.4 of the *International Code of Zoological Nomenclature* and suggested that it was probably a distinct species. Reid (1962), commenting on the *bancroftii* group, noted discrepancies in existing descriptions: "*A. bancroftii* var. *barbiventris* from Celebes seems to merit specific rank; in addition to the striking tufts of black and white scales on the abdominal sternites [sterna], the large leaflets on the phallosome [aedeagus] appear to be longer than those of *bancroftii* and *pseudobarbirostris* and have fine teeth [serration]; doubtless there are other differences." Herein, in addition to evidence of allopatry, we agree with Reid (1962) and Harbach & Howard (2007) that *barbiventris* should be afforded species status: ***Anopheles* (*Anopheles*) *barbiventris* Brug, 1938**. *Anopheles barbiventris* is currently listed as a species in the Encyclopedia of Life.

Note. A species complex is suggested by a molecular and morphological study (Beebe *et al*. 2002; Beebe *et al*. 2013) demonstrating the probability of four *bancroftii*-related sibling species in northern Australia and Papua New Guinea.

Anopheles (*Anopheles*) *eiseni* Coquillett

subspecies ***eiseni*** Coquillett, 1902a—original combination: *Anopheles eiseni*. Distribution: Belize, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, El Salvador, French Guiana, Guatemala, Guyana, Honduras, Mexico, Nicaragua, Panama, Peru, Suriname, Trinidad and Tobago, Venezuela (Wilkerson *et al*. 2021).

subspecies ***geometricus*** Corrêa, 1944—original combination: *Anopheles* (*Anopheles*) *enseni* [*sic*] subsp. *geometricus* (varietal status by Stone *et al*. 1959; original subspecific status re-confirmed by Harbach & Howard 2007). Distribution: Brazil (Corrêa 1944).

Coquillett (1902a) described *An*. *eiseni* from a female and two males from Aguna [*sic*], Guatemala. The female bears a type label and Coquillett's determination label (Stone & Knight 1956b). Belkin *et al*. (1965) cited the type locality as Aguná (Escintila), elevation 2,000 ft. The most likely location is Finca Aguná. This estimation is based on the cited elevation that corresponds to one of a number of nearby places with the same name: Coordinates 14.38955 -91.07121 (uncertainty 3,250 m); Municipio de Santa Lucía Cotzumalguapa, Escuintla Province, Guatemala (Chapman & Wieczorek 2020; D. Pecor pers. comm.). *Anopheles eiseni sensu lato* females have easily recognized morphological characters throughout its reported range: Hindtibia with broad apical band; apex of hindfemur with a few pale scales; costa of wing dark-scaled except for a preapical pale spot on it and vein R_1; sector pale spot only on R_1; apical fringe spot present; scutum with broad pruinose silvery gray central area; proboscis dark; palpomere 5 pale with small dorsal dark spot, palpomere 4 dark laterally, palpomere 3 with narrow apical pale band. There is a wide variety of depictions of wing characters in *eiseni sensu lato*: Sector pale present on costa (Lane 1953); *eiseni sensu stricto* with fringe spots at apices of veins R_2, R_3 and R_{4+5}, but *eiseni geometricus* without the R_2 fringe spot (Sallum *et al*. 2020); with pale fringe at apices of all veins and in addition a basal pale fringe spot (Pelaez 1945). Recent observations and photographs of the wing of the holotype female (by D. Pecor) show only preapical pale and sector pale spots as described above, no pale fringe spots. These examples could indicate the presence of a species complex.

Subspecies *geometricus* was described for specimens from Guarujá, Ilha de Santo Amaro, São Paulo, Brazil. Corrêa (1944) based his description on previously illustrated observations (Corrêa 1942), which were made in comparison to specimens of *An*. *eiseni* from Mexico. He noted that the São Paulo "geographical race" was different from specimens from the Guatemala type locality and Mexico. The Guarujá population (*eiseni geometricus*) was abundant in larval habitats but absent from animal-bait captures and light traps, in contrast to Guatemala, where adults are very easy to find. The primary difference between the two was the morphology of the egg. The egg of *geometricus* from Guarujá exhibits lozenge-shaped (diamond) features on the outer chorion (thus the name *geometricus*), while in Mexico (see also Vargas 1942) the outer chorion is smooth with some granular formations at both ends. We assume that the Mexican and Guatemalan specimens are conspecific. Given the great geographical distance between the populations, apparent behavioral differences and distinctive egg features we conclude that *geometricus* should be afforded species status: ***Anopheles* (*Anopheles*) *geometricus* Corrêa, 1944**. *Anopheles geometricus* is currently listed as a species in the Encyclopedia of Life.

Anopheles eiseni has a single synonym, *An. niveopalpis* Ludlow, 1919 (type locality: Comacho Reservoir, Empire, Canal Zone, Panama). Until proven otherwise, *niveopalpis* should remain a synonym of *An. eiseni*.

Anopheles (*Anopheles*) *gigas* Giles

subspecies ***crockeri*** Colless, 1955—original combination: *Anopheles gigas* ssp. *crockeri*. Distribution: Sabah, Malaysia [Saung-Saung, Sunsuran Trace, North Borneo] (Colless 1955).

subspecies ***danaubento*** Mochtar & Walandouw, 1934—original combination: *Anopheles gigas* var. *danaubento*. Distribution: Sumatra (Mochtar & Walandouw 1934).

subspecies ***formosus*** Ludlow, 1909a—original combination: *Anopheles formosus*. Distribution: Indonesia, Philippines (Wilkerson *et al*. 2021).

subspecies ***gigas*** Giles, 1901b—original combination: *Anopheles gigas*. Distribution: India (records from other countries listed in Wilkerson *et al*. 2021 either apply to the other subspecies, are doubtful or require verification).

subspecies ***oedjalikalah*** Nainggolan, 1939—original combination: *Anopheles gigas* var. *oedjalikalah* [as Oedjali Kalah]. Distribution: Sumatra (Nainggolan 1939).

subspecies ***pantjarbatu*** Waktoedi Koesoemawinangoen, 1954—original combination: *Anopheles gigas* var. *pantjarbatu*. Distribution: Sumatra (Waktoedi Koesoemawinangoen 1954).

subspecies ***refutans*** Alcock, 1913—original combination: *Anopheles gigas* var. *refutans*. Distribution: Sri Lanka (Alcock 1913).

The nominotypical subspecies, from India, is a member of the Gigas Complex, Gigas Subgroup of the Lindesayi Group. A coordinate grouping, the Baileyi Complex (Somboon *et al.* 2020b; Namgay *et al.* 2020), is also included in the Gigas Subgroup. Knight & Stone (1977) treated all of what is now the Baileyi Complex (*An. baileyi* Edwards, 1929b; *An. simlensis* James, 1911) (in James & Liston 1911) plus the Gigas Complex (the above plus *An. sumatranus* Swellengrebel & Rodenwaldt, 1932) as varieties of the nominotypical subspecies. Another species of the Gigas Complex, *An. prachongae* Rattanarithikul & Harrison, 2017 (in Harbach *et al.* 2017), was described subsequently. Species of the Gigas Complex are large mosquitoes found at higher elevations (≥ 1,000 m) in mountainous areas of the Oriental, Palearctic and Australasian Regions. It is generally accepted that changes in climate can isolate populations on mountain refugia, which then lead to fragmented distributions of related species (reviewed by Harbach *et al*. 2017), as appears to be the pattern here.

The nominotypical subspecies occurs in southwestern India (type locality: Conoor (2,000 m), Nilgiri Hills, Madras, India). None of the other subspecies has been found in India. Subspecies *crockeri* is the only member of the complex found in Borneo (type locality: Saung-Saung, Sunsuran [Sunsuron?] Trace, northern Borneo). Characters to separate it from the other subspecies have been discussed and illustrated by Colless (1955), Reid (1968) and Harbach *et al*. (2017). The last authors also questioned its subspecific status. It is characterized as follows. Female: Maxillary palpus dark at apex; costa of wing without preapical pale spot (only present on costa in *An*. *simlensis*), fringe spots present at apices of veins R_{4+5} and M_{3+4} and between veins CuA and 1A, fringe spot absent between apices of M_{3+4} and CuA (only present in *An*. *sumatranus*). Larva: Seta 2-C long, longer than 0.5 length of head; 3-C long, about 0.67 length of 2-C, with 2,3 basal branches; 4-C stout, single or branched at apex. Given the allopatric distribution in comparison to the other subspecies, and its distinctive morphological characters, it is likely that *crockeri* is genetically distinct and should therefore be afforded specific status: ***Anopheles*** **(*Anopheles*)** ***crockeri*** **Colless, 1955**. *Anopheles crockeri* is currently listed as a species in the Encyclopedia of Life.

Subspecies *formosus* is the only member of the complex described from the Philippines (type locality: Camp John Hay, Benguet, Philippines). Characters separating it from other subspecies of the complex are listed in Harbach *et al*. (2017). King (1931) described and illustrated distinguishing characters, a few of which are given here, as follow. Female: Maxillary palpus pale apically; wing without fringe spots except for one between the tips of veins CuA and 1A; preapical pale spot present on costa and veins R_1 and R_2. Larva: Seta 2-C usually single; 3-C 0.5 or more length of 2-C, with 2–6 branches; 4-C nearly as long as 3-C, with 3–8 basal branches. Given the allopatric distribution in comparison to the other subspecies, and its distinctive morphological characters, it is likely that *formosus* is genetically distinct and should therefore be afforded specific status: ***Anopheles*** **(*Anopheles*)** ***formosus*** **Ludlow, 1909a**. *Anopheles formosus* is currently listed as a species in the Encyclopedia of Life.

Subspecies *refutans* is the only member of the complex described from Sri Lanka. The maxillary palpus of the female has three or four narrow white bands, one usually terminal (Alcock 1913). The wing fringe is all dark except for a pale spot between the tips of veins CuA and 1A (Christophers 1933). Christophers also noted a small pale spot dorsally on the midfemur, as in *simlensis*, which is not noted in Harbach *et al*. (2017). Additional study, especially of the probable types in the Natural History Museum, London (Townsend 1990), and the larval stage, are needed to better characterize this taxon. However, we think that its allopatric distribution in comparison to the other subspecies, the characters of the maxillary palpus and wing fringe, along with the dorsal spot on the midfemur (which needs to be verified) indicate that *refutans* is probably genetically distinct and should therefore be afforded species status: ***Anopheles*** **(*Anopheles*)** ***refutans*** **Alcock, 1913**. *Anopheles refutans* is currently listed as a species in the Encyclopedia of Life.

There are four nominal members of the Gigas Complex in Sumatra. One, *An*. *sumatranus*, was elevated to species status by Harbach *et al*. (2017). Subspecies *danaubento* and *oedjalikalah* were both described from near Mt Kerintji. The type locality of subspecies *danaubento* is Lake Danau Bento [danau = lake, bento = a kind of grass] in North Kerintji in Central Sumatra. Verbatim coordinates of 1° 40′ S, 101° 16′ E are very close to the gazetteer entry for Danau Gunung Labuh (coordinates: -1.7381, 101.2673) and match the text description, "Lake Bento lies at about 1400 m on the Southern Slope of Mt. Kerintji on the borders of Djambi and Sumatera Barat Provinces" (Kitzmiller 1982; D. Pecor pers. comm.). The type locality of subspecies *oedjalikalah* has verbatim coordinates of 1° 42′ S, 101° 16′ E. Oedjali Kalah is an old Kerintji word, which means Land of the Gods; situated on the southern slopes of Mt Kerentji, it was the source area of the Soengei Sioelak Deras. The elevation at this location is 1,451 m, which matches the locality description of 1,400–1,800 m (coordinates -2.13333, 101.38333) (Kitzmiller 1982; D. Pecor pers. comm.). Subspecies *danaubento* and *oedjalikalah* apparently have sympatric distributions and there are no obvious diagnostic characters that distinguish them, though a minor character given by Nainggolan (1939), the apex of vein CuP dark-scaled in *oedjalikalah* rather than narrowly pale-scaled as in *danaubento*.

The third subspecies of the Gigas Complex in Sumatra is *pantjarbatu*, which was collected as larvae from undisclosed localities. Characters to distinguish it from the previous two nominal forms are weak and overlapping. The following table (Table 5) is derived from the tabular comparison of a few larval characters for these three Sumatran forms provided by Waktoedi Koesoemawinangoen (1954).

TABLE 5. Comparison of larval characters for the three Sumantran subspecies of *Anopheles gigas*.

Character	***danaubento***	***oedjalikalah***	***pantjarbatu***
Seta 4-C length / seta 3-C length	~ 0.5	0.5	0.5–0.67
Seta 4-C distance to seta 3-C	Not so distant	Distant	Distant
Seta 4-C, branches	3,4 branches near tip	Single, simple or with a few barbs	Single or 2-branched
Seta 1-P, branches	8–10 with very thin main stem	7–9 with very thin main stem	7–9 with very thin main stem

Given the probability that the three nominal forms are sympatric and there are no diagnostic characters to separate them, we conclude that they are conspecific and that allopatry and key morphological characters indicate the species is distinct from other members of the Gigas Complex. Therefore, subspecies *danaubento* is afforded specific status: ***Anopheles* (*Anopheles*) *danaubento* Mochtar & Walandouw, 1934**, and *oedjalikalah* and *pantjarbatu* are hereby recognized as synonyms of that species: ***oedjalikalah* Nainggolan, 1939 and *pantjarbatu* Waktoedi Koesoemawinangoen, 1954, junior subjective synonyms of *Anopheles* (*Anopheles*) *danaubento* Mochtar & Walandouw, 1934**. *Anopheles danaubento* is currently listed as a species in the Encyclopedia of Life. Subspecies *oedjalikalah* Nainggolan, 1939 and *pantjarbatu* Waktoedi Koesoemawinangoen, 1954, which are currently listed as species therein, need to be removed from the list of recognized species of the genus *Anopheles*.

Anopheles (*Anopheles*) *parapunctipennis* Martini

subspecies ***guatemalensis*** de León, 1938—original combination: *Anopheles* (*Anopheles*) *chiriquiensis* var. *guatemalensis* (subspecific status by Wilkerson 1990). Distribution: Guatemala (Wilkerson 1990).

subspecies ***parapunctipennis*** Martini, 1932—original combination: *Anopheles parapunctipennis*. Distribution: Guatemala, Mexico (Wilkerson 1990).

The nominotypical subspecies belongs to the Pseudopunctipennis Group (Reid & Knight 1961). Most members of the group are large, high elevation species which share a number of distinctive morphological characters (see the treatment of *An. pseudopunctipennis* Theobald below). Wilkerson (1990) established that a synonym of *An. parapunctipennis*, *i.e. Anopheles* (*Anopheles*) *chiriquiensis* Komp, 1936, was a valid species. However, he left *guatemalensis* as a subspecies of *parapunctipennis* and stated that a single character in the female (but not the male) separated it from the nominotypical species: Vein R_1 dark at the subcostal pale spot, pale in *parapunctipennis*. The type locality of the nominotypical subspecies is San Cristóbal de las Casas, Chiapas Mexico (coordinates: 16.73176, -92.64126) and the type locality of subspecies *guatemalensis* is Cumbre del Aire, Department of Totonicapán, Guatemala (coordinates: 15.11667, -91.56667). The two localities are only 213 km apart in the same mountain range (coordinates and distance: D. Pecor pers. comm.). Given there is insufficient morphological indication that these nominal forms are genetically distinct, and that the type localities are geographically close enough to assume sympatry, we hereby recognize *guatemalensis* as a synonymous name: ***guatemalensis* de León, 1938, junior subjective synonym of *Anopheles* (*Anopheles*) *parapunctipennis* Martini, 1932**. The nominal *guatemalensis*, which is listed as a species in the Encyclopedia of Life, must be removed from the list of valid species of *Anopheles*.

Anopheles (*Anopheles*) *pseudopunctipennis* Theobald

subspecies ***levicastilloi*** Levi Castillo, 1944—original combination: *Anopheles pseudopunctipennis* var. *levicastilloi* (subspecific status by Leví Castillo 1945). Distribution: Ecuador (Levi Castillo 1944).
subspecies ***neghmei*** Mann, 1950—original combination: *Anopheles pseudopunctipennis* ssp. *neghmei*. Distribution: Chile (Mann 1950).
subspecies ***noei*** Mann, 1950—original combination: *Anopheles pseudopunctipennis* ssp. *noei*. Distribution: Chile (Mann 1950).
subspecies ***patersoni*** Alvarado & Heredia, 1947—original combination: *Anopheles* (*Anopheles*) *pseudopunctipennis* var. *patersoni* (subspecific status by Lane 1953). Distribution: Argentina (Alvarado & Heredia 1947).
subspecies ***pseudopunctipennis*** Theobald, 1901c—original combination: *Anopheles pseudopunctipennis*. Distribution: Aruba, Curaçao, Granada, Margarita Island (Venezuela), Trinidad and Tobago (historical), Venezuela [to be verified] (revised here).
subspecies ***rivadeneirai*** Leví Castillo, 1945—original combination: *Anopheles* (*Anopheles*) *pseudopunctipennis* var. *rivadeneirai* (subspecific status by Lane 1953). Distribution: Ecuador (Leví Castillo 1945).
syn. *argentinus* Brèthes, 1912—original combination: *Proterorhynchus argentinus*.
syn. *peruvianus* Tamayo, 1907 (in Tamayo & García 1907)—original combination: *Anopheles peruvianus*.
syn. *tucumanus* Lahille, 1912—original combination: *Anopheles tucumanus*.

Overview. *Anopheles pseudopunctipennis sensu lato* (herein the Pseudopunctipennis Complex) has a wide distribution from the southern United States to northern Argentina and Chile. In some localities it is an important malaria vector, in others it is seldom attracted to humans (Rozeboom 1941). This complex belongs to the Pseudopunctipennis Group, which also includes *An. chiriquiensis* Komp, 1936, *An. eiseni* Coquillett, 1902a, *An. franciscanus* McCracken, 1904, *An. geometricus* Corrêa, 1944, *An. hectoris* Giaquinto Mira, 1931 and *An. parapunctipennis* Martini, 1932 (Reid & Knight 1961). The Pseudopunctipennis Complex (as *An. pseudopunctipennis*) has been diagnosed throughout its range in keys and descriptions using the following characters. Female: Maxillary palpus with narrow pale bands at articulations, palpomere 5 pale; scutum with broad silvery gray central area; legs mostly dark and unmarked; costa of wing dark except for subcostal pale and apical pale spots (according to Wilkerson & Peyton 1990), vein R_1 pale except at presector dark, sector dark and subapical dark spots, sector pale spot present at radial crossvein (r_1-r_s), vein Cu pale with postbasal and preapical dark spots, vein 1A pale basally, dark apically except for pale apex, and all posterior veins terminating at pale fringe spots. Male: Aedeagus with 1–3 pairs of small curved serrate leaflets. Larva: Seta 3-C single; 9-M,T about 2 times length of seta 10-M,T; 6-IV,V prominent, plumose; 2-IV single; median plate of spiracular apparatus with a pair of distinctive posterior-directed projections. Egg: Characters vary but an egg with the collar separate from the floats is the character state most cited and illustrated. Currently, not including the nominotypical subspecies, the complex includes five subspecies and three synonyms. We use literature-based morphological, ecological, geographic, cytological and genetic evidence to propose elevation of four subspecies and two synonyms to specific status, and synonymy of one subspecies. We transfer one elevated synonym to *nomen dubium* because of the lack of a primary type, or any other specimens for study, and a contradictory original description. Two junior synonyms remain associated with one of the elevated synonyms. No subspecies are retained.

Anopheles pseudopunctipennis sensu stricto

The nominotypical species of the Pseudopunctipennis Complex was redescribed, illustrated (except for the egg) and a neotype designated using specimens from the type locality, Granada (Rueda *et al*. 2004). There are two publications of note that distinguish *An. pseudopunctipennis sensu stricto* from other members of the complex. Manguin *et al*. (1995), in an isoenzyme study, sampled across the entire range of *An. pseudopunctipennis sensu lato*, identified three groups/clusters: 1) Granada, 2) USA, Mexico and Guatemala, and 3) Argentina to Belize. They judged that the three groups represented a single species. We agree that their method did not provide the resolution needed to separate all of the species in this complex but we think their results clearly separate the populations at the type locality as a distinct species. In addition, crossing experiments between specimens from Mexico, the USA and Granada (Coetzee *et al*. 1999) produced non-viable offspring and extensive asynapsis of polytene chromosomes. Coetzee *et al*. treated their results as evidence of a species complex. We are confident that the results of these two studies, along with adequate distances for genetic isolation, are sufficient to distinguish *An. pseudopunctipennis sensu stricto* from all other taxa discussed below. The distribution of *An. pseudopunctipennis sensu stricto* is not clear. It was reported by van der Kuyp (1953) from Curaçao, Margarita [now Venezuelan territory] and Aruba. Shannon *et al*. (1927) wrote that Puerto España, Trinidad was probably the eastern-most limit of this species. There are extensive records for *An. pseudopunctipennis* in Venezuela (Gabaldon & Cova-Garcia 1946; Sutil O. 1980). We assume these are conspecific with the Granada population, but this has not been verified. The occurrence of *An. pseudopunctipennis sensu stricto* in adjoining Colombia should also be considered. Taking into account the evidence/inferences of the validity and distributions of other related species in the complex summarized below, we think the distribution of *An. pseudopunctipennis sensu stricto* should be changed from the currently listed countries that represent all the species in the complex, found in many publications, to that shown above.

Anopheles pseudopunctipennis sensu lato in Argentina

Three taxa of the Pseudopunctipennis Complex have been described from Argentina: *Proterorhynchus argentinus* Brèthes, 1912 (currently a junior synonym of *pseudopunctipennis*), type locality: Tucumán (Belkin *et al*. 1968 [list of "type locality" sites repeated in the literature refers only to where Brèthes thought this species transmitted malaria]); *Anopheles tucumanus* Lahille, 1912 (currently a junior synonym of *An*. *pseudopunctipennis*), type locality: Banks of the Rio Salí, Tucumán and Santiago del Estero Provinces; and *Anopheles patersoni* Alvarado & Heredia, 1947 (currently a subspecies of *An*. *pseudopunctipennis*), type locality: Tucumán.

Dantur Juri *et al*. (2014), in a population genetics study using the cytochrome oxidase I (*COI*) gene, sampled 12 localities, that included the above type localities, in the Yungas ecological region in northwestern Argentina. The Yungas is a highland zone on the eastern slope of the Andes Mountains, which has a rainy, humid and warm climate (https://en.wikipedia.org/wiki/Yungas, accessed 4 June 2021). Similar Yungas regions also occur in Bolivia and Peru, suggesting potential additional habitat for the species discussed below. Dantur Juri *et al*. stated: "The demographic pattern [of *COI* haplotypes] suggests that *An*. *pseudopunctipennis* has undergone a single colonization process, and the ancestral haplotype is shared by specimens from all localities, indicating mitochondrial gene flow. Genetic differentiation was minimal, observed only between one northern and one southern locality." Since no other related species have been recorded in this area, we conclude that the above three names represent the same species. Extensive geographic distance, egg morphology and different habitat ecologies all enforce our opinion that the Argentinian taxon is genetically distinct from *An*. *pseudopunctipennis sensu stricto* found on Granada (see above under *An. pseudopunctipennis sensu stricto*). Subspecies *patersoni* (as a *pseudopunctipennis* variety) was named based on egg characters in comparison to "typicus", *i.e. pseudopunctipennis sensu stricto* and *An*. *franciscanus* and two of its synonyms, *An*. *boydi* Vargas, 1939 and *An*. *willardi* Vargas, 1941. The two current synonyms of *An*. *pseudopunctipennis*, *argentinus* Brèthes, 1912 and *tucumanus* Lahille, 1912, both have priority over *patersoni*, with publication dates of 27 July and 4 October, respectively, thus making *argentinus* Brèthes the senior synonym, not *patersoni*. Accordingly, ***Anopheles* (*Anopheles*) *argentinus* (Brèthes, 1912)** is retrieved from synonymy with *pseudopunctipennis*, *patersoni* is made a junior synonym of *argentinus* and *tucumanus* is changed from a junior synonym of *pseudopunctipennis* to a junior synonym of *argentinus*: ***patersoni* Alvarado & Heredia, 1947 and *tucumanus* Lahille, 1912, junior subjective synonyms of *Anopheles* (*Anopheles*) *argentinus* (Brèthes, 1912)**. Consequently, "*Anopheles patersoni*" should be removed from the list of *Anopheles* recorded in the Encyclopedia of Life, and *Anopheles argentinus* should be added to the list.

Anopheles pseudopunctipennis sensu lato in Ecuador and Colombia

Two varieties of *An*. *pseudopunctipennis* were described from Ecuador by Leví Castillo, both currently subspecies of *pseudopunctipennis*. *Anopheles pseudopunctipennis levicastilloi* Levi Castillo, 1944, type locality: Guayas Province, and *An*. *pseudopunctipennis rivadeneirai* Leví Castillo, 1945, type locality: Cited as having been found in the provinces of Carchi, Imbabura, Pichincha, Cotopaxi, Tungurahua, Chimborazo, Cañar, Azuay and Loja. An adequately detailed map of collection records for the two varieties is in Leví Castillo (1945). The following is a brief summary [paraphrased translation of selected text from Spanish] from that publication.

> In Ecuador, there are two varieties in the Pseudopunctipennis Complex, completely different from each other; one coastal, *An. pseudopunctipennis* var. *levicastilloi*, and one montane, *An. pseudopunctipennis* var. *rivadeneirai*. The former is relatively small, wing length about 4 mm, the latter is the largest anopheline in Ecuador, wing length about 5 mm. The eggs of the two varieties are the best way to recognize them. Coastal *levicastilloi* eggs are more characteristic [of the genus *Anopheles*], boat-shaped with floats that give the appearance of a wasp nest [no collar is mentioned or apparent in the illustration]. The montane *rivadeneirai* egg is boat-shaped with the appearance of a grain of wheat, dorsocentrally concave with rounded ends, but lacks floats. Instead of floats there are many vacuoles filled with an unknown substance. Female. Wing vein R_2 in *levicastilloi* has a median pale spot, in *rivadeneirai* vein R_2 is completely dark. Coastal *levicastilloi* is not involved in malaria transmission while the montane *rivadeneirai* is the principal vector of malaria in the warm valleys of the Ecuadorian Andes.

This distinction of lowland and highland Ecuadorian subspecies (as varieties) was also noted by Pinault & Hunter (2011), who collected *Anopheles* extensively in both ecological/altitudinal areas. They found *An. pseudopunctipennis sensu lato* in both lowland and montane areas but did not recognize or mention the two varieties of Leví Castillo. They described, however, finding *pseudopunctipennis* at very different altitudes and in different climates.

In a comprehensive study of *Anopheles* in western Colombia using *COI* barcode sequence, this lowland-highland distribution of *An. pseudopunctipennis sensu lato* was also reported by Ahumada *et al*. (2016). They found highly supported groups representing northwestern and southern Pacific coastal populations, but only referred to them as "s.l." and did not compare their sequences with sequences from the type locality of *An. pseudopunctipennis* in Granada.

We believe that Leví Castillo clearly described two species that differ from *An. pseudopunctipennis sensu stricto*, and each other, both geographically and morphologically. Furthermore, we think that Pinault & Hunter (2011) and Ahumada *et al*. (2016) studied these same species in Ecuador and Colombia. Accordingly, we elevate both to species status: ***Anopheles* (*Anopheles*) *levicastilloi* Levi-Castillo, 1944** and ***Anopheles* (*Anopheles*) *rivadeneirai* Levi-Castillo, 1945**. Further studies are needed to clarify their overall distributions. *Anopheles levicastilloi* and *An. rivadeneirai* are both currently listed as species in the Encyclopedia of Life.

Anopheles peruvianus Tamayo, 1907

Currently a junior synonym of *An. pseudopunctipennis sensu stricto*, we can find no justification for its taxonomic status. It was cited as a synonym in Howard *et al*. (1917), Shannon & del Ponte (1928) and Lane (1953). A type does not exist for comparison, the original description is ambiguous and the illustrations that accompany the description of the nominal species lack detail. Unlike other species in the complex, the illustrations show the wing with a sector pale spot, no apical pale spot nor pale fringe scales at the ends of the veins. In contrast, the text (interpreted by RCW) agrees with characters on other species in the complex with the costal vein dark except for subcostal pale and apical pale spots, and the sector pale spot is on the subcosta and vein R_1, but not on the costa. Pale fringe is not noted in the description. In addition, the text and illustration show the femur (femora?) slightly speckled, which is not seen elsewhere in the complex. Lacking evidence, we do not think this nominal species should remain a junior synonym of *An*. *pseudopunctipennis sensu stricto*. It is possible it could be a senior synonym of one of the other species, especially *rivadeneirai*. In addition to the type locality, Tamayo also mentioned its occurrence in Peru: San Pedro de Lloc, San Pedro Province, La Libertad Region; environs of Lima; and, Chanchamayo, Junín Region. Lane (1953) said "Levi-Castillo (1944–1945) described two subspecies (*rivadeneirai* and *levi-castilloi*). We [?] believe that there is quite a probability that his subspecies *rivadeneirai* is *A. peruvianus* Tamayo, 1927 [*sic*] while *levi-castilloi* is the typical form. The work on subspecies of *A. pseudopunctipennis* will be subject to error up to the time when the cycle of this species is described in detail from the type locality." Until more information becomes available, we surmise that *An*. *peruvianus* should be considered a *nomen dubium*. If its validity is established as conspecific with *An*. *rivadeneirai*, it would replace it as the senior synonym. We here elevate *An. peruvianus* from synonymy with *pseudopunctipennis* and formally recognize it as a ***nomen dubium*: *Anopheles* (*Anopheles*) *peruvianus* Tamayo, 1907**.

Both the female and male of *peruvianus* were described in Tamayo & García (1907). The last paragraph of the description of the male is a bit of a puzzle: "*Fórmula ungueal*. Uno de nosotros lo considera como especie distinta, habiendo propuesto el nombre de *Anopheles multimaculatus* que no le ha conservado en la citada descripción." [English translation: "*Claw formula*. One of us considers it as a different species, having proposed the name of *Anopheles multimaculatus* which has not been preserved in the aforementioned description."] How this statement came to follow the heading for the "claw formula" is not clear. What is clear is that one of the authors thought that the male, we assume, was a different species and assigned it a name not employed elsewhere in the description. We propose that *Anopheles multimaculatus* Tamayo, 1907 (or Tamayo & García?) should be considered a synonym of *An*. *peruvianus* until it is shown that there is another distinct species sympatric with *peruvianus* that can be associated with the name *multimaculatus*. Or until such time a better explanation is offered.

***Anopheles pseudopunctipennis sensu lato* in western Chile**

Mann (1950) described two subspecies from the Tarapacá Region of Chile, *An. pseudopunctipennis neghmei* and *An. pseudopunctipennis noei* from La Quebrada de Miñimiñe and Oasis de Suca, respectively. The two sites are only about 2.5 km apart but they are "perfectamente aislados por fajas de desierto absoluto", absolutely and completely isolated by desert. The projections of the median plate of the spiracular apparatus are much shorter in the two subspecies than in the nominotypical subspecies. They have very different eggs from each other and *An*. *pseudopunctipennis sensu lato* (a key is given to eggs of related species), and *neghmei* is described as distinctly more melanistic than *noei*. Ecological studies were carried out by Mann with the intention of future publication, of which we can find no record. However, there is reference (Anonymous 1950) to a fire that destroyed the School of Medicine and the Department of Parasitology of the University of Chile in 1949, which might explain why the information was not published. However, a brief result of that unpublished study is given in his description. Mann (1950) described rearing many individuals of the two subspecies in each other's habitats to see if environment affected their morphological characters, which to him was an alternative explanation for their differences [phenotype affected by environment]. He reported that characters for each remained true no matter where they were raised. It is an intriguing question if hybrids or introgression occurred because of this manipulation. Because of distance and morphological differences from the nominotypical subspecies, and striking egg and color differences between these two subspecies, we elevate both to species status: ***Anopheles* (*Anopheles*) *neghmei* Mann, 1950** and ***Anopheles* (*Anopheles*) *noei* Mann, 1950**. *Anopheles neghmei* and *An. noei* are both currently listed as species in the Encyclopedia of Life.

Perspective

Manguin *et al*. (1995), cited above, carried out comprehensive field collections and isozyme electrophoresis of *An. pseudopunctipennis sensu lato* throughout its range. They concluded that it was a single species. We propose that while their method has utility as a population genetics tool, it is not the best procedure for species discovery. For instance, they did not detect the two species in lowland and montane areas of Ecuador, a separate species in northern Chile or conclude that the Granada population was distinct. We think other data published in the studies cited above indicate otherwise. Manguin *et al*. did report, however, three clusters: Granada, USA to northern Mexico and Guatemala, and Belize to Argentina and Chile. Along with what others have reported, summarized above, we think this validates *An. pseudopunctipennis sensu stricto,* and suggests that the USA/Mexico/Guatemala cluster could be an unnamed species (see also Estrada-Franco *et al*. 1993a, 1993b) and the South American cluster, that extends north to Belize could be, at least in part, *An. rivadeneirai*.

***Anopheles* (*Cellia*) *cinereus* Theobald**

subspecies ***cinereus*** Theobald, 1901a—original combination: *Anopheles cinereus*. Distribution: Algeria, Chad, Egypt, Eritrea, Eswatini, Ethiopia, FYRO Macedonia, Georgia, Greece, Guinea-Bissau, Israel (and Gaza Strip and West Bank), Italy (includes Sardinia and Sicily), Jordan, Libya, Lithuania, Kenya, Madeira, Malawi, Morocco, Mozambique, Namibia, Niger, Portugal, Republic of the Congo, Republic of South Africa, Saudi Arabia, Somalia, Spain, Sudan, Tanzania, Tunisia, Uganda, Ukraine, Yemen, Zimbabwe (Wilkerson *et al*. 2021).

subspecies ***hispaniola*** (Theobald, 1903a)—original combination: *Myzomyia hispaniola* (subspecific status by Senevet & Rioux

1960 and Ribeiro *et al.* 1980). Distribution: Algeria, Bulgaria, France, Greece, Italy, Morocco, Spain (including Canary Islands), Yemen (Wilkerson *et al*. 2021).

Theobald (1901a) described *cinereus* from Salisbury, Mashonaland [Harare, Zimbabwe] (Townsend 1990). Selected characters include: Maxillary palpus with four white bands, including one at the apex; antenna with a few white scales on one side of the proximal flagellomeres (not shown in Theobald's fig. 43b). A text description of the wing markings was provided but the accompanying illustration (fig. 44) shows only venation. However, there is a color illustration of the habitus in Theobald (1901a [plates]: fig. 7, pl. II). He wrote in summary: "At first sight they look like large *A. funestus*, but the clear pale bases to the legs separate it at once, as well as the large wings and the marked character of the jet-black legs with the white spots at the knees and apices of the tibiae." Theobald (1903a) described and contrasted *Myzomyia hispaniola* to *Myzomyia turkhudi* Liston, 1901, noting that both species shared a black palpomere 5 [in contrast to *cinereus*]. The nominal taxon *hispaniola* has "tarsi unbanded, and apices of all the femora and tibiae with a pale yellow spot." As for *cinereus* in Theobald (1901a), the wing of *hispaniola* was described but only the venation illustrated. A color habitus illustration was not provided, as it was for *cinereus*. For *cinereus*, Theobald (1901a [plates]) illustrated pale fringe scales at the apices of all veins except 1A. Theobald (1903a) described *hispaniola* with "fringe brown, with pale spots where the veins join the costa except at the lower branch of the fifth and the sixth", *i.e.* at the apices of veins Cu and 1A. For *hispaniola*, both Romero Viamonte (1949) and Ribeiro *et al*. (1980) illustrated pale fringe spots at the apices of all veins, including 1A, while Gillies & de Meillon (1968) showed *cinereus* with all the veins, except at 1A, ending at pale fringe. We have not found this character noted elsewhere, but it could have diagnostic value.

Below we describe the unstable taxonomic history of the nominal species *cinereus* and *hispaniola.* This has been the result of an incomplete understanding of morphological variability and dubious use of the subspecies concept. Currently, the commonly understood distributions for these nominal taxa are Afrotropical for *cinereus* and Mediterranean for *hispaniola*. Much morphological and biological diversity remains to be understood, which we think will eventually be explained by the existence of a species complex.

The two nominal taxa are quite similar morphologically but occur in very different biogeographical zones. Since they are so similar, the two names have been used inconsistently. Evans (1938) treated *cinereus* as a species in the Afrotropical Region (as Ethiopian Region) and included *hispaniola* as a possible synonym of *turkhudi*. Romeo Viamonte (1949, 1950) and Aitken (1953) both treated *hispaniola* as a species. De Meillon (1947) provided the most comprehensive and illustrated description of *cinereus*, including the egg. Gillies & de Meillon (1968) updated the description of de Meillon (1947) and addressed the possibility that *hispaniola* was a subspecies of *cinereus*. They stated: "As pointed out by Mattingly & Knight (1956), the separation of this species [*hispaniola*] from *cinereus* is very difficult if not impossible, which led Senevet & Rioux (1960) to reduce it to the status of a subspecies of *cinereus*. They summarized the characteristics of *hispaniola* as follows: adult, reduction or absence of apical pale band on ♀ palps [maxillary palpi]; pupa, hair [seta] l-IV more often simple [single]; larva, most specimens with mouth-brushes [palatal brushes] not mounted laterally." The biological and taxonomic significance of the lateral position of the palatal brushes in these species has not been investigated further. Mattingly (1969) pointed out that species in the Cinereus Group (of Gillies & de Meillon 1968) have eggs that lack floats and a much reduced frill, which remain "only as a small patch near the anterior end. These eggs hang vertically in the water and sink readily. Loss of the float is thought to be adaptive to oviposition among the filamentous algae on which the larvae feed by means of specialized mouthparts." We note that the extent of the frill seems to vary in published illustrations (*e.g.* Edwards 1921d, fig. 1l; Romeo Viamonte 1949: fig. 1; Romeo Viamonte 1950: fig. 27; Gillies & de Meillon 1968, pl. 100g), but this has not been documented. As explained by Romeo Viamonte (1949, 1950), Edwards's figure 11 is incorrectly labelled as the egg of *An. turkhudi*.

Gillies & de Meillon (1968) agreed [with caveats] with Raffaele & Coluzzi (1961) that differences in the pharynx [cibarial teeth of adult females] justified the recognition of *cinereus* and *hispaniola* as separate species. Dahl & White (1978), however, synonymized *hispaniola* with *cinereus* in the Balkans without comment. This synonymy was followed by Ward (1984) and Ramsdale (1998). Ribeiro *et al.* (1980) referred to the taxon in Portugal as *cinereus hispaniola*. Hammadi *et al*. (2009) considered *hispaniola* as a species in Algeria and Kyalo *et al.* (2017) considered *cinereus* to be a species in the Afrotropical Region, but did not mention *hispaniola*. Robert *et al*. (2019) acknowledged the two names, and identification problems, in their distribution chart for Euro-Mediterranean mosquitoes but did not attempt to resolve the issue, and instead combined them as "*sensu lato*". Irish *et al.* (2020) used the name *cinereus* but also noted several instances of usage of the name *hispaniola* in the Afrotropical Region.

Becker *et al*. (2020) are the only authors who considered and compared both nominal taxa in the same publication, but wrote: “Therefore, *An*. *cinereus* is described here, despite the complicated situation of its real distribution”, and further noted: “The status of *hispaniola* is still rather undefined.” They discussed and gave descriptions of both *cinereus sensu stricto* and *cinereus hispaniola*, with keys to adult females, male genitalia and larvae of the latter form. Their treatment was only for the separation of the taxon from other European species of the subgenus *Cellia*, with no attempt to resolve the composition of *cinereus sensu lato*.

To justify retaining *hispaniola* as a subspecies, Ribeiro *et al.* (1980) stated: “In the absence of other information concerning experimental or natural hybridization between both forms, it is classical to adopt a subspecific treatment in such a situation [Mayr *et al*. (1953); Mayr (1963); Mayr (1969)]” [the dates of the three publications are replacements here for the original reference numbers 32, 33 and 34, respectively]. As stated by Mayr *et al.* (1953), “It is preferable for various reasons to treat doubtful allopatric populations as subspecies.” We believe this approach is arbitrary and has caused considerable confusion. Further work is needed to morphologically and genetically characterize the two nominal taxa. Morphological differences are not well documented and there is a very significant difference in biogeographical occurrence. To further confuse the issue, we think there is enough morphological variability to suggest that this is probably a complex of species. For these reasons, and to draw attention to the need to fully understand *hispaniola* in comparison to *cinereus*, we herein afford it species status: ***Anopheles* (*Cellia*) *hispaniola* Theobald, 1903**. The country occurrence records listed above, especially for *hispaniola*, should be used with caution until the genetic identities of the two species are resolved. *Anopheles hispaniola* is currently listed as a species in the Encyclopedia of Life.

Anopheles cinereus has a single synonym, *An. jehafi* Patton, 1905 (type locality: Jebel Jehaf, D’thalia, Yemen); *An. hispaniola* has three sysnonyms, *Pyretophorus myzomyifacies* Theobald, 1907 (type locality: Algeria), *An. italicus* Raffaele, 1928 (type locality: Calabria, Italy) and *Myzomyia rifenus* Baeza Cuéllar, 1933 (type locality: Er Rif, Morocco). In addition to the uncertainty about the genetic identities of *cinereus* and *hispaniola*, these synonymized nominal species further suggest the existence of a species complex. Until further data become available, it seems appropriate to retain the current synonymies.

***Anopheles* (*Cellia*) *garnhami* Edwards**

subspecies ***basilewskyi*** Leleup, 1957—original combination: *Anopheles garnhami* sbsp. *basilewskyi*. Distribution: Tanzania (Mount Meru) (Leleup 1957).

Subspecies ***garnhami*** Edwards, 1930—original combination: *Anopheles garnhami*. Distribution: Burundi, Democratic Republic of the Congo (eastern), Eritrea, Ethiopia, Kenya, Lesotho, Malawi, Mozambique, Rwanda, Somalia, South Africa, South Sudan (southeastern), Tanzania, Uganda, Zimbabwe (derived from Gillies & de Meillon 1968, fig. 52; Somalia from Irish *et al*. 2020).

Edwards (1930) described the nominotypical subspecies based on specimens from Kenya: Kericho, 6,000 ft. (2♂♂, 3♀♀); Saiwa (1♀); Londiani, Kenya, 7,500 ft. (1♀); Uasin Gishu, 6,000 ft. (11♀♀); locality not specified (3♂♂, 3♀♀), and additionally from Karambo, 6,000 ft. (1♀), a village in Rwanda. Townsend (1990) found 22 of the above 25 specimens in the Natural History Museum, London, and referred to them as “syntypes”. Edwards, however, clearly referred to the specimens from Kericho as including the type specimens, but did not state what sort of specimens, which leaves designation of a lectotype, if needed, for the future.

As a basis for comparison to the forms treated here, we quote portions of Edwards’s (1930) original description of *garnhami* based on the specimens from the localities listed above. All are from highland locations in the general vicinity of Lake Victoria.

> ♀. *Head* with the usual [?] dense upright scales, pale yellowish in middle, black at sides; frontal tuft long and pure white.... Palpi... [with] scales on first segment shaggy; a very narrow white ring at tip of first segment [palpomere], a somewhat broader one embracing tip of second and base of third, tip of third and whole of fourth white; third and fourth segments [palpomeres] together about equalling third in length, fourth short, scarcely more than one-third as long as third [*i.e*. maxillary palpus with three white rings]….
>
> *Thorax* as seen from above greyish in middle (for about one-third of its width), sides of mesonotum [scutum] very broadly dark brown, but extreme margins again narrowly grey; a small dark brown area immediately in front of

> scutellum in middle. Median greyish area of mesonotum densely covered with narrow scales (about 6–8 times as long as broad), mostly creamy-white in colour....
>
> *Abdomen* brownish above, lateral and posterior margins of tergites [terga] dark brown; sternites [sterna] with large and rather conspicuous whitish-grey basal lateral patches. No scales; hairs [setae] pale.
>
> *Legs* blackish; coxae and trochanters pale; tips of femora and tibiae and of first two or three tarsal segments [tarsomeres] of all legs very narrowly creamy-white.
>
> Wings.... Costa mainly black, with three or four yellowish spots; first very small (sometimes scarcely distinguishable), placed just before base of cubital fork [sector pale and accessory sector pale spots joined on costa (C), subcosta (Sc) and vein R_1]; second larger and always distinct, above stem of radial fork [subcostal pale spot on C, Sc and R_1]; third small (often absent), above middle of radial fork [preapical pale spot on C and R_1]; fourth small, close to tip [apical pale spot at ends of veins R_1 and R_2]. First vein [R] pale at base, and with three pale yellowish spots corresponding with those on costa, otherwise black. Radial fork [veins R_2 and R_3] mainly black. Third vein [R_{4+5}] pale except narrowly at base and tip. No dark area on fifth vein [CuA] at base of fork [mcu]. Sixth vein [1A] with three dark areas, basal one short (sometimes absent). Small fringe-spots present opposite tips of all veins except sixth [pale fringe spot also illustrated at the middle of cell 1A]. Base of radial fork [R_s?] much proximal to that of the median. Knob [capitellum] of halteres black....
>
> ♂. …club [fused setae on dorsal lobe of the claspette] long and rather narrow; claspette with long apical hair [seta], but apparently without accessory hair; innermost of the four spines [parabasal setae] of the coxite [gonocoxite] stout on basal half, very slender and curved on apical half.

A great deal of variability is reported for "typical" *garnhami* from throughout its considerable range (approximately 4,800 km). Examples follow.

Evans (1938) separated *garnhami* into "typical" and "atypical" forms and Gillies & de Meillon (1968) resolved *garnhami* in two places in their keys to adult females (Sections VIII and X).

Apparently, there is bionomical variability of possible consequence. Horsfall (1955) noted: "De Meillon (1947a) [1947 herein] noted that variations in reported sites appear in the literature. The form in southern Africa does not inhabit houses, and, similarly, D. B. Wilson (1938) [not seen by us] regards the form in Tanganyika [Tanzania] as no inhabitant of houses. Symes (1931) [not seen by us], on the other hand, found large numbers of adults in huts in Kenya where goats as well as humans were housed."

Corradetti (1940) described variation of the nominotypical subspecies throughout its range in Africa to include specimens from Dessiè, Ethiopia, which is approximately 400 km north of the capital Addis Ababa and about 1,300 km north of the type locality of *garnhami*. He explained the variation as follows (translated from the Italian, some intervening text omitted).

> During my research on malaria in Abissinia [Ethiopia] I had occasion to observe *An. garnhami* in Dessiè and in some surrounding areas around this city. The study of the Ethiopian material caused me to observe that the variability of some characters is considerably wider than it had previously been described.
>
> [Heading] Morphological variability of *A. garnhami* in the Dessiè area.
>
> *Adult*. ...In the wings the sector pale spot is complete or incomplete (limited to the subcosta and the 1st longitudinal vein [Sc, vein R] and totally absent on the costa). The subapical dark spot may be complete, incomplete or absent [reflects presence and/or size of preapical pale spot]....
>
> *Pupa*. Considerable variability is observed in the bristles B [seta 5] of segments V–VII, they may appear simple [single], with a small lateral branch, or divided into various branches. Consistency may not be observed in this respect in the various segments of the same nymph [pupa] and sometimes not even in the two halves of the same segment....
>
> [Heading] Considerations on the systematic value of the morphological variants of *A. garnhami*.
>
> From the study of the literature hitherto known on this anopheline it is evident that the limits of variability of the characters presented by the species appear markedly different in different parts of Africa. Knowledge in this regard can be summarized as follows:
>
> 1) Kenyan material (typical). Wing length mm. 5–5.5 (5.5–6 in Uasin Gishu). Female palpi with 3 spots. Strong variability in the wing spots, and absence of basal spots on the costa. Bristle B [seta 5] of the pupa on segments VI–VII with 3–7 branches. Absence of small accessory tergal plates on the abdominal segments of the larva.
>
> 2). Material from Uganda (Mt. Elgon). Female palpi with 4 spots. Strong variability in wing spots and absence

> of basal spots on the costa. Bristle B [seta 5] of the pupa on segments V–VII sometimes simple [single]. Absence of small accessory tergal plates on the abdominal segments of the larva.
>
> 3) Variety *walshi* (South Africa). Wing length about 4 mm. Female palpi with 4 spots. Very little variability in the wing spots: little tendency for sector [pale] and subapical [pale] spots to disappear; presence of basal spots on the costa. Marked tendency for the development of small accessory tergal plates on segments VI–VII of the larva.
>
> 4) Dessiè material. Wing length: males mm. 3.4–4.1; female mm. 3.7–4.5. Female palpi with 3 spots. Strong variability in the wing spots and absence of basal [pale] spots on the costal vein. Strong variability in the characters of the bristle B [seta 5] of the pupa. Presence of small plates on the metathorax of the larva. Strong variability regarding the presence or absence of accessory tergal plates on abdominal segments of the larva from [segment] IV onwards.
>
> From these observations [there is] the need to extend the research on *A. garnhami* of the various African regions in order to determine the limits of variability of the species in the various zones from the study of sufficient material from each locality.

Subspecies *basilewskyi* was described by Leleup (1957) from a subalpine prairie characterized by the monotypic plant genus *Hagenia* [*Hagenia abyssinica* (Bruce), which is found at high elevations in Afromontane regions in East Africa]. The collection site was a marsh at 2,900 m elevation on a vegetated volcanic mountain (Mount Meru) isolated by a large arid area. Leleup (1960) re-published the brief 1957 description and provided further detail and illustrations of a wing, dorsal lobe of the claspette and aedeagal leaflets. The type series consists of a female holotype, a male allotype and seven female and three male paratypes. The author was unable to preserve immature stages for study. Leleup reported several unambiguous diagnostic characters that distinguish *basilewskyi* from the nominotypical form: Wings lack pale fringe spots, except for the pale scales of the apical pale spot, and pale spots at the bifurcation of R_2 and R_3 and at the base of M_{3+4} (crossvein mcu) (pale spots present in the nominotypical form); the dorsal lobe of the claspette with a distinctly broadened club with a shorter accessory seta (longer narrow club with a longer accessory seta in nominotypical *garnhami*); aedeagal leaflets about equal in number but thinner with less serration in *basilewskyi.* Leleup (1960) summarized the purported differences by stating: "All zoologists will agree in admitting that when all the individuals of an isolated colony offer common characteristics differentiating them from the typical form, it is indeed a subspecies and not of a simple variety [translated from the French]." Stone *et al.* (1959) and Lips (1960) also treated *basilewskyi* as a subspecies but Gillies & de Meillon (1968) considered variation throughout the range of *garnhami* and concluded that "…it appears impossible to define *basilewskyi* in any satisfactory way, and it must be regarded simply as a variant at below the subspecific level." Given the inconclusive and poorly documented variation of *garnhami* over such a large range, we think Gilles & de Meillon's decision to synonymize *basilewskyi* with *garnhami* was incorrect. Overlapping characters are not a valid criterion to combine different forms. This opinion was shared by Brunhes *et al*. (1998) who resurrected *basilewskyi* from synonymy with *garnhami*, stating that "The geographical isolation of this population, the absence of apparent sympatry, with *An. garnhami*, and the concern not to attribute to *An. garnhami* too large a set of characters [great variability], lead us to consider *An. g. basilewskyi* as a valid taxon. It has been very frequently argued that mountain species are genetically isolated from each other, as are island populations. The gene flow these populations receive is probably much reduced, which causes faster speciation. The many morphological variations observed in the orophilic [thriving in mountainous or subalpine regions] *Anopheles* would, in this hypothesis, be the consequence of a **speciation in progress or already carried out** [emphasis ours]. As Corradetti (1940) suggested, all available information should be re-examined on orophilic species and in particular for *An. garnhami* [translated from the French]."

We also consider the distinct differences found for *basilewskyi*, along with its apparent isolation on a volcanic mountain surrounded by a large arid area, to provide more than sufficient evidence of an independently evolving species and therefore accord *basilewskyi* species status: ***Anopheles* (*Cellia*) *basilewskyi* Leleup, 1957**. *Anopheles basilewskyi* is currently listed as a species in the Encyclopedia of Life.

Anopheles garnhami has one synonym, *An. garnhami* var. *walshi* Evans & de Meillon, 1933. From its original description, it is "Only known up to the present from Drakensberg, 3,000 to 4,000 ft., near Tzaneen, Transvaal, and Tzaneen itself, 2,380 ft., 15 miles from the mountains, where a few specimens have been collected. Cotype ♂♂ and ♀♀ from Magoeba's Kloof, Tzaneen, North Transvaal...".

Evans & de Meillon (1933) described and contrasted *walshi* to the "type form" of *garnhami*. However, some illustrated wing spot characters of their "type form" do not entirely agree with the original description of Edwards (1930). Present on the South African "type form", not found on nominotypical *garnhami*, are a discrete accessory sector pale spot (only on vein R); base of M_{3+4} (crossvein mcu) dark, as in *basilewskyi*; pale fringe spot on the border of cell 1A not depicted. Variety *walshi* was described as differing from the South African "type form" by having prehumeral and humeral pale spots and a discrete accessory sector pale spot on vein R. Subsequently, de Meillon (1947), while still retaining the validity of variety *walshi,* stated: "Resembles *garnhami* very closely and it is doubtful if it deserves even varietal rank. Re-examination of a series of cotypes leads me to believe that it cannot be separated from the type form with certainty." He, however, then listed distinguishing characters. Stone *et al*. (1959) listed *walshi* as a synonym of *garnhami* but Lips (1960) treated it as a variety. Gillies & de Meillon (1968) stated: "As pointed out by De Meillon (1947), *garnhami* var. *walshi* grades into typical *garnhami* in all characters and cannot be separated with any certainty. It is accordingly regarded here as falling within the limits of variation of the normal form."

We think the status of *walshi* and the "type form" in southern Africa merit further examination since *walshi* is inadequately compared to "normal" *garnhami*, which has not been characterized throughout its range. Synonymous variety *walshi* and nominotypical *garnhami* have both been reported from the Drakensburg Mountains in Transvaal, South Africa. We note that the high elevation habitat typical of nominotypical *garnhami* is disjunctive with *garnhami* and the purported synonymous *walshi* from South Africa found in a mountain range a very great distance from the Kenyan highlands. This suggests to us the probability that a species complex related to *garnhami* exists in East Africa south of Ethiopia.

***Anopheles* (*Cellia*) *ludlowae* (Theobald)**

subspecies ***ludlowae*** (Theobald, 1903a)—original combination: *Myzomyia ludlowii*. Distribution: India, Indonesia, People's Republic of China, Philippines, Singapore, Sri Lanka, Taiwan, Thailand (Wilkerson *et al*. 2021).

subspecies ***torakala*** Stoker & Waktoedi Koesoemawinangoen, 1949—original combination: *Anopheles* (*Myzomyia*) *ludlowi* var. *torakala* (subspecific status by Harbach & Howard 2007). Distribution: Indonesia (Sulawesi) (Stoker & Waktoedi Koesoemawinangoen 1949).

Theobald (1903a) described *ludlowii* (also spelled *ludlowi*; emendation to *ludlowae* by Stone 1957) from a series of six female syntypes from "Luzon, Philippine Islands (Miss Ludlow)." Later authors debated whether *ludlowae* was a fresh water, blackish water or salt water species. Ludlow (1914) further clarified the type locality: "taken by Dr. Graves in the Province of Abra, Island of Luzon, on the Benguet Road during the construction of that road. The location is definitely inland… there is no sea or blackish water within many miles."

Nominotypical *ludlowae* can be recognized in the adult female by the following: Maxillary palpus with three white bands, two apparently at the apices of palpomeres 2 and 3 and third at the apex of palpomere 4 continuing onto palpomere 5; wing with four main dark spots (presector, sector, preapical, apical), with an apical pale spot, an accessory sector pale spot on R_1 (sometimes continuing onto subcosta but not costa), with pale spots and pale fringe at apices of all veins, pale fringe not evident between any of the veins, vein CuA with three dark spots and 1A with two dark spots; legs with distinct speckling, speckles on the hindlegs often extending onto hindtarsomeres 2 and 3, tarsomeres usually banded apically and sometimes basally (specifically described as basal and apical by Theobald 1903a); abdomen without obvious scales; aedeagal leaflets about five or six per side with the longest leaflet somewhat serrate and sinuous (Russell & Baisas 1936). Characteristics of the larva and pupa of the nominal taxon *ludlowae* from the Philippines were described by King (1932) and Baisas (1936), respectively, but observations are not available for comparison to subspecies *torakala*. According to Urbino (1936), the egg of *ludlowae* does not have floats; the egg of subspecies *torakala* has not been documented. Subspecies *ludlowae* is not known as a vector of malarial parasites in the Philippines (Basio 1971).

Since there are many species with the overall appearance of the adult female of *ludlowae,* the name was associated with other taxa as a variety or subspecies. There was initial recognition of a "salt water *ludlowae*" in the Philippines. King (1932) determined this to be a separate species (currently *An*. (*Cel*.) *litoralis* King, 1932). Bonne-Wepster & Swellengrebel (1953) wrote: "Early writers used the name *ludlowi* for the common speckled-legged *Anopheles* species which occurs all over the Sunda Islands, Malaya and the Andamans and which in later years was also found in India, along the coast in brackish and fresh water. Rodenwaldt (1925) noted several important characters in which the species from Indonesia differs from that on the Philippine Islands and described it as *ludlowi* var. *sundaica*." This variety was later elevated to species rank by Christophers (1933). Harrison *et al*. (1991) reinforced this idea in a rationale for a list of mosquitoes of Thailand and nearby countries: "*Anopheles* (*Cel.*) *ludlowae* (Theobald) was listed as doubtful and needing further confirmation. Additional confirmation is not necessary. The old records of '*ludlowi*' by Barnes (1923), Barraud and Christophers (1931) and Thurman (1959) were based on misidentified specimens of *An. sundaicus* (Rodenwaldt) as noted by Scanlon *et al*. (1968). *Anopheles ludlowae* is an insular species, not found on mainland Southeast Asia, and should not be included in the Thailand list."

Harbach & Howard (2007) noted that subspecies *torakala* was first published in 1938 in Dutch but neither they nor we have been able to obtain a copy of the publication. Therefore: "it is not known whether or not the name was originally introduced in 1938" or at what rank/status. Subspecies *torakala* is recognized as an important vector of human malarial parasites (van Hell 1952; Basio 1971). A brief description, with illustrations of the maxillary palpus of both sexes, a wing and a hindleg, was later published in English by Stoker & Waktoedi Koesoemawinangoen (1949) as a variety of *ludlowi*. The type locality, discussed by Kitzmiller (1982), is in South Sulawesi Province. No type specimens are known. Stoker & Waktoedi Koesoemawinangoen briefly described and illustrated, not only *torakala,* but also *Anopheles* (*Myzomyia*) *ludlowi* (*sensu* Walch & Soesilo 1929) and *Anopheles* (*Myzomyia*) *ludlowi* "*typicus*" (= *sensu* Theobald 1903a, *i.e.* the nominotypical form). The descriptions are brief and do not provide a differential diagnosis or an explanation about specimens or literature examined, but we surmise the following: *torakala* does not have an accessory sector pale spot on the subcosta and the accessory sector pale spot on vein R_1 is not demarcated by the additional dark mark between it and the sector pale spot ("*typicus*" has a distinct accessory sector pale spot on the subcosta and R_1, with three pale spots on R_1 below the sector dark); *torakala* does not have a pale fringe spot between CuA and 1A ("*typicus*" has a continuous pale fringe spot from CuA to 1A); in *torakala* it is difficult to interpret but it appears that vein R_3 does not end in a pale fringe spot ("*typicus*" has a continuous pale fringe spot between the ends of veins R_3 and R_{4+5}); *torakala* has CuA with two dark spots ("*typicus*" has CuA with three dark spots); *torakala* has three dark spots on the subcosta ("*typicus*" with two dark spots on the subcosta). In addition, judging from the illustrations, we do not see significant differences in banding on the maxillary palpi or the speckling of the legs.

From the above, a likely significant character is the pale fringe between CuA and 1A, the presence of which is used in keys to distinguish Indonesian *ludlowae* from *torakala*, which does not have the spot. In contradiction, this fringe spot is not present on the wing of Philippine *ludlowae* (*sensu stricto*). Lee *et al*. (1987) did not distinguish between *ludlowae* and *ludlowae* var. *torakala* in the Australasian Region and combined them in their key, in which they state that there is usually a pale fringe spot between CuA and 1A. Since only the nominotypical form has been characterized in all life stages, no certain comparisons can be made with Indonesian forms, except for one character of the male genitalia. Bonne-Wepster & Swellengrebel (1953) compared the aedeagal leaflets of Philippine *ludlowae* with the aedeagal leaflets of males from Sulawesi (the Celebes). Their figure 51 shows that the leaflets of Celebes specimens are long and numerous whereas the leaflets of Philippine specimens, as discussed above, have only five or six leaflets on each side, with the longest sinuous or S-shaped.

In summary, because of commonly shared characters in this group of species, we think that the concept of *ludlowae* from the Philippines has been mixed and confused with what probably is a species complex in Sulawesi, and elsewhere in Indonesia. How to adequately characterize *torakala* is not possible without further study, especially utilizing molecular methods. Because of noted differences in the transmission of malarial parasites, the presence of pale fringe between CuA and 1A in *torakala* and differences in the form of aedeagal leaflets, we think these are probably separate species, and therefore elevate *torakala* to species status: ***Anopheles*** **(*Cellia*)** ***torakala*** **Stoker & Waktoedi Koesoemawinangoen, 1949**. *Anopheles torakala* is currently listed as a species in the Encyclopedia of Life.

Three names (*formosaensis*, *hatorii*, *cabrerai*) are currently in synonymy with *ludlowae*/*torakala*. Since those nominal species do not occur in the geographical range of *An. torakala*, we believe all three are synonyms of *An. ludlowae*. *Anopheles ludlowii* var. *formosaensis* Koidzumi, 1917 was preoccupied and replaced by *An. hatorii* Koidzumi, 1920, as explained by Yamada (1925): "Koidzumi (1917) pointed out, however, the Formosan form differs slightly from *ludlowii* and placed the former as a variety of the latter, giving it a name, *Anopheles ludlowii* var. *formosensis*. After that, Koidzumi (1920) leaned to separate the Formosan form specifically from *ludlowii* and gave it provisionally another name *A. hatorii* nov. sp. (?) replacing *formosensis* preoccupied. But the provisional name was lately made valid by the author (1924). It was, however, placed again as a synonym of *ludlowii* by Christophers (1924)." *Anopheles* (*Cellia*) *ludlowae* ssp. *cabrerai* Cagampang-Ramos & Darsie, 1969 (in Darsie & Cagampang-Ramos 1969) was described in comparison with *ludlowae* as having three dark spots on vein 1A instead of two. The authors (Darsie & Cagampang-Ramos 1977) later determined that this single character was variable and recognized *cabrerai* as a synonym of *ludlowae.*

Anopheles (*Cellia*) *moucheti* Evans

subspecies ***moucheti*** Evans, 1925b—original combination*:* *Anopheles marshalli* var. *moucheti* (specific status by Evans 1931). Distribution: Burundi, Central African Republic, Côte d'Ivoire, Democratic Republic of the Congo, Equatorial Guinea, Gabon, Ghana, Kenya, Republic of the Congo, Rwanda, Sierra Leone, South Sudan, Tanzania, Uganda (Wilkerson *et al*. 2021, Cameroon, Guinea and Nigeria are excluded).

subspecies ***nigeriensis*** Evans, 1931—original combination: *Anopheles moucheti* var. *nigeriensis*. Distribution: Cameroon, Guinea, Niger, Nigeria (Wilkerson *et al*. 2021).

Anopheles moucheti was originally described as a variety of *An. marshallii* (Theobald, 1903a) and elevated to species status by Evans (1931). The taxon was described from a series of adult males and females from the Belgium Congo, present-day Democratic Republic of the Congo. The holotype male was collected at Buta, which today is a city and capital of Bas-Uiele Province located in the northern area of the country. When Evans recognized *moucheti* as a distinct species, she also described *nigeriensis* as a variety of the species based on a series of syntypes ("co-types"), including one male and two females with associated larval and pupal exuviae, collected at Yaba, a suburb of Lagos, Lagos State in southern Nigeria. Townson (1990) verified the presence of nine syntypes in the Natural History Museum, London—two females from Yaba, and two males, two females and three larvae from near Lagos.

Gillies & de Meillon (1968) and Gillies & Coetzee (1987) did not distinguish the adults of *moucheti sensu stricto* and *nigeriensis* in their keys to the *Anopheles* of the Afrotropical Region; however, they did distinguish the larvae based on the development of head seta 3-C—with three or more branches in *moucheti sensu stricto* and single, occasionally bifid in *nigeriensis*. The complete chaetotaxy of the larvae, and also the pupae, has not been 8studied comparatively. Gillies & de Meillon (1968) specified that *nigeriensis* "Differs from the nominate subspecies only in the following characters: *Pharynx* [cibarium]*:* Spines on pediment of cone apparently rather longer. *Wing:* In a series of specimens from Lagos, reared from eggs and with associated larvae from the same egg-batch (C. D. Ramsdale), a 6th pale fringe spot is present in 4 out of 5 females. *Outer clypeal hairs* [seta 3C]*:* Simple or bifid apically. We have not been able to confirm Evans's description of the mesonotal hairs as being narrower than in the type form."

The taxonomic history of *An. moucheti* (Moucheti Complex, Brunhes *et al*. 1998b) involves the closely related *An. bervoetsi* D'Haenens, 1961, which was originally described as a subspecies of *moucheti*. It was afforded specific status by Gillies & de Meillon (1968) based on distinctive features of the larva, and returned to subspecific status by Brunhes *et al*. (1998b), who also considered *nigeriensis* to be a synonym of *moucheti*: "All of these [published] observations lead us, at least while awaiting new information, to consider *An. moucheti* as a polymorphic species and *An. moucheti nigeriensis* as a synonym of *An. moucheti* Evans, 1925 [translated from the French]." In agreement with Gillies & de Meillon, *bervoetsi* was reinstated as a separate species by Antonio-Nkondjio *et al*. (2008) based on high levels of differentiation between 10 microsatellite loci of non-coding DNA.

Kengne *et al*. (2007) investigated the use of the mitochondrial cytochrome oxidase b (*CytB*) gene and the ribosomal internal transcribed spacers ITS1 and ITS2 to distinguish *bervoetsi*, *moucheti sensu stricto* and *nigeriensis*, which were recognized as subspecies of *moucheti* at the time. The results of their study suggested that *moucheti sensu stricto* occurs in the forested areas of central Africa while *bervoetsi* and *nigeriensis* are only found in areas of the Democratic Republic of the Congo and Nigeria, which encompass their type localities, respectively. For ITS1, the mean genetic distance was found to be greater between *nigeriensis* and *bervoetsi* (0.166) than between *moucheti sensu stricto* and *bervoetsi* (0.141), and lower between *moucheti sensu stricto* and *nigeriensis* (0.084). The authors stated that "This degree of differentiation between morphological forms is relatively high, indicating significant genetic divergence among the three taxa, which is comparable with that among species." In comparison, the ITS2 sequences exhibited a lower degree of divergence, ranging from 0.03 between *moucheti sensu stricto* and *nigeriensis* to 0.063 between *moucheti sensu stricto* and *bervoetsi*. Sequence differences included 30 fixed indel or substitutions between *moucheti sensu stricto* and *bervoetsi*, 29 between *nigeriensis* and *bervoetsi*, and 16 between *moucheti sensu stricto* and *nigeriensis*. For the *CytB* gene, 26 fixed differences in the first codon position were identified among the three forms. The *CytB* gene sequences, in agreement with the ITS2 sequences, showed consistent but low divergence of 0.035–0.047 between the three forms. The authors concluded that "The concordance of genetic variability of the three markers and the lack of intraspecific geographical variation suggests that the three members of the group are true species." In summary they stated that "The three genomic regions revealed sequence differences between the three morphological forms similar in degree to the differences shown previously for members of other anopheline species groups or complexes (genetic distance d = 0.047–0.05 for *CytB*, 0.084–0.166 for ITS1 and 0.03–0.05 for ITS2)." In view of the genetic evidence, we are suprised that Kengne *et al*. did not formally elevate *nigeriensis* to specific rank. But having said that, the taxonomic status of *nigeriensis* was not relevant to the objective of their study, which was to elucidate molecular means for distinguishing and identifying the three nominal forms.

Despite the available morphological, molecular and distribution data, *nigeriensis* continued to be recognized as a subspecies (Harbach 2018; Coetzee 2020; Irish *et al*. 2020; Wilkerson *et al*. 2021). In fact, *nigeriensis* as a separate entity has largely been ignored, *e.g.*, in the recent list of countries in which Afrotropical species of *Anopheles* have been recorded (Irish *et al*. 2020), the authors stated "As *An. nigeriensis* refers to a subspecies of *An. moucheti*, it is not included here."

In view of the morphological, distributional and in particular the molecular distinctions detailed above, we are compelled to formally recognize *nigeriensis* as a separate species of the Moucheti Complex: ***Anopheles* (*Cellia*) *nigeriensis* Evans, 1931**. *Anopheles nigeriensis* is not currently included as a species in the Encyclopedia of Life and should be added to the list of species of the genus. As currently understood, the Moucheti Complex includes three species, *bervoetsi* D'Haenens, *moucheti* Evans and *nigeriensis* Evans.

Anopheles (*Cellia*) *rhodesiensis* Theobald

subspecies ***rhodesiensis*** Theobald, 1901a—original combination: *Anopheles rhodesiensis*. Distribution: Angola, Benin, Botswana, Burkina Faso, Cameroon, Central African Republic, Chad, Côte d'Ivoire, Democratic Republic of the Congo, Djibouti, Eritrea, Eswatini, Ethiopia, Gabon, Ghana, Guinea, Kenya, Malawi, Mali, Mauritania, Morocco, Mozambique, Namibia, Niger, Nigeria, Republic of the Congo, Republic of South Africa, Saudi Arabia, Senegal, Seychelles, Sierra Leone, Somalia, South Sudan, Sudan, Tanzania, Uganda, Zambia, Zimbabwe (Wilkerson *et al*. 2021).

subspecies ***rupicolus*** Lewis, 1937—original combination: *Anopheles* (*Myzomyia*) *rupicolus* (subspecific status by Mattingly & Knight 1956). Distribution: Algeria, Chad, Egypt, Eritrea, Ethiopia, Jordan, Lebanon, Morocco, Niger, Saudi Arabia, Sudan, Syria, Yemen (Wilkerson *et al*. 2021).

The nominotypical subspecies was described from Mashonaland, British Central Africa, now in northern Zimbabwe. Theobald (1901a) noted that the species had been sent "in numbers" from "Central Africa". It has since been documented throughout the Afrotropical Region (Kyalo *et al.* 2017; Irish *et al.* 2020, who treated all records as *rhodesiensis*). Theobald provided a color illustration of the habitus of the adult female (Theobald 1901a [plates]: fig. 14, pl. IV), which matches the verbal description. Of note were: Head scales erect, dark laterally, pale on occiput and frontal tuft; scutum reddish brown with a dorsocentral ash-gray stripe; maxillary palpus with three narrow pale bands, one near apex of palpomere 2, one between palpomeres 3 and 4 and one encompassing most of palpomere 5; wing with distinct pale spots on the costa and vein R_1 as follows, sector pale (on R_1 only, illustrated by others on both veins), subcostal pale, preapical pale and apical pale spots (as defined by Wilkerson & Peyton 1990); legs entirely dark brown; abdomen brown with basal and median light brownish yellow mottling. These characters have been used in most keys to identify *rhodesiensis*, *e.g.* de Meillon (1947), Gillies & de Meillon (1968) and Gillies & Coetzee (1987). Characters of the adult, larva, pupa and male genitalia are well documented and illustrated in the three publications. According to Gillies & de Meillon (1968), larvae are found in a variety of habitats, including "rock pools, stream beds, seepages with little shade, margins of streams, springs and pools, ditches and hoof-prints, artificial containers such as concrete tanks and swimming-baths, whether in exposed water or in shade." Females are not known to feed on humans or to be a factor in malaria transmission (Gillies & de Meillon 1968).

Subspecies *rupicolus* was described from Gebel Moya near Sennar, Blue Nile Province, southeastern Sudan. Lewis (1937) remarked that the species had almost all dark wings resembling some species of the subgenus *Anopheles.* The color of the head scales was described as like those of subspecies *rhodesiensis*, with dark scales on the back of the occiput, white scales on the vertex and a conspicuous white vertical frontal tuft. The maxillary palpus and legs were described as all dark and the wing as having variably faint to absent sector pale, subcostal pale and preapical pale spots on the costa and/or vein R_1. Specimens were collected from a metal tank but most from a deep cleft in a rock. Lewis stated: "The wing markings and characters of the pharyngeal armature [cibarial armature] and male hypopygium [genitalia] indicate that the species is allied to *A. rhodesiensis* Theo. It differs from the latter in having 37 teeth on the mandible which is expanded at the tip, dark palpi with a higher index [length in relation to proboscis length], very faint pale marks, less than four, on the costa, no pale area on the basal third of the first longitudinal vein [R_1], and in the larva the clypeal hairs [setae 2,3-C] usually simple [single]. The mandible of *A. rhodesiensis* is not expanded at the end and has 80 teeth (Christophers [& Puri] 1931).” No apical pale spot was noted. De Meillon (1947) provided full descriptions of both subspecies (as species), and included illustrations showing contrasting wing spot characters and allopatric distributions (*rupicolus* Saharan, *rhodesiensis* Afrotropical), but then noted after the description of *rupicolus*: “It is questionable if this species is distinct from *rhodesiensis*. The adult is paler, the wings and palps [maxillary palpi] with less distinct pale making but otherwise there is little to separate them. The larvae and pupae, when considering the range of variation seen in *rhodesiensis*, appear to be inseparable from that species.” Mattingly & Knight (1956) cited de Meillon’s (1947) note and agreed that they too doubted the two were distinct species and provisionally preferred to treat them as subspecies. In addition, they mentioned that Lewis agreed with them. The logic and utility of this decision is not clear. However, the two nominal taxa have been treated as subspecies since that time (Gillies & de Meillon 1968; Gillies & Coetzee 1987; Knight & Stone 1977; Harbach 2018; Wilkerson *et al*. 2021). Gillies & de Meillon (1968) included the two nominal taxa in their key to adult females but they are combined in the larval key as *rhodesiensis*. They stated that *rupicolus* “is not separable from the nominate form.”

An important indicator of separate species status is evidence of sympatry. Kyalo *et al*. (2017) did a comprehensive review of literature records of all *Anopheles* in the Afrotropical Region. Their dataset (Snow 2017) was used by David Pecor (Walter Reed Biosystematics Unit) to map *rhodesiensis* and *rupicolus*. This allowed visualization of numerous instances of co-occurrence and overlapping ranges of the two nominal taxa. Also, Verrone (1962), in a paper not indexed by Kyalo *et al.* (2017), recorded both subspecies in close proximity in Ethiopia. The accuracy of these records is enhanced by an illustrated key to adult females clearly showing the diagnostic characters discussed above.

The above nominal taxa have been closely associated since the description of *rupicolus*. All stages are very similar, except for diagnostic differences in the adult female (wing with an apical pale spot, banded proboscis and many fewer mandibular teeth in *rhodesiensis*). The assumption was made that differences in adult characters were due to clinal variation related to hotter temperatures in the Saharan taxon *rupicolus*. However, we can find no published evidence of clinal variation, and it is apparent the two forms are sympatric. This obviates the assumption of subspecific status. We therefore believe they are two genetically distinct species and formally reinstate *rupicolus* to its original specific status: ***Anopheles* (*Cellia*) *rupicolus* Lewis, 1937**. *Anopheles rupicolus* is currently listed as a species in the Encyclopedia of Life.

Anopheles rupicolus currently has two synonyms, which we retain: *An. aegypti* Salem, 1938 (type locality: Wadi Taba, Sinai, Egypt) and *An. rhodesiensis* var. *dthalisimilis* Corradetti, 1939 (type locality: Semien District, Ethiopia). Both were treated as questionable synonyms by Edwards (1941), which leaves some doubt about their status and lays open the possible existence of a species complex.

***Anopheles* (*Cellia*) *rufipes* (Gough)**

subspecies ***broussesi*** Edwards, 1929a—original combination: *Anopheles* (*Myzomyia*) *broussesi* (subspecific status by Rioux 1961). Distribution: Algeria, Burkina Faso, Chad, Egypt, Ghana, Libya, Mali, Niger, Nigeria (Wilkerson *et al*. 2021).

subspecies ***rufipes*** (Gough, 1910)—original combination: *Nyssorhynchus pretoriensis* var. *rufipes* (specific status by Edwards 1912c). Distribution: Algeria, Angola, Benin, Botswana, Burkina Faso, Cameroon, Central African Republic, Chad, Côte d’Ivoire, Democratic Republic of the Congo, Eritrea, Eswatini, Ethiopia, Gabon, Gambia, Ghana, Guinea, Guinea-Bissau, Kenya, Madagascar, Malawi, Mali, Mauritania, Mozambique, Namibia, Niger, Nigeria, Republic of the Congo, Republic of South Africa, Senegal, Seychelles, Sierra Leone, South Sudan, Sudan, Tanzania, Togo, Uganda, Zambia, Zimbabwe (Wilkerson *et al*. 2021).

The taxa discussed here have very similar larval, pupal and male genitalic characters. Most are illustrated or discussed in Gillies & de Meillon (1968). The adult females are distinguished from other species of the subgenus *Cellia* by the following combination of characters: Lack of shaggy palpus; uniformly brownish leg coloration; various extent of white banding on the hindtarsomeres; medium to broad pale scutal scales either in a regular pattern or grading to evenly distributed; usually with 6 distinct pale wing spots and pale fringe spots at the ends of all veins except the anal vein; abdomen uniformly without scales; gonocoxite of male with 4 parabasal setae and aedeagus with several pairs of unmodified leaflets; larval setae 2,3-C long with sparse branches; blades of palmate setae with very short stumpy filaments, the setae resembling blunt-looking fans.

Gough (1910) described *rufipes* as a variety of *Nyssorhynchus pretoriensis* Theobald, 1903a (not *pretoriensis* Gough, 1910, a synonym of *An. squamosus* Theobald, 1901a) from collections made in Onderstepoort, Transvaal, Republic of South Africa. Gough's description is brief but he noted that variety *rufipes* has "uniformly ruddy brown" legs, quite different from *pretoriensis*, which has speckled femora and tibiae. Other distinctive adult and larval characters that separate *pretoriensis* from *rufipes* are also evident. Without comment, in a key, Edwards (1912c) recognized *rufipes* as a species and also placed *An. watsoni* Edwards, 1911a, from Katagumm Northern Provinces, Nigeria, in synonymy with it.

Edwards (1929a) described *broussesi* from "Djanet, the most southerly post in the Algerian Sahara… on the southern extremity of the Tasili n Ajjer [*sic*] mountains." Djanet is the capital of Djanet Province, an oasis city in a hot desert climate in southeastern Algeria. The adult female has a combination of distinguishing characters: "Palpi of ♀ slender, dark, with three very narrow white rings on joints, last segment almost entirely dark…"; scutum with well-defined lines of supraalar, dorsocentral and acrostichal scales; vein R_{4+5} mostly dark with a pair of small subbasal pale spots (illustrated but not noted by Edwards); legs with "extremely faint pale rings present at tips of first four segments [tarsomeres 1–4] of hind tarsi; last hind tarsal segment [tarsomere 5] in several specimens entirely cream-coloured, but in others apparently dark like remainder of tarsi."

Evans (1938) described the nominotypical form in detail but did not compare it with *broussesi*. She did, however, recognize *rufipes* var. *ingrami* Edwards, 1929b, a current synonym of ssp. *broussesi*, as listed by Harbach (2018) and Wilkerson *et al*. (2021) or as ssp. *rufipes* per Gillies & de Meillon (1968). Evans noted several features that can be contrasted with Edwards's (1929a) characters for *broussesi*: Female palpus with 3 pale bands, the first 2 broad; scutum nearly evenly covered with somewhat broad pale scales; vein R_{4+5} with a single small subbasal pale spot and long median pale spot (illustrated but not noted by Evans); hindtarsomere 2 pale on apical 0.4 and on all of tarsomeres 3–5; larval seta 2-C single or with fine aciculae.

De Meillon (1947) treated *An. rufipes* and *An. rufipes* var. *ingrami* in keys, descriptions and illustrations, but did not mention *broussesi*, perhaps because he considered it to be a Saharan taxon. Senevet & Andarelli (1956), in a treatise on species of North Africa and the Mediterranean basin, used Edwards's (1929a) characters and illustration of the wing, and considered *broussesi* to be a species. It is to be noted that *broussesi* and *rufipes* both were listed as separate species in Stone *et al*. (1959).

Rioux (1961) discussed geographic distribution, variation in the extent of hindtarsal pale scaling, and the extent and distribution of pale scutal scales, to determine that *rufipes* consisted of three subspecies: *An. rufipes rufipes*, *An. rufipes broussesi* and *An. rufipes seneveti* Rioux, 1959. This was the first time *broussesi* was considered as a subspecies of *rufipes*. The taxonomic treatment of Gillies & Coetzee (1987) and catalog listings (Knight & Stone 1977; White 1980; Harbach 2018; Wilkerson *et al*. 2021) followed the recognition of *rufipes rufipes* and *rufipes broussesi*. Hamon *et al*. (1961) named a new variety, *An. rufipes* var. *brucechwatti*, and also recognized *An. broussesi* as a species and *An. rufipes* as a species with varieties *ingrami* and *seneveti*. Dubose & Curtin (1965), who stated they used the collection of the U. S. National Museum extensively, presumably with Alan Stone's input, retained *broussesi* as a species. Variety *seneveti* was later placed in synonymy with *An. rufipes broussesi* by Gillies & de Meillon (1968), as was *brucechwatti*. We note that the illustration of the wing of *seneveti* differs from illustrated wings of the other nominal forms in having a nearly entirely pale-scaled vein CuA, suggesting its possible validity. Gillies & de Meillon (1968) recognized only *An. rufipes rufipes* and *An. rufipes broussesi* and included *ingrami* as a synonym of subspecies *rufipes* and not *broussesi* as indicated by Harbach (2018) and Wilkerson *et al*. (2021). We do not know the source of this placement, or which is correct.

Ribeiro & da Cunha Ramos (1975) also recognized subspecies *rufipes rufipes* and *rufipes broussesi.* They stated: "*A. rufipes rufipes* is a widespread subspecies of African savannas, while *A. rufipes broussesi* is restricted to the western portion of the Northern Savanna of Moreau." Julvez *et al*. (1998) reported that subspecies *rufipes rufipes* and *rufipes broussesi* are sympatric in Chad.

We believe that the above provides evidence of two species, *rufipes* and *broussesi*. *Anopheles rufipes* is a variable, widespread Afrotropical species, or species complex, and *An. broussesi* is a hot-dry climate Saharan and Mediterranean species. The observed variability, mostly in the pattern of palpal and hindtarsal pale scales, has been expressed by authors using varietal or subspecies names, which have been used over time in many different combinations. We see no empirical evidence of genetic independence other than between these two species, and therefore return *broussesi* to species status: ***Anopheles* (*Cellia*) *broussesi* Edwards, 1929a**. *Anopheles broussesi* is currently listed as a species in the Encyclopedia of Life.

Anopheles (*Cellia*) *sergentii* (Theobald)

subspecies ***macmahoni*** Evans, 1936—original combination: *Anopheles* (*Myzomyia*) *macmahoni* (subspecific status by Mattingly & Knight 1956). Distribution: Algeria, Burkina Faso, Côte d'Ivoire, Djibouti, Eritrea, Ethiopia, Ghana, Guinea, Kenya, Mali, Republic of South Africa, Senegal, Somalia, South Sudan, Sudan (Wilkerson *et al.* 2021).

subspecies ***sergentii*** (Theobald, 1907)—original combination: *Pyretophorus sergentii*. Distribution: Albania, Algeria, Bulgaria, Burkina Faso, Cameroon, Chad, Côte d'Ivoire, Djibouti, Egypt, Eritrea, Greece, Iran, Iraq, Israel, Italy, Jordan, Libya, Kenya, Morocco, Pakistan, Portugal, Saudi Arabia, Senegal, Spain, South Sudan, Sudan, Tunisia, Turkmenistan (Wilkerson *et al.* 2021).

The female of the nominotypical form was described by Theobald (1907) based on two adult females from an unspecified locality in Algeria (see below). He described them as a gray to brown species with three palpal bands, one of them the entire palpomere 5; with the abdomen brown without scales; legs brown, unbanded, and "Wings dark scaled; costal border with five large dark spots, four spreading evenly on to first long vein [R]; a few pale spots on wing field, notably at the cross-veins and bases of the fork-cells [R_2 and M_1]." All primary wing veins except 1A end at a pale fringe spot. There was no explicit mention of the nature of the dark and pale areas on vein R_{4+5} but "most of the veins" were described as "uniformly dark scaled". Subsequently, Christophers (1933) described all life stages from specimens collected in presesnt-day Pakistan.

Subspecies *macmahoni* was described as a species by Evans (1936) based on two larval cotypes and a male and a female with associated larval and pupal exuviae from Isiolo, Kenya. She noted: "The larvae of this species can be identified easily by the characters of the tergal plates…", which are unusually broad. In the adult female, the maxillary palpus has three narrow pale bands, the tarsi lack definite pale rings and the wings are predominantly dark with the third vein (R_{4+5}) mainly or entirely dark-scaled. Based on additional specimens from the same locality, Evans stated that the hindtibia has a "rather distinct white spot at the base, as well as the usual apical spot." Two years later, in her treatise on Afrotropical anophelines, Evans (1938) more precisely described variation observed for vein R_{4+5}: "Third vein ranging from entirely dark to about ⅔ pale, usually about ¼–½ pale; pale area when present usually situated distally as in *A. funestus*, but in 3 cases it was median in the vein." Subspecies *sergentii* was not mentioned in Evans (1936) or Evans (1938).

De Meillon (1947) followed the descriptions of Evans (1936, 1938) and additionally noted the presence of five parabasal setae on the gonocoxite of the male, the innermost borne on a prominent eminence, and vein R_{4+5} all dark and the pale area, when present, at the center or with a long basal dark spot and a small apical one. Subspecies *sergentii* was also not mentioned in this publication.

Mattingly & Knight (1956) in "Mosquitoes of Arabia" examined larvae of subspecies *macmahoni* from the Western Aden Protectorate (Yemen) "and consider them to be those of *An. sergenti* [*sic*] of which *An. macmahoni* is, in our view, a subspecies probably mainly confined to the African portion of the Somali-Arid District. The latter is therefore eliminated from our list." Differences they noted in the cibarial armature of females, also noted by others, were deemed to be too variable to be indicative of separate species. However, two principal differentiating characters were noted. Vein R_{4+5} in *macmahoni* "is normally extensively pale scaled in the middle and only exceptionally dark." Subspecies *sergentii*, in contrast, "is constantly dark except at base and extreme tip". The other feature used to separate the two nominal taxa was the large size of the main tergal plates present in larvae of *macmahoni*.

Senevet *et al*. (1959) conducted a comprehensive study of the larval tergal plates of *sergentii* and *macmahoni* in Algeria. Whereas Theobald (1907) merely indicated that the type specimens of *sergentii* were collected in Algeria by Dr E. Sergent, Senevet *et al*. revealed that the specimens were found by Edmond Sergent in "El Outaya (région de Biskra, partie N. du Sahara algérien)." Based on this revelation, we hereby restrict the type locality of *Anopheles sergentii* Theobald, 1907 to El Outaya (35.040868, 5.56491), Biskra Province, Algeria. Senevet *et al*. noted that one of them had collected *sergentii* on the south side of the Aurès Mountains at the northern limit of the Sahara. For comparison, they obtained specimens from Tassili N'Ajjers, a national park in the Sahara located north of Djanet in southeastern Algeria. El Outaya and Djanet are about 1,000 km apart. The authors summarized their findings as follow: “we are dealing with two types: the group «small plates» corresponds to the variety «*typicus*» [*sergentii*]; the «large plates» group corresponds to the subspecies *macmahoni*. The first of these groups does not in fact differ much from the form considered as typical by most authors [translated from the French].”

The two nominal taxa belong to the *demeilloni* section of Gillies & de Meillon (1968) (= Demeilloni Group in Wilkerson *et al*. 2021). Gillies & de Meillon placed adult females of subspecies *macmahoni* in their key in Section XI, with the following characters: “Mosquitoes with 1 pale spot on upper branch of 5th vein [M_{3+4}], no pale interruption on 3rd dark area [preapical dark spot] of 1st vein [R_1]; costa with at least 1 pale spot on basal half; palps [maxillary palpi] with less than 4 bands, pale at apex; legs not speckled, hind tarsus 4 and 5 [hindtarsomeres 4 and 5] not entirely pale; abdomen without laterally projecting tufts of scales.” We point out that both nominal taxa have dark tarsomeres, maxillary palpus with three pale bands, two narrow ones, plus the entire palpomere 5, basal area of vein R_1 entirely pale-scaled, all veins except 1A ending in a pale fringe spot. Gillies & de Meillon placed fourth-instar larvae of both subspecies in their key in Section VI: “Larvae with wide abdominal plates [tergal plates], equalling on segment 5 three quarters or more the distance between bases of palmate hairs [setae]; saddle hair [seta 1-X] with less than 5 branches; no coarse spicules on sides of thorax and abdomen; outer clypeal hairs [seta 3-C] with less than 8 branches; inner clypeal hairs [seta 2-C] wide apart and not strongly branched.” Both nominal taxa have one of the long mesopleural “hairs” [seta 9- or 10-M] plumose and the inner shoulder “hair” [seta 1-P] with 15–20 branches inserted on a well-developed tubercle. In subspecies *sergentii*, the width of the main tergal plate on segment V is at most four-fifths the distance between the palmate setae, whereas in subspecies *macmahoni* the main tergal plate on segment V is equal to greater than four-fifths the distance between the palmate setae.

Gillies & de Meillon (1968) summarized their view of the two taxa as follows. *Anopheles sergentii sergentii*: “A widespread and important vector of malaria, extending into southern Arabia. As pointed out by Mattingly and Knight (1956) it differs from subsp. *macmahoni* only in the larval stage. From this it is separable by the width of the main tergal plates, which are at most ⅘ the distance between the palmate hairs [setae].” “LARVAL HABITAT: According to Senevet and Andarelli (1956), *sergentii* occurs in oases and irrigated areas in many types of water, shaded and unshaded, with and without vegetation.” “ADULT BIOLOGY: Attacks man readily, often entering houses to do so. Often found resting indoors by day, but also makes extensive use of outdoor shelters which are sometimes remote from dwellings. It was formerly, at least, an important vector of malaria...”. Gillies & de Meillon illustrated the distribution of the two subspecies in map form (fig. 53), on which they drew a non-overlapping line of demarcation. They further commented that “We ourselves would note in passing that, despite the close similarity between *sergentii* and *macmahoni*, the behaviour of the adults of the two is very different, suggesting that there are more profound biological differences between them than their morphology would suggest.”

The nature of the dark and pale spots on vein R_{4+5} (“third vein”) has often been used to separate *Anopheles* species. In the case of *sergentii* and *macmahoni*, a great deal of variation has been noted or illustrated for R_{4+5} in subspecies *macmahoni*. This could be an indicator of cryptic species or normal variation. Subspecies *sergentii*, according to Theobald (1907), Christophers (1933), Mattingly & Knight (1956) and Senevet & Andarelli (1956), has vein R_{4+5} all dark or only with a median pale spot and/or small pale spots at the base and apex. In comparison, the scaling of vein R_{4+5} in subspecies *macmahoni* has been characterized differently by several authors: “Third vein ranging from entirely dark to about ⅔ pale, usually about ¼–½ pale; pale area when present usually situated distally as in *A. funestus*, but in 3 cases it was median in the vein” (Evans 1938); “all dark, pale area if present may be at the center” or pale with a long dark basal spot and a small apical dark spot (de Meillon 1947); “it appears that it is normally extensively pale scaled in the middle and only exceptionally dark [all dark?]” (Mattingly & Knight 1956); and Gillies & de Meillon (1968) illustrated the wing showing R_{4+5} with a long (⅓ of total length) pale area subapically and perhaps small pale spots at the base and apex, and stated that “3rd vein variable, sometimes broadly pale as figured, in others entirely dark except at base and apex as in subsp. *sergenti* [*sic*].”

A problem with recognizing subspecies as legitimate ranks, at least for mosquitoes, is illustrated by Irish *et al*. (2020), who only recognized the nominotypical subspecies and therefore listed the occurrence of only *sergentii* in countries of sub-Sharan Africa, and Coetzee (2020) who did not include subspecies *macmahoni* in keys to the adult females of *Anopheles* in the Afrotropical Region. This prevents *macmahoni* from being known and confuses records and recognition of both putative subspecies.

The two nominal taxa, *sergentii* and *macmahoni*, were not recognized as related taxonomically (Evans 1936, 1938; de Meillon 1947) until Mattingly & Knight (1956) considered *macmahoni* to be a subspecies of *sergentii*. Subspecies *macmahoni* is probably mainly confined to the “African portion of the Somali-Arid District” (Mattingly

& Knight 1956) and zoophilic, while subspecies *sergentii* is a north African-Mediterranean anthropophilic malaria vector (Gillies & de Meillon 1968). There exists abundant morphological variation but the only reliable way to separate the two forms is by the relatively large size of the larval tergal plates that characterize *macmahoni* (Gillies & de Meillon 1968). In a recent review of the mosquitoes of Algeria, Merabti *et al*. (2021) stated that "Subspecies *macmahoni* is an Afrotropical form that occurs in many of the countries where the typical form is also found, which suggests that Evans (1936) may have correctly recognized it as a distinct species." Mattingly & Knight (1956) eliminated subspecies *macmahoni* from their list for mosquitoes in Arabia while distinguishing it morphologically and bionomically from *sergentii*. These observations conform to our criteria for species status, *i.e.* allopatry (and sympatry) with morphological and bionomical distinctions. We therefore reinstate *macmahoni* to species status: ***Anopheles* (*Cellia*) *macmahoni* Evans, 1936**. *Anopheles macmahoni* is currently listed as a species in the Encyclopedia of Life.

Anopheles macmahoni has a single synonym, *An. macmahoni* var. *barkhuusi* Giaquinto-Mira, 1950 (type locality: Valley of Becilo, Ethiopia), synonymy by Stone *et al*. 1959. It is possible that *barkhuusi* may be a distinct species, but until proven otherwise, it is retained as a synonym of *An. macmahoni*.

***Anopheles* (*Cellia*) *tessellatus* Theobald**

subspecies ***kalawara*** Stoker & Waktoedi Koesoemawinangoen, 1949—original combination: *Anopheles* (*Myzomyia*) *tessellatus* var. *kalawara* (subspecific status by Harbach & Howard 2007). Distribution: Indonesia [Celebes = Sulawesi] (Stoker & Waktoedi Koesoemawinangoen 1949; Waktoedi Koesoemawinangoen 1954).

subspecies ***orientalis*** (Swellengrebel & Swellengrebel de Graaf, 1920)—original combination: *Neomyzomyia punctulata* var. *orientalis* (subspecific status by Harbach & Howard 2007). Distribution: Indonesia (Wilkerson *et al.* 2021).

subspecies ***tessellatus*** Theobald, 1901a [often misspelled *tesselatus*]—original combination: *Anopheles tessellatus* [first published in error as *Anopheles punctulatus* Dönitz, see below]. Distribution: Bangladesh, Bhutan, Cambodia, Guam, India, Indonesia, Laos, Malaysia, Maldives, Myanmar, Nepal, Papua New Guinea, People's Republic of China, Philippines, Solomon Islands, Sri Lanka, Taiwan, Thailand, Timor, Vietnam (Wilkerson *et al.* 2021).

Bourke *et al.* (2021) analyzed *COI* sequences from populations of *An. tessellatus sensu lato* from Sri Lanka, Southeast Asia, Indonesia to the Philippines and identified six genetically diverse OTUs (operational taxonomic units), which they called the Tessellatus Complex (Tessellatus Group of Rattanarithikul *et al*. 2006b). The complex currently consists of the nominotypical *tessellatus* and subspecies *kalawara* and *orientalis*, with six associated synonyms.

The nominotypical form was first described from a single female from Taipang [= Taiping], Perak, Malaya [Malaysia]. Townsend (1990) documented the presence of the holotype in the Natural History Museum, London. Theobald originally described the species as *Anopheles punctulatus* Dönitz, to which he gave the manuscript name *tessellatus*. He incorrectly believed that *tessellatus* was the same as *punctulatus* Dönitz, 1901. However, *punctulatus* is a different allopatric species found in the Australian Region. Stanton (1913) recounted the history as follows: "The species here referred to under the name *tessellatus* was first described by Theobald from specimens taken in Malaya. In his manuscript he gave it the name *Anopheles tessellatum*, but before publication, having seen Dönitz' description of his *Anopheles punctulatus*, he considered the two to be identical and used his description as that of *Anopheles punctulatus*, Dönitz. In a later volume of his monograph (iii, p. 55) Theobald states that, as pointed out by Dönitz, *tessellatus* is distinct from *punctulatus*; the former species he includes in the genus *Myzomyia* and the latter in the genus *Cellia*—to this opinion he adheres in his volumes iii and iv. In volume v I can find no reference to *tessellatus*, but *punctulatus* is again referred to under the genus *Cellia*." Some confusion persisted as various authors continued to use *punctulatus* instead of *tessellatus*.

Theobald's description is accompanied by illustrations of the scutum, wing, hindtibia and hindtarsomeres. There is also a color drawing of the adult female in a separate accompanying volume (plates). Selected characters from the original description follow.

> [Diagnosis] Thorax brown with frosty-grey tomentum, two dark spots in front and another near the scutellum; abdomen almost black with golden hairs [setae]; costa yellow, with four large and four small black spots, wing field with very numerous dark spots. Legs yellow with dusky scales, banded; [Theobald used "metatarsis" for what is now tarsomere 1 and his "tarsus" refers to tarsomeres 2–5] fore tarsi apically and basally pale banded; mid and hind tarsi apically pale banded only.

> ♀. Head black, with white scales in front, black scales behind and at the top; eyes black... proboscis yellow with black scales towards the base and a small dark ring near the apex; palpi black scaled at the base, then a small ring of white scales, then a broad ring of black, the remainder white, with two small rings of black; the apical joint yellowish.
>
> Thorax... scutellum dusky towards the middle....
>
> Abdomen dark brown, almost black, with golden hairs.
>
> [Next paragraph omitted here.]
>
> Halteres pure white.
>
> Anterior legs with the femora much swollen, yellow with dusky scales, showing more or less banding; tibiae yellow, with dark scales scattered about [speckled]; metatarsus [tarsomere 1] dark scaled at the base, white at the apex, and with several white bands towards the apex; first three tarsal joints apically and basally banded white, last apically white only; the femora and the tibiae of the mid legs as in the fore ones; metatarsus mostly black scaled, the apex banded yellow; tarsi [tarsomeres 2–5] all apically yellow banded; hind legs with the tibiae more or less banded; metatarsus very long and banded, the apex white; and the tarsi apically whitish-yellow.

The wing has the full complement of costal spots as defined by Wilkerson & Peyton (1990). Of possible key character significance, the accessory sector pale spot is present on the costa and all of the posterior veins end in pale fringe spots. The accessory sector pale spot is not present on the costa in depictions of *tessellatus* from Indonesia (Stoker & Waktoedi Koesoemawinangoen 1949) or Taiwan (Tanaka *et al.* 1979).

In Theobald's original description of the proboscis—"yellow with black scales towards the base and a small dark ring near the apex"—differs somewhat from subsequent descriptions which indicate that the apical third to half of the proboscis is distinctly pale.

The following are distinguishing characters of adult females and larvae summarized from Reid (1968, Malaysia and Borneo) and Rattanarithikul *et al.* (2006b, Thailand).

Adult. Proboscis with pale scales on apical half; maxillary palpus with four pale bands; antepronotum without scales; upper proepisternal seta present; tibio-tarsal articulation with a narrow, white band; femora and tibiae speckled; hindtarsomeres 3–5 mostly dark but with narrow apical pale bands [Reid 1968]; hindtarsomeres 1–4 with narrow apical pale bands [Rattanarithikul *et al*. 2006b]; abdominal sterna without tufts of black scales.

Larva. Seta 2-C not closely approximated, distance between their bases about 1.5–2.0 times distance between bases of 2-C and 3-C; seta 3-C slender, at least apically without branches or aciculae; seta 1-P reduced, 2–5-branched, arising from small, lightly pigmented basal tubercle not attached to tubercle of seta 2-P; setae 9,10-P and 9,10-M all single, not aciculate; abdominal seta 1-II not palmate, with filamentous branches; abdominal tergal plates on segments IV–VII small, not as wide as the distance between the bases of each pair of palmate setae, small tergal plates not enclosing small median posterior plates.

Stoker & Waktoedi Koesoemawinangoen (1949) are currently credited with naming subspecies *kalawara*, as *Anopheles* (*Myzomyia*) *tesselatus* (*sic*) var. *kalawara*. They stated: "This illustrated map of the Anopheline Imagines [adults] of Indonesia is a corrected and supplemented edition (English translation of the Indonesian text) of the „Kaart [*sic*] en determinatietabel der Anophelinen in Ned. Oost Indie" (edition Public Health Service, section malariacontrol [*sic*] 1938)." We have not seen the original 1939 publication, and we do not know, as Harbach & Howard (2007) noted, what status was intended for *kalawara* (infrasubspecific or other). Two articles are mentioned in the translation that we have not seen but which could shed light on the question. The translation of Stoker & Waktoedi Koesoemawinangoen (1949) does not indicate that *kalawara* was intended to be a new variety, but the name was distinctly listed as a variety of *tessellatus*. It is noteworthy that Stoker & Waktoedi Koesoemawinangoen placed "(Brug 1938)" directly after the name *kalawara* in their key to the *Anopheles* of subgenus "*Myzomyia*" in Indonesia. This appears to be an indication of prior taxonomic treatment rather than an indication of taxon authorship, which is further indicated by citations of non-authors that follow many other species names in the key.

Apparently, Brug (1938) was the source of the only differential character used in the putative 1949 original description. He did not mention the name *kalawara*, but described a palpal difference later used by Stoker & Waktoedi Koesoemawinangoen (1949) to distinguish *kalawara* and *tessellatus*: Presence of pale scales dorsally on palpomeres 2 and 3 in *tessellatus*, all dark dorsal scaling on those palpomeres in *tessellatus* var. *kalawara*—"In nine females, bred from larvae collected at Kalawara" (see below). Brug (1938) referred to these morphotypes as *tesselatus* [*sic*] "normaal" and *tesselatus* "abnormaal". Presumably, "abnormaal" corresponded to variety *kalawara*.

We translated Brug (1938) and report here a type-written, annotated, anonymous translation included with our copy of Waktoedi Koesoemawinangoen (1954). That translation and ours closely agree. In summary, the scattered pale scales supposedly found dorsally on palpomeres 2 and 3 of *tessellatus* versus no pale scales on those palpomeres of *kalawara*, are either variable and/or other concordant characters have not yet been noted.

> The anonymous translator: "Here is the text on which Waktoedi based *Anopheles tesselatus* [*sic*], the variety name *kalawara*." And, "He just uses the village name, even in the key there is no differentiation from the other variety [*orientalis*] or the type either [*tessellatus*]."

> Translation of Brug (1938) [figure numbers as in original]:
>
> Introduction. "In the investigation of the transmitters of *Filaria malayi* in Kalawara (this magazine, 1937, LXXVII, 1462) and of *Filaria bancroffi* at Kabaena 1) (the results will be published in the Med. D.V.G., 1938) showed some aberrant Anophelines found, which will be described in more detail below."
>
> Description of *An. tesselatus* [*sic*]. "The palps [maxillary palpi] of the female usually show, viewed from above, in addition to four light bands, two light spots, one located between the basal band pair [middle of palpomere 2] and the other between base and first band [middle of palpomere 1] (fig. 4a). In nine females bred from larvae collected at Kalawara, these spots were missing and the decoration of the palps therefore consisted exclusively of four pale bands (fig. 4b). Only one female showed the [extra] spots. The hypopygia [genitalia] of the males, bred from the same brood, showed no difference from those of males from other regions van den [from the] Archipelago, where, as far as our collection showed, the female palps as shown in Fig. 4a. However, there was some [some had a] peculiar nodule on the grasping pincers [gonostyli] (fig. 3), but this was far from constant, sometimes only present on [one] the side. Barraud (1934, p. 318) describes the same deviation too, occurring inconstantly, in *Armigeres kuchingensis* and *A. obturbans*)."

Variety *kalawara* was listed as such in catalogs by Stone *et al*. (1959) and Knight & Stone (1977), but it was excluded from keys to Indonesian anophelines by O'Connor & Soepanto (1979) due to lack of distributional data and specimens. In compliance with Article 45.6.4 of the *International Code of Zoological Nomenclature*, *kalawara* was raised to subspecific rank by Harbach & Howard (2007) because the original designation did not provide any indication that the name was intended for an infrasubspecific form. To our knowledge, *kalawara* was not explicitly designated as the name of a new taxon, it is based on a single apparently variable character and type specimens do not exist. Until further information might come to light, we believe ***kalawara* Stoker & Waktoedi Koesoemawinangoen, 1949 should be formally treated as a *nomen dubium***. "*Anopheles kalawara*" should be removed from the list of *Anopheles* species recorded in the Encyclopedia of Life.

Swellengrebel & Swellengrebel de Graaf (1920) described *orientalis* as a variety of *An*. *punctulatus* (see explanation of the name *punctulatus* above) from northern Celebes [Sulawesi], Moluccas and eastern Java. Without explanation, Bonne-Wepster & Swellengrebel (1953) cited the type locality as Paleleh, Celebes [a village in Central Sulawesi Province]. The original description follows [figure numbers as in the original]: "This variety is founded on larval characters only, the adult not differing from the type, [*sic*] Here follow the distinctive character [*sic*]: 1). The leaflets of the fans [palmate setae] are very slender, not serrate and show pigmentation up to the apex ([pl. 2,] fig. 4). 2). There is no fanshaped [*sic*] hair [seta] on the 2nd abdominal segment but only a small cocade [*sic*; Dutch word veder should instead have been translated as feather] ([pl. 2,] fig. 5)."

The character of the palmate setae (seta 1) on abdominal segments III–VII with smooth or very slightly serrate margins has been used to distinguish *orientalis* in Indonesia from the "type" form of *tessellatus* by Bonne-Wepster & Swellengrebel (1953), Waktoedi Koesoemawinangoen (1954) and Reid (1968). However, specimens of nominal *tessellatus* in the Philippines (Baisas & Dowell 1967) and Taiwan (Tanaka *et al*. 1979) were also found to have smooth or slightly serrate margins. The leaflets in Taiwanese larvae appear a bit different in that they are "rather broad, transparent, usually simple...".

There seem to be multiple character states related to the form of the leaflets of palmate setae in the Tessellatus Complex. Subspecies *orientalis* has no known type material and only an uncorroborated type locality. Larvae characteristically have the leaflets of palmate setae without serration and adults may or may not have dorsal pale scales on palpomeres 2 and 3.

Subspecies *orientalis* occurs in an area where Bourke *et al*. (2021) identified two sympatric OTUs in their molecular study. It is not possible, however, without further study, to determine if one of those refers to *orientalis*.

For now, we think that the name ***orientalis* Swellengrebel & Swellengrebel de Graaf, 1920 should be considered a *species inquirenda*,** *i.e.* a "species of doubtful identity requiring further investigation" (Glossary, *International Code of Zoological Nomenclature*, International Commission on Zoological Nomenclature 1999). "*Anopheles orientalis*", currently recognized as a species in the Encyclopedia of Life, should be removed from the list of *Anopheles* species until its taxonomic status is resolved.

The nominotypical subspecies currently has six synonyms (type localities from Wilkerson *et al.* 2021): *Anopheles formosae* Hatori, 1901 (type locality: Taihoku, Kielun and Tansui, Formosa [Taiwan]); *Anopheles deceptor* Dönitz, 1902 (type locality: Sumatra [Indonesia]); *Myzomyia thorntonii* Ludlow, 1904a (type locality: Cottabato [Cotabato], Mindanao, Philippines); *Dactylomyia ceylonica* Newstead & Carter, 1910 (type locality: Trincomalee, Ceylon [Sri Lanka]); *Anopheles kinoshitai* Koidzumi, 1917 (type locality: Ryukokosho, Taihoku (Taipei), Formosa [Taiwan]); *Anopheles taiwanensis* Koidzumi, 1917 (type locality: Garden of Central Institute, Formosan government and Banshoryo, Ako Prefecture, Formosa [Taiwan]).

It is not yet known what differential characters might be associated with the component taxa of the Tessellatus Complex. We should therefore be mindful that published keys and descriptions were sometimes based on characters of specimens from throughout the range of what was assumed to be a single species. For examples see Peyton & Scanlon (1966), Baisas & Dowell (1967), Reid (1968), Basio (1971), Rattanarithikul & Harrison (1973), Tanaka *et al.* (1979) [characters of Taiwanese specimens], Lee *et al.* (1987), Darsie & Pradhan (1990), Oo *et al.* (2006) and Rattanarithikul *et al*. (2006b).

Anopheles (*Cellia*) *turkhudi* Liston

subspecies ***telamali*** Saliternik & Theodor, 1942—original combination: *Anopheles turkhudi* var. *telamali* (subspecific status by Harbach & Howard 2007). Distribution: Israel (Saliternik & Theodor 1942).

subspecies ***turkhudi*** Liston, 1901—original combination: *Anopheles turkhudi*. Distribution: Afghanistan, Algeria, Bangladesh, Djibouti, Egypt, Eritrea, Ethiopia, India, Iran, Iraq, Israel, Jordan, Morocco, Nepal, Pakistan, Saudi Arabia, Somalia, Sudan, Yemen (Wilkerson *et al*. 2021).

Anopheles turkhudi sensu lato comprises the nominate form, subspecies *telamali* and four synonyms. It ranges from Nepal (Darsie & Pradham 1990), India, Bangladesh (Bashar *et al*. 2013), southwestern Asia (not currently recorded, however, from Bahrain, Cyprus, Kuwait, Lebanon, Syria, Turkey, Qatar and the U.A.E. (Glick 1992) and Saharan Africa (Gillies & de Meillon 1968). The species is a member of the Cinereus Group (Gillies & de Meillon 1968) of the Paramyzomyia Series (Christophers & Barraud 1931), which also includes *An. azevedoi* Ribeiro, 1969, *An. cinereus* Theobald, 1901a and *An. hispaniola* (Theobald, 1903a). Larvae of species of the Cinereus Group have laterally oriented palatal brushes and eggs without floats (see *An. cinereus* above). However, we are not certain this applies to the palatal brushes of *An. azevedoi* and *An. hispaniola*. Gillies & de Meillon (1968) noted for *An. cinereus* that the "eggs hang vertically in the water and sink readily. Loss of the float is thought to be adaptive to oviposition among the filamentous algae on which the larvae feed by means of specialized mouthparts." Also, the larvae typically orient vertically, as do most non-anophelines, probably facilitated by lack of palmate setae on the first few abdominal segments. We also noted this combination of palatal brush orientation and eggs without floats in *An.* (*Ano.*) *rivadeneirai* Levi-Castillo, 1945 (see above).

The nominotypical subspecies was described from a female from Ellichpur, India [Amaraoti District, Central Provinces; also called The Deccan]. The number of specimens examined was not stated; only the holotype is known (Townsend 1990). In summary: Wing with six costal pale spots, including one at apex [basal] pale, prehumeral pale and accessory sector pale spots not present; vein R_1 with corresponding pale spots, lacking the humeral pale but including an accessory sector pale not continuous with the costa; vein M white-scaled at base; vein 1A with a single white-scaled area [size and position not stated]; pale fringe spots present at ends of all veins except 1A; maxillary palpus with three white bands at articulations of palpomeres 2–3, 3–4 and 4–5, apex of palpomere 5 dark [description stated pale spot present at middle of terminal segment but subsequent descriptions and illustrations show palpomere 5 dark apically, white basally; a key character]; thorax covered with white [slender] scales arranged in lines along median and sublateral areas, lateral areas with brown scales often tipped with white scales; legs dark except for white scales at apices of femora and tibiae.

Other characters mentioned in the literature for species in the Cinereus Group are as follow: Larvae with stout dorsal head setae, 2–4-C single, 5–7-C with few branches, 8-C single or double, and 9,10-M plumose; leaflets of the palmate setae short with irregular shoulders and short median filaments. Senevet (1931) described the lateral margin of the pupal paddle with short blunt tooth-like serration. There is variability of possible note on two wing veins: The costa with or without humeral and presector pale spots, and vein 1A either mostly pale with dark spots at ends, mostly dark-scaled or apical half dark with small basal dark spot.

Synonym *An. azriki* Patton, 1905 (synonymy with *turkhudi* by Edwards in Evans 1938) was described from the Aziriki spring near D'thala [West Aden Protectorate, Yemen]. It was distinguished as having five white scale spots on the costa, vein M with two black spots, one at base and the other at apex, and no pale fringe spots at the ends of primary veins. The observed lack of pale fringe spots can be explained by difficulty seeing them on a pale wing, especially without proper illumination. Edwards, in Evans (1938), stated: "The variety *azriki* according to Christophers [1933] differs from the type only in having the wing-fringe entirely dark, but the fringe-spots are in any case faint, and as suggested by Christophers, *azriki* is probably not a true variety, but merely another synonym."

Synonym *An. flaviceps* Edwards, 1921c (synonymy with *turkhudi* by Edwards in Evans 1938) was described from Erkowit, Sudan. It was distinguished from *turkhudi* by having about five rather narrow aedeagal leaflets, instead of 12–15 broader ones; claspette with a more basally situated club than *turkhudi sensu lato*, with one seta about as long as the club and another smaller seta, in contrast to various descriptions of *turkhudi*, which have the claspette with one seta twice as long as the club and two much shorter setae.

Synonym *An. persicus* Edwards, 1921d (synonymy by Christophers 1933) was described from East Persia [Iran]. Christophers dismissed the proposed name since its very short description was based on a single damaged male.

Synonym *An. amutis* de Burca, 1943 (synonymy by Gillies & de Meillon 1968) was described from a single male from Seganeiti, Eritrea. The corresponding larva, however, was a different species, *An. squamosus* Theobald, 1901a. De Burca noted that vein 1A was mainly pale and that pale fringe spots were absent. Male *Anopheles* are typically much paler than females, making comparison to *Anopheles* females problematic.

Subspecies *telamali* was collected at Tel Amal, Plain of Esdraelon, Israel and described based on characters from four larvae, one adult male and two females (Saliternik & Theodor 1942). The authors compared the specimens to a single specimen of *turkhudi* from Chakdara, India [Afghanistan] and to literature accounts by Puri (1931) and Iyengar (1930) as follow: Two white spots present on basal third of costa in the Indian specimen [humeral and presector pale spots], which are not found on *telamali*; base of R_1 dark in the Indian specimen, base of R_1 white in *telamali* [not evident in illustration]; vein R_{4+5} all dark in the Indian specimen, nearly all white in *telamali* [not evident in illustration]; well-defined white area in middle of 1A in the Indian specimen, but only four or five scattered white scales in *telamali*. Saliternik & Theodor (1942) noted that the male genitalia agreed with the illustration of Christophers (1915) except for the presence of many more aedeagal leaflets in *telamali*: "There are only 3 to 4 indicated in his figure while there are 10 to 11 in our specimen." Additionally, the hindfemur of *telamali* was described (and illustrated) with "a well-defined white longitudinal stripe which ends a short distance before tip. On the other femora the white stripe is less clearly defined." This last character was not mentioned as diagnostic, but we have not seen reference to it elsewhere. Regarding the male genitalia, it is obvious that Saliternik & Theodor erred when they stated that Christophers (1915) indicated the presence of three to four aedeagal leaflets in his figure of the male genitalia. Christophers's figure (pl. XXIII, fig. 19), clearly diagrammatic, distinctly shows two apical leaflets on only one side of the aedeagus. In his brief description, he stated that the genitalia were "As in *rhodesiensis*", *i.e.* "Theca [aedeagus] Y shaped, with about four strongly chitinised leaflets, the inner, the longest, ·5 [0.5] of the length of the theca." It is obvious that Saliternik & Theodor compared the total number of leaflets in their specimen, *i.e.* the sum of leaflets on both sides, with the number on one side (5–7) indicated in the descriptions and illustrations of Christophers (1915, 1933); thus, the number of leaflets does not distinguish subspecies *telamali* from the typical form of *An. turkhudi*.

Subspecies *telamali* has not been explicitly reported from Israel since the original description in spite of continued collecting (Margalit *et al.* 1973; Margalit & Tahori 1974). However, the nominotypical form has been reported in some of the same publications. In addition, neither Mattingly & Knight (1956) nor Rodhain *et al.* (1977) mention *telamali* in their treatments. Glick (1992), in a key to adult female *Anopheles* from southwestern Asia and Egypt, stated in an explanatory note (no. 2) that "The variety *An.* (*Cel.*) *turkhudi telamali* described by Saliternik and Theodor (1942) from 'Palestine' was not seen during this study" and "J. Margalit (personal communication) feels that the status of *An. turkhudi telamali* as a valid subspecies may be in doubt." Recently, Bromley-Schnur (2021), in an illustrated guide to the mosquitoes of Israel and neighboring areas, reiterated that the validity of subspecies *telamali* is doubtful and noted that *An. turkhudi* is rare in Israel and has not been found in the country since it was last identified as larvae collected in 1969 at Eine et Turabe Springs near the northwestern side of the Dead Sea (Margalit *et al*. 1973).

Although further study could prove differently, we believe that subspecies *telamali* is a synonym of *An. turkhudi* [*sensu lato*]. However, variation reported from the wide geographical range of *An. turkhudi* suggests a species complex. We agree with the opinion of Gillies & de Meillon (1968) that "The discrepancy between the terminalia [genitalia] of specimens from Peninsular India and the rest of its distribution has already been noted, which raises the question as to whether Edwards, in Evans (1938), was correct in synonymizing *flaviceps* with *turkhudi*. It seems possible that specimens from the north-west of the Indian subcontinent and from Arabia and Africa may not be conspecific with the *turkhudi* of the Deccan." Until further studies prove otherwise, *telamali* is here considered to be conspecific with the nominate species: ***telamali*** **Saliternik & Theodor, 1942, junior subjective synonym of** ***Anopheles*** **(*****Cellia*****)** ***turkhudi*** **Liston, 1901**. Consequently, "*Anopheles telamali*" should be removed from the list of species of *Anopheles* recorded in the Encyclopedia of Life.

Anopheles (*Cellia*) *wellcomei* Theobald

subspecies ***ugandae*** Evans, 1934—original combination: *Anopheles distinctus* var. *ugandae* (subspecific status by Gillies & de Meillon 1968). Distribution: Angola, Botswana, Burundi, Democratic Republic of the Congo, Gabon, Gambia, Kenya, Senegal, Tanzania, Uganda (Ribeiro & Ramos 1975; Gillies & Coetzee 1987; Wilkerson *et al.* 2021).

subspecies ***ungujae*** White, 1975—original combination: *Anopheles* (*Cellia*) *wellcomei ungujae*. Distribution: Island of Zanzibar, Tanzania (White 1975).

subspecies ***wellcomei*** Theobald, 1904—original combination: *Anopheles wellcomei*. Distribution: Angola, Benin, Botswana, Burkina Faso, Cameroon, Central African Republic, Chad, Côte d'Ivoire, Democratic Republic of the Congo, Eritrea, Ethiopia, Gabon, Gambia, Ghana, Guinea, Kenya, Mali, Mauritania, Mozambique, Niger, Nigeria, Senegal, Seychelles, South Sudan, Sudan, Tanzania, Togo, Uganda, Zambia, Zimbabwe (Wilkerson *et al.* 2021).

The nominal taxa treated here are members of the Wellcomei Group (Gillies & de Meillon 1968) of the Myzomyia Series (Christophers 1924), which also includes *An. distinctus* (Newstead & Carter, 1911), *An. erepens* Gillies, 1958 and *An. theileri* Edwards, 1912c. Species in the Wellcomei Group lack aedeagal leaflets (except *theileri*) and have adaptations in the immature stages for climbing out of the water (Evans 1934). The larvae have large dense hair-like spicules on the thorax and abdomen, and pupae have a row of ventrally directed hooks on the cephalothorax and the paddle is fringed externally with coarse spines. Verification of these characters for subspecies *ungujae* is still needed, because it is known only from a single female.

The original description of *An. wellcomei* (adult female) includes an informative color illustration. Theobald's (1904) diagnosis follows: "Head black with dense white, yellow and brown upright forked scales, the white ones in front and two long hair-like projecting white tufts; palpi yellow, black at the base with two white bands on the yellow area. Thorax ashy, chestnut-brown at the sides and with hair-like golden scales; abdomen brown, unbanded with brownish golden hairs. Wings mostly yellow scaled, costa jet black with two yellow spots and three or four black spots on the wing field." Also of note are other characters from the original description and subsequent observations. The maxillary palpus is black basally and ochreous (yellow orange to orange) on approximately the distal two-thirds, with two broad white bands and a third narrow band apically. The proboscis is dark on the proximal half, and the distal half is ochreous like the palpus. The wing is distinctive and was later described by Evans (1927): "To the naked eye the wings seem yellow with a narrow, black anterior border." Also from the original description: Costal wing spots, on costa and vein R_1, include subcostal, preapical and apical pale spots. There is also a small sector pale spot on R_1, which is almost entirely pale proximally. Wing mostly pale yellowish with small dark spots (noted by Theobald to vary) on veins R_2, R_3, R_{4+5}, M_1, M_2 and 1A. Fringe scales pale at ends of all veins, wing apex and entire border of the anal cell. "Legs brown with very narrow apical yellow bands." Legs subsequently described by Gillies & de Meillon (1968) as: "Tarsus 1–3 of fore legs [foretarsomeres 1–3] with distinct but narrow apical pale bands; mid legs similar but pale bands less distinct; hind legs with tarsus 1–4 [hindtarsomeres 1–4] distinctly banded apically."

Anopheles wellcomei was described from three females from Baro and Pibor, Sudan (now in South Sudan). "Dr. Balfour states that 'it boarded the steamer in the evening at Baro and bit freely.'" Also, "It is abundant on the Baro [River]." Townsend (1990) recorded the label data for the three syntypes as "*wellcomei* Theobald, 1904c: 64–66

(*Anopheles*). Syntypes (3) – Sudan: 1 female, [Eastern Equatoria], Baro [5°45′N 31°42′E]; 2 females, [Sobat], Pibor." David Pecor (pers. comm.) interprets the Baro and Pibor collection localities to be place names with coordinates of 5.75, 31.7 and 6.79853, 33.13045, respectively (see: https://arcg.is/0D4nD).

Two other nominal species were included with the above species by Evans (1934) in the "*distinctus* series" (*Anopheles walravensi* Edwards, 1930 and *Anopheles schwetzi* Evans, 1934). They "share a peculiarity in wing markings, namely, the reduction or loss of some of the pale costal spots, especially of the sector and subcostal, at least the basal 2/3 of the costa being entirely dark...". The relative vagueness of the lack of pale spots on the costa and few dark spots on the rest of the wing (along with similarity in leg coloration) presumably led taxonomists to include similar-looking species in the concept of the "*distinctus* series". Also vague to us is the ill-defined designation of varieties and subspecies throughout the taxonomic history of this group of species. To illustrate, it is perhaps informative to look at name combinations over time.

Pyretophorus distinctus Newstead & Carter, 1911: To genus *Anopheles* by Evans (1927).
Pyretophorus distinctus var. *melanocosta* Newstead & Carter, 1911: To synonym of *An. distinctus* by Evans (1934).
Anopheles theileri Edwards, 1912c: New name for *Pyretophorus albipes* Theobald, 1911a.
Anopheles theileri var. *brohieri* Edwards, 1929b: To species rank, *An. brohieri*, by Gillies & de Meillon (1968).
Anopheles distinctus var. *ugandae* Evans, 1934: To *An. wellcomei* subspecies *ugandae* by Gillies & de Meillon (1968) (elevated to species herein).
Anopheles walravensi Edwards, 1930: No change.
Anopheles schwetzi Evans, 1934: No change.
Anopheles theileri var. *septentrionalis* Evans, 1934: To synonym of *An. brohieri* Edwards, 1929b by Gillies & de Meillon (1968).
Anopheles walravensi var. *milesi* de Meillon & Evans, 1935: To synonym of *An. wellcomei* subspecies *ugandae* by Gillies & de Meillon (1968).
Anopheles michaeli de Meillon & Leeson, 1940: To synonym of *An. schwetzi* by Gillies & de Meillon (1968).
Anopheles wellcomei subspecies *erepens* Gillies, 1958: To species rank, *An. erepens*, by Gillies & Coetzee (1987).
Anopheles wellcomei subspecies *ungujae* White, 1975 (elevated to species herein).

Subspecies *ugandae* was described from Kampala, Uganda. The two type localities of *wellcomei*, Baro and Pibor, are 606 km and 716 km, respectively, north of Kampala. Larvae, pupae and adult females were available to Evans (1934), and were illustrated in part. A holotype female with associated larval and pupal exuviae is in the Natural History Museum, London. Evans (1934) did not clearly distinguish *ugandae* from other taxa in the "*distinctus* series" but instead alluded to differences between it and "pale forms of *distinctus*", "the type of the former var. *melanocosta*", pupal paddle "Shape more nearly ovoid than usual, but apparently less so than in *theileri* and the type form of *distinctus*", "Larvae and pelts [exuviae] resembled those of the type form and of *A. theileri*", "Outer clypeals, as in type form and some specimens of *theileri*, very short and bluntly pointed distally" and, in addition, there were vague comparisons to the antennae and abdominal setae of *theileri*. The distinguishing character, however, provided in a key to adult females, is "Outer half of proboscis with creamy or whitish scales; palpi with dark brown scales confined to the basal one-third" in *wellcomei*, and "Outer half of proboscis dark-scaled; palpi with dark-scaled areas on outer two-thirds" in *walravensi*, *distinctus* var. *ugandae*, *distinctus* "type form" and *schwetzi*. These same characters were used by Gillies & Coetzee (1987) to distinguish *wellcomei wellcomei* from *wellcomei ugandae*. Gillies & Coetzee were not able to separate the larvae or pupae of species in the Wellcomei Group (as the *wellcomei* section).

Gillies & de Meillon (1968) mapped the distributions of subspecies *wellcomei* and *ugandae* (their fig. 47). Subspecies *wellcomei* is shown across central sub-Saharan Africa and subspecies *ugandae* is distributed more in southeastern Africa, but with a large overlap of the two in Uganda, Republic of Congo, Tanzania, Kenya and southern South Sudan. Gillies & Coetzee (1987) stated that "Gillies and De Meillon (1968) recognised the 3 subspecies, *w. wellcomei*, *w. ugandae* and *w. erepens*. The last named was a very dark form from an isolated area in Tanzania and Kenya. The pale form with flavescent palps and proboscis (*wellcomei*) is typical of the northern savanna while, from Uganda southwards, forms lacking this overlay of pale scales predominate (*ugandae*). However, material collected more recently from the western limits of the northern savanna in Senegal (Dr M Cornet) and from adjacent parts of The Gambia lacks the flavescent scales and has a rather darker wing, both characters diagnostic of subsp. *ugandae*.

This pattern of variation, in which there is a tendency for certain peripheral as well as southern populations to become darker, means that *ugandae* is a rather less satisfactory taxon than appeared when Gillies and De Meillon redefined it. However, the name *ugandae* must be applied to Sene-gambian specimens even though this invalidates to a certain extent the picture of distribution previously presented." This uncertainty suggests to us that the variability could indicate a species complex.

Given the diagnostic character of the pale coloration of the apical half of the maxillary palpus and proboscis in subspecies *wellcomei*, which are dark in subspecies *ugandae*, the relative closeness of type localities and the extensive overlapping distributions, we believe these are genetically distinct taxa. Therefore, we hereby elevate subspecies *ugandae* to specific status: ***Anopheles* (*Cellia*) *ugandae* Evans, 1934**. *Anopheles ugandae* is currently listed as a species in the Encyclopedia of Life. As indicated above, we agree with Gillies & de Meillon (1968) that *An. walravensi* var. *milesi* de Meillon & Evans, 1935 (type locality: Victorian Falls, Zimbabwe) is probably a synonym of *An. ungandae* (type locality: King's Lake Area, Kampala, Uganda). However, the possibility that further study could reveal that *milesi* is a separate species cannot be ruled out.

White (1975) named and designated a holotype for *An*. *wellcomei* subspecies *ungujae* based on a brief description by Gillies (1958) of a single female from Zanzibar, which Gillies called both *Anopheles wellcomei* subsp. indet. and *A*. *wellcomei*, Zanzibar form. Gillies noted that "The finding of *A*. *wellcomei* on the island of Zanzibar extends the known range of the species right across Africa. It is interesting to note that moderately intensive collecting on the adjacent East African coast has failed to reveal this species, although *erepens* is abundant in the arid regions 100 or so miles inland." White (1975) stated that "Apart from its discreet distribution, this subspecies is readily separable from other forms of *wellcomei* by extension of the pale sector wing-spot onto the costa and by the almost completely pale first wing vein (vide Figure 4 in Gillies, 1948:10; Plate 82b in Gillies & De Meillon, 1968:177)." However, a complete description of the holotype is needed. Based on the stated discrete characters and distribution we believe, pending further morphological and molecular study, that subspecies *ungujae* should be afforded species status: ***Anopheles* (*Cellia*) *ungujae* White, 1975**. *Anopheles ungujae* is currently listed as a species in the Encyclopedia of Life. Without a complete description of the holotype and collection and study of the adult male and immature stages, its placement in the Wellcomei Group remains uncertain.

Culex (*Culex*) *andersoni* Edwards

subspecies ***abyssinicus*** Edwards, 1941—original combination: *Culex* (*Culex*) *andersoni* ssp. *abyssinicus*. Distribution: Ethiopia (Edwards 1941).

subspecies ***andersoni*** Edwards, 1914—original combination: *Culex andersoni*. Distribution: Comoros, Democratic Republic of the Congo, Eritrea, Kenya, Malawi, Republic of South Africa, Rwanda, Tanzania, Uganda (Wilkerson *et al*. 2021).

subspecies ***bwambanus*** Edwards, 1941—original combination: *Culex* (*Culex*) *andersoni* ssp. *bwambanus*. Distribution: Lesotho, Republic of South Africa, Uganda (Wilkerson *et al*. 2021).

Edwards (1914) described *Culex andersoni* from specimens collected at Kabete, located outside the borders of Nairobi in the Central Province of Kenya, based principally on features of the male habitus and male genitalia.

Subspecies *abyssinicus* is only known from Ethiopia, and according to Edwards (1941) the adult is ornamented differently than the typical form but the male genitalia are essentially the same. Because the treatment of the genitalia is rather superficial, it is likely that some differences might be evident upon closer examination. Based on differences in ornamentation and allopatry, *abyssinicus* is hereby considered a separate species: ***Culex* (*Culex*) *abyssinicus* Edwards, 1941**. This species should be added to the species of *Culex* listed in the Encyclopedia of Life.

Subspecies *bwambanus* and the nominotypical form are both reported from Uganda, and Edward (1941) indicated that they both occur in the Ruwenzori Mountains. However, Edwards described *bwambanus* from a Ruwenzori location while recognizing the presence of the typical form elsewhere in the same mountains. Although the Ruwenzori Mountains appear to be the only place where the two forms may be in sympatry, Edwards described *bwambanus* as a new subspecies because of differences in the pale scaling of the hindfemur of the adults, and nearly "hairless" maxillary palpi ("may be rubbed in the type"), gonocoxite with a more prominent subapical lobe and a narrower gonostylus in the male. Since the available evidence indicates that *bwambanus* is morphological distinct in the absence of clinal variation, it is hereby afforded species status: ***Culex* (*Culex*) *bwambanus* Edwards, 1941**. *Culex bwambanus* is currently listed as a species in the Encyclopedia of Life.

Culex (*Culex*) *annulirostris* Skuse

subspecies ***annulirostris*** Skuse, 1889—original combination: *Culex annulirostris*. Distribution: Australia, Bismarck Archipelago, Cook Island, Easter Island, Fiji, French Polynesia, Guam, Indonesia, Kiribati, Nauru, New Caledonia, Palau, Papua New Guinea, Philippines, Samoa, Solomon Islands, Tahiti, Timor, Tonga, Tuvalu, Vanuatu, Wake Island (Wilkerson *et al*. 2021, except Mariana Islands).

subspecies ***marianae*** Bohart & Ingram, 1946b—original combination: *Culex* (*Culex*) *annulirostris marianae*. Distribution: Mariana Islands (Bohart & Ingram 1946b).

The nominotypical subspecies is widely distributed in the Australasian Region and occurs in eastern islands of Indonesia (Maluku Islands and Timor) and northward into the Philippines. As indicated by Bohart (1957), "The typical subspecies is replaced in the Mariana Islands by subspecies *marianae*", which he recorded from Aguiguan, Anatahan, Pagan, Saipan and Tinian Islands in the contemporary Northern Mariana Islands and from Guam, the southernmost of the Mariana Islands (Bohart & Ingram 1946b; Yamaguti & LaCasse 1950; Bohart 1957). The adults of subspecies *marianae* differ from those of the typical subspecies mainly in having a narrow line of pale scales on the caudal margins of abdominal terga II–IV and sometimes also on terga V–VII or VIII. Larvae usually have blunter dorsomental teeth and shorter anal papillae, normally shorter than the saddle (Yamaguti & LaCasse 1950; Bohart 1957). Based on these seemingly consistent differences and the great distances between the Mariana Islands and islands that harbour populations of the typical form, and because evidence suggests that *Cx. annulirostris* is a complex of species (Lee *et al*. 1989a), it seems likely that *marianae* is genetically distinct and should therefore be afforded specific status: ***Culex* (*Culex*) *marianae* Bohart & Ingram, 1946b**. *Culex marianae* is currently listed as a species in the Encyclopedia of Life.

Five nominal species are recognized as junior synonyms of *Cx. annulirostris*: *Cx. jepsoni* Bahr, 1912 (type locality: Fiji Islands), *Cx. somerseti* Taylor, 1912 (type locality: Somerset, Queensland, Australia), *Culicelsa consimilis* Taylor, 1913 (type locality: Ayr, Queensland, Australia), *Culicelsa simplex* Taylor, 1914 (type locality: Townsville, Queensland, Australia) and *Cx. palmi* Baisas, 1938 (type locality: Parañaque, now officially Pasay, Rizal Province, Luzon, Philippines). The type locality of *Cx. annulirostris* is located in the Blue Mountains of New South Wales, Australia. As it is probable that *Cx. annulirostris* is a complex of species (Lee *et al.* 1989a), it is possible that the five nominal forms may represent at least three separate species: One in the Fiji Islands (*Cx. jepsoni*), one in the Philippines (*Cx. palmi*) and a third species in Queensland (*Cx. somerseti*, *Culicelsa consimilis* and *Culicelsa simplex*). For the time being, however, these nominal forms are retained as synonyms of *Cx. annulirostris* pending further consideration of their taxonomic status.

Culex (*Culex*) *argenteopunctatus* (Ventrillon)

subspecies ***argenteopunctatus*** (Ventrillon, 1905)—original combination: *Heptaphlebomyia argenteopunctata*. Distribution: Only known with certainty from Madagascar (see below).

subspecies ***kingii*** (Theobald, 1913c)—original combination: *Heptaphlebomyia kingii* (subspecific status by Edwards 1941). Distribution: Angola, Burkina Faso, Cameroon, Central African Republic, Democratic Republic of the Congo, Ghana, Kenya, Namibia, Nigeria, Republic of the Congo, Republic of South Africa, Senegal, Sierra Leone, South Sudan, Sudan (Wilkerson *et al*. 2021). These and the following countries listed for *argenteopunctatus sensu stricto* by Wilkerson *et al*. (2021) most likely also pertain to *kingii*: Benin, Côte d'Ivoire, Mali, Mozambique, Nigeria and Togo.

Culex argenteopunctatus was described and named based on specimens (adult male and female) collected in the environs of Antananarivo, formerly Tananarive, Madagascar. Subspecies *kingii* was originally described as a species distinct from *Cx. argenteopunctatus* based on two females, one collected at Nyumbe and the other at Alenga in the former Lado District (current Dokolo State) of present-day South Sudan. Theobald (1913c) stated that *kingii* "can be distinguished from the allied *H. argenteopunctata*, Ventrillon, by the abdomen having only small basal lateral spots and not ornamented as in Ventrillon's species from Madagascar; the antennae are also black in the ♀, not yellowish, and the thoracic adornment differs." Additionally, Edwards (1941) noted that *kingii* differs from the typical form in having broad and flat postspiracular scales as on other areas of the thoracic pleura, mesokatepisternal scales more numerous with the upper patch large and extending over the prealar area, and the hindfemur "white all round on basal fourth or more." In his study of the adult, larval and pupal stages of *Cx. argenteopunctatus* in Madagascar (the larva and pupa of the typical form were not previously known), Brunhes (1967) pointed out morphological characters specific to the typical form as follows: "The most important of these distinctive characters seem to us to be in the larva; the comb of segment VIII formed by scales [not spine-like] and the spines [seta 2-S] of the dorsal valves of the siphon which do not have a plane of symmetry [elongate and not identical]; in adults, the narrow and curved postspiracular scales, the sternopleural [mesokatepisternal] spot of white scales which does not reach the prealar area, the two patches of pale scales on the nape of the neck [occiput] and the male terminalia [genitalia] which are different from those drawn by Edwards from a male of subspecies *kingi* [translated from the French]." Despite "these morphological peculiarities, allied to a geographical isolation", Brunhes elected to maintain the typical form as a subspecies. On the contrary, in view of the morphological distinctions, as well as other differences in the adults, larva and pupa of the typical form noted by Brunhes, and its geographical isolation, we conclude, in agreement with Theobald (1913c), that *kingii* is not conspecific with the Madagascan species. Thus, the continental form is hereby formally returned to its original specific status: ***Culex* (*Culex*) *kingii* (Theobald, 1913c)**. *Culex kingii* is currently listed as a species in the Encyclopedia of Life.

Culex (*Culex*) *comorensis* Brunhes

subspecies ***comorensis*** Brunhes, 1977—original combination: *Culex* (*Culex*) *comorensis*. Distribution: Anjouan and Mohéli Islands, Union of the Comoros and Ankaratra Massif, Madagascar (Brunhes 1977).

subspecies ***kartalae*** Brunhes, 1977—original combination: *Culex* (*Culex*) *comorensis* ssp. *kartalae*. Distribution: Grande Comore [Union of the Comoros], Mayotte [overseas department of France] (Brunhes 1977).

Culex comorensis was described and named from specimens discovered on Anjouan Island, an autonomous high island that forms part of the Union of the Comoros. Brunhes (1977) indicated that it was also found on Mohéli Island and the Ankaratra Massif of Madagascar. Subspecies *kartalae* was briefly described and named in the same publication from specimens collected on Grande Comore Island. Brunhes pointed out morphological "peculiarities" of the male genitalia and larvae that distinguish the two forms. In the typical form, the subapical lobe of the gonocoxite bears a few minute setae at the bases of setae *a-f*; in the larva, head seta 13-C is long (0.6 mm), seta 1-S of the siphon usually has 4 pairs of setae on the posterior margin, the pecten consists of 10–14 spines (mean 11.2), and the dorsal and ventral anal papillae are equal in length. In subspecies *kartalae*, the subapical lobe of the gonocoxite bears a dense cluster of minute setae at the bases of setae *a-f*; the larva differs in having a short seta 13-C (0.2–0.3 mm), the siphon usually has 5 pairs of seta 1-S on the posterior margin, the pecten consists of 4–10 spines (mean 7.2) and the dorsal pair of anal papillae are longer than the ventral pair. The author, however, overlooked some additional important differences of the male genitalia. Subspecies *kartalae* differs from the typical form as follows: The ventral arms of the phallosome are longer and more slender, the dorsal arms are more distinctly minutely toothed and more sharply pointed, setae *a*, *b*, *c* and *h* of the subapical lobe are distinctly longer than seta *g*, setae *a* and *b* are stouter and more distinctly hooked apically and the insertion of seta *c* is borne mesad of setae *a* and *b* whereas it is inserted distal to these two setae in the typical form. The complexity of morphological distinctions and the geographical isolation are a clear indication that *kartalae* is a distinct species; thus, this form is hereby afforded specific status: ***Culex* (*Culex*) *kartalae* Brunhes, 1977**. *Culex kartalae* is currently listed as a species in the Encyclopedia of Life.

Culex (*Culex*) *grahamii* Theobald

subspecies ***farakoensis*** Hamon, 1955—original combination: *Culex grahami* [*sic*] var. *farakoensis* (subspecific status by Harbach & Howard 2007). Distribution: Southern Mali (Hamon 1955).

subspecies ***grahamii*** Theobald, 1910—original combination: *Culex grahamii* [*nomen novum* for *Culex pullatus* Graham, 1910]. Distribution: Angola, Benin, Burkina Faso, Cameroon, Central African Republic, Côte d'Ivoire, Democratic Republic of the Congo, Ghana, Guinea, Kenya, Liberia, Madagascar, Mali, Nigeria, Republic of the Congo, Senegal, Sudan and South Sudan, The Gambia, Togo, Uganda (Knight & Stone 1977; Wilkerson *et al*. 2021).

Graham (1910) described the male and female of this species (as *Cx. pullatus*) from specimens collected in the vicinity of Lagos, Nigeria (Stone *et al*. 1959; Townson 1990). The larva was described by Wesché (1910), as *Cx. pullatus*, from specimens collected around Lagos, described by Macfie & Ingram (1923) from specimens collected in the vicinity of Accra, Ghana (as Gold Coast) and by Hopkins (1936, 1952) from undisclosed localities, except for reference to specimens described by Macfie & Ingram. Hamon (1955) described *farakoensis* from specimens collected "aux cascades de Farako, Cercle et Subdivision de Sikasso, Soudan Français" (at Farako waterfalls, Sikasso Cercle and Subdivision, French Sudan = Mali). Farako Waterfalls are located about 30 km east of Sikasso in Sikasso Cercle, which is one of seven administrative subdivisions of the Sikasso Region of southern Mali. Based on this, the type locality of *farakoensis* that is listed as "Farako, Sikasso, French Sudan" in the catalogs of Stone *et al*. (1959), Knight & Stone (1977) and Wilkerson *et al*. (2021) must be corrected to Farako Waterfalls, Sikasso Cercle, Mali (formerly French Sudan). The listing of Nigeria in the distribution given by Wilkerson *et al*. (2021) appears to be in error.

Hamon (1955) provided a brief description of *farakoensis*, stating that the adults are "almost identical to the typical form and probably not separable with certainty. Male terminalia [genitalia] do not show any difference…" and the "general morphology [of the larva] is that of *Cx. grahami* [*sic*] except for the eighth abdominal segment…" (translated from the French). Hamon recorded the following distinctions: Comb with 13–19 spine-like scales, siphon index 7.9–10.4, pecten with 6–9 simple spines, seta 1-S with about 16 setae (this is misleading as the illustration provided includes a ventral row of 12 setae beyond the pecten and a lateral row of 5 setae on the distal half of the siphon) with 2–4 branches and the 8 proximal setae at least as long as the diameter of the siphon; anal papillae 2.5–4.0 times as long as the saddle. Hamon stated that the dorsal pair of anal papillae were usually longer than the ventral pair, but the illustration shows the ventral pair are longer than the dorsal pair. In the typical form, these morphological traits, based on the descriptions of Wesché (1910), Macfie & Ingram (1923) and Hopkins (1936, 1952), are characterized as follows: Comb with 14–25 spine-like scales, siphon index 12–15, pecten also with 6–9 simple spines, seta 1-S with about 4 setae (6 are illustrated by Hopkins), minute, with 1–3 branches, one seta inserted within the pecten; anal papillae slightly longer than the saddle, usually equally long or dorsal pair slightly longer. Thus, only three of these characters are distinctive for *farakoensis*, *i.e.* the significantly shorter siphon, the more numerous and longer siphonal setae all borne distal to the pecten and the greater length of the anal papillae. However, the comb scales illustrated for *farakoensis* appear to differ from those illustrated for the typical form. The lateral spicules progressively increase in length to the sides of the median apical spine in *farakoensis* whereas in the typical form they comprise lateral fringes of equal length borne proximal to a stronger apical spine.

Hamon (1955) concluded the description of *farakoensis* with the following observation: "This species [*farakoensis*] was already known from various places of the A. O. F. [Afrique-Occidentale française (French West Africa)], but the only locality having given us larvae identical to the description of Hopkins is Danané (Forest Zone of lower Côte d'Ivoire). All the larvae collected in the savannah zone: Agba-titoé (Togo), Thiès (Senegal), Bobo Dioulasso (Upper Volta) [Burkina Faso] and in various sites of Casamance [Senegal] have in fact the color and chaetotaxy of the typical form but their siphon indexes rarely exceed 11 [translated from the French]." This indicates that the siphon index of *farakoensis* may be slightly greater than noted in the description, but it is still smaller than that of the typical form. This observation, the morphological distinctions noted above and the apparently close association with savannah strongly suggest that *farakoensis* is likely to be genetically distinct from *Cx. grahamii sensu stricto*; accordingly, this nominal form is formally elevated to species status: ***Culex*** **(*Culex*)** ***farakoensis*** **Hamon, 1955**. *Culex farakoensis* is currently listed as a species in the Encyclopedia of Life, however the date of authorship for the former species needs to be corrected from 1954 to 1955.

Culex **(*Culex*)** ***guiarti*** **Blanchard**

subspecies ***guiarti*** Blanchard, 1905—original combination: *Culex guiarti* [*nomen novum* for *Culex viridis* Theobald, 1903a]. Distribution: Benin, Burkina Faso, Cameroon, Central African Republic, Côte d'Ivoire, Democratic Republic of the Congo, Gabon, Gambia, Ghana, Kenya, Liberia, Madagascar, Mali, Mozambique, Nigeria, Republic of the Congo, Republic of South Africa, Senegal, South Sudan, Tanzania, Uganda (Wilkerson *et al*. 2021, but not Sudan, see Simsaa *et al*. 2021).

subspecies ***sudanicus*** Edwards**,** 1941—original combination: *Culex guiarti* var. *sudanicus* (subspecific status by Harbach & Howard 2007). Distribution: Ghana, Nigeria (Wilkerson *et al*. 2021).

Culex guiarti sudanicus was originally described and named as a variety that was considered to be morphologically "Intermediate between *C. guiarti* and *C. weschei*" (Edwards 1941). It was recognized as a subspecies of *Cx. guiarti* by Harbach & Howard (2007).

Edwards (1941) noted that *sudanicus* resembled the nominotypical form in having the proboscis entirely dark-scaled, the abdominal sterna with dark apical bands and the distal half of the midfemur extensively dark-scaled dorsally in posterior view, but exhibited the following differences: Scutal integument uniformly brownish, not paler on the fossae (shoulders), scales nearly entirely pale and coarser; mesokatepisternal scales more numerous, the upper and lower patches almost contiguous; proepisternal scales and setae also more numerous; anterior scales of forecoxa all pale; male genitalia as in the typical form, gonostylus not unusually broad (moderately broad and rather suddenly narrowed apically in the typical form). The larva is known for the typical form (Hopkins 1952), but it is not known for *sudanicus*. The typical form has been recorded from many countries in sub-Sharan Africa whereas *sudanicus* is only recorded from Ghana and Nigeria (Wilkerson *et al*. 2021). Based on the paucity of morphological data and the fact that the typical form has also been recorded from Ghana and Nigeria, we believe that Edwards (1941) was correct in describing *sudanicus* as a morphological variant of *Cx. guiarti*. Consequently, it seems prudent to formally recognize *sudanicus* as a synonymous name: ***sudanicus* Edwards, 1941, junior subjective synonym of *Culex* (*Culex*) *guiarti* Blanchard, 1905**. "*Culex sudanicus*" should be removed from the list of *Culex* species included in the Encyclopedia of Life. We retain a second synonym of *Culex guiarti*, *Culex viridis* Theobald, 1903a, described from Buse, Uganda.

Culex (*Culex*) *invidiosus* Theobald

subspecies ***invidiosus*** Theobald, 1901d—original combination: *Culex invidiosus*. Distribution: Sub-Saharan Africa, countries north of approximately 10° S latitude—including Benin, Burkina Faso, Cameroon, Côte d'Ivoire, Democratic Republic of the Congo, Gabon, Gambia, Ghana, Kenya, Liberia, Mali, Nigeria, Republic of the Congo, São Tomé and Príncipe, Senegal, Sierra Leone, South Sudan, Sudan, Tanzania, Uganda (Wilkerson *et al*. 2021).

subspecies ***vexillatus*** Edwards, 1941—original combination: *Culex* (*Culex*) *invidiosus* var. *vexillatus* (subspecific status by Harbach & Howard 2007). Distribution: Cameroon, Democratic Republic of the Congo, Nigeria, Republic of the Congo, Uganda (Wilkerson *et al*. 2021).

subspecies ***vicinalis*** de Meillon & Lavoipierre, 1944—original combination: *Culex* (*Culex*) *invidiosus* ssp. *vicinalis*. Distribution: Democratic Republic of the Congo (de Meillon & Lavoipierre 1944).

Like many species of Afrotropical *Culex*, *Cx. invidiosus* is very poorly known. It was last treated by Edwards (1941), who distinguished *vexillatus* as a variety based on five males and a female from Kampala, Uganda (Mattingly 1956) that closely resembles the typical form except for the shape of seta *f* of the subapical lobe of the male gonocoxite. Three years later, de Meillon & Lavoipierre (1944) described *vicinalis* as a subspecies of *Cx. invidiosus* based on a single male collected at Yangambi, a town located on the Congo River in the central region of present-day Democratic Republic of the Congo.

A review of the taxonomic history of *Cx. invidiosus* following its original description by Theobald (1901c) begins with Edwards (1911b), who indicated that it belonged to a group of species that are "very difficult to classify" because they lack "clearly marked distinctions." Ironically, Edwards formally recognized *Cx. euclastus* Theobald, 1903b, *Cx. chloroventer* Theobald, 1909 and *Cx. aquilus* Graham, 1910 as synonyms of *Cx. invidiosus*, and those names have remained as synonyms of *Cx. invidiosus* to the present.

Wesché (1910) described the larva of *Cx. invidiosus* (as *Cx. aquilus*) and included it in a key to the larvae of African Culicidae. Edwards (1912d) updated the key and illustrated the head and terminal abdominal segments of *Cx. invidiosus*. Although Edwards was "unable to separate the larvae of *C. decens* [now considered a valid species]… and *C. invidiosus*", and found that the characters given by Wesché were unreliable, he believed the two species were distinct because *Cx. decens* could be distinguished by the reddish thorax (brown in *Cx. invidiosus*) and the banded abdominal segments of males. Despite treating them as separate species, he concluded that "It is therefore quite possible that the two are really only forms of one species; they generally occur together, but specimens bred from one batch of larvae exhibit little variation."

Edwards (1914) acknowledged that species of *Culex* are most readily separated by features of the male genitalia, but indicted "As previously stated, I can detect no difference whatever between the hypopygia [genitalia] of this species [*Cx. invidiosus*] and of *C. decens*." Despite this comment, Edwards treated *Cx. invidiosus* as a distinct species and surmized that it "is probably a purely West African species." He illustrated the phallosomes and gonocoxites of *Cx. invidiosus*, *Cx. antennatus* (Becker, 1903) (as Cx. *laurenti* Newstead, 1907, in Newstead *et al*. 1907) and Cx. *perfuscus* sp. nov. to show the close similarity of the genitalia of seemingly unrelated species.

Macfie & Ingram (1920) conducted a detailed comparison of the pupae of *Cx. decens* and *Cx. invidiosus*, but were unable to find differences to distinguish them. In summary, they stated: "The question then arises, are *C. decens* and *C. invidiosus* separate species or are they varieties of a single mosquito. There are indeed certain differences in the adults, but the genitalia of the males are identical according to Edwards, the larvae cannot be separated [reiterated by Hopkins 1936, 1952], and the same remark applies to the pupae. Under these circumstances we think there can be little doubt that they should be regarded as varieties and not as distinct species; we propose to retain for the species the name *C. decens*." Based on these findings, Edwards (1932a) listed *invidiosus* as a variety of *Cx. decens*, with the three synonyms noted above.

Edwards (1941) is the last reviser of the subgenus *Culex* in the Afrotropical Region. He reiterated his earlier observation (Edwards 1912d) that the adults of *Cx. invidiosus* differ from those of *Cx. decens* in having brown instead of reddish mesonotal (scutal) scales and abdominal terga without pale bands, and added that the male genitalia of *Cx. invidiosus* differ from those of *Cx. decens* in having seta *f* longer and distally expanded on one side and seta *h* with a kink at mid-length. He concluded that "Since it has now been found that small differences exist in the male terminalia [genitalia], supporting the more obvious differences in colouring, it may be more correct to treat *C. invidiosus* as a distinct species rather than as a variety of *C. decens*." He then described *vexillatus* as a variety with male genitalia that "Closely resemble those of *C. invidiosus* in all respects except as regards the shape of appendage *f* of the coxite lobe [gonocoxite subapical lobe]; this is greatly expanded at the tip, like a small flag; seta *h* sinuous as in typical *invidiosus*." In addition to the character of seta *f*, comparison of Edwards's illustrations of the partial phallosomes of *invidiosus* and *vexillatus* reveals a difference not noticed by Edwards, *i.e.* the dorsal arms of the lateral plates are larger, distally tapered and project beyond the largest tooth of the lateral arm in the type form whereas in *vexillatus* the dorsal arms are smaller, slightly enlarged distally and do not reach beyond the largest tooth of the lateral arm.

Culex invidiosus vicinalis was described by de Meillon & Lavoipierre (1944) as "agreeing with *invidiosus* Theo. in all respects the only differences to be found in the male terminalia [genitalia]", *i.e.* seta *f* of the subapical lobe is not enlarged apically, seta *h* is not sinuous and a unique double row of rather sharply bent setae is borne adjacent to the subapical lobe on the lateral surface of the gonocoxite. The authors pointed out that a similar double row of setae is present in an unnamed variety of *Cx. ornatothoracis* Theobald, 1909 (see Edwards 1941: fig. 118g), but because *vicinalis* bears an overall closer resemblance to *Cx. invidiosus*, de Meillon & Lavoipierre regarded it "as a subspecies of that species rather than of *ornatothoracis*."

Based on many years of taxonomic work (REH) on species of the genus *Culex*, especially species of the subgenus *Culex*, it is apparent that seemingly minor differences in features of the male genitalia are indicative of separate species. In the case of *vexillatus* and the typical form, differences now apparent in the development of the dorsal arms of the phallosome, supporting the previously noted differences in the form of setae *f* and *h* of the subapical lobe, it is more appropriate to treat *vexillatus* as a distinct species: ***Culex* (*Culex*) *vexillatus* Edwards, 1941**. The situation with *vicinalis* is very different. Based on the diagnostic presence of a unique double row of setae on the gonocoxite, coupled with the distinctive development of setae *f* and *h*, it is surprising that *vicinalis* was not originally recognized as a distinct species; thus, it is hereby afforded specific status: ***Culex* (*Culex*) *vicinalis* de Meillon & Lavoipierre, 1944**. Both *Cx. vexillatus* and *Cx. vicinalis* are listed as species in the Encyclopedia of Life. The larva of *Cx. invidiosus* is partially known (Wesché 1910; Edwards 1912d); the larvae of *Cx. vexillatus* and *Cx. vicinalis* are unknown. Once the larvae of all three species are known and have been studied and compared in detail, it is likely that morphological differences will be found that support their recognition as separate species. Molecular data are also expected to support their specific status.

Three nominal species are recognized as junior synonyms of *Cx. invidiosus*: *Cx. euclastus* Theobald, 1903b (type locality: Gambia), *Cx. chloroventer* Theobald, 1909 (type locality: Accra, Ashanti Region, Ghana) and *Cx. aquilus* Graham, 1910 (type locality: Lagos, Nigeria). The type locality of *Cx. invidiosus* is the island town of Bonny in Rivers State in southern Nigeria. As there is no evidence that one or more of the three nominal forms might be conspecific with either *Cx. vexillatus* (type locality: Kampala, Uganda) or *Cx. vicinalis* (type locality: Yangambi, Tshopo Province, Democratic Republic of the Congo), they must remain as junior synonyms of *Cx. invidiosus*.

Culex (*Culex*) *pipiens* Linnaeus

subspecies ***pallens*** Coquillett, 1898—original combination: *Culex pallens* (subspecific status by Tanaka 2004). Distribution: China, Japan, Mexico, South Korea, United States (continental) (Wilkerson *et al*. 2021).

subspecies ***pipiens*** Linnaeus, 1758—original combination: *Culex pipiens*. Distribution: Temperate regions of Africa, Asia, Australia, Europe and North and South America (for specific country records, see Wilkerson *et al*. 2021).

Without question, the taxonomic status of *Cx. pipiens* and its allied forms has received more attention than any other culicine taxon. As pointed out in a review of the taxonomic history of the species (Harbach 2012), the essence of decades of work conducted on *Cx. pipiens* was to determine whether it is a single polytypic species or a species complex. As a starting point, Edwards (1932a) listed *Cx. pipiens* and its sister species *Cx. quinquefasciatus* Say, 1823 (as *Cx. fatigans* Wiedemann, 1828) as separate species, and *Cx. pallens* as a variety of the former. In a review of the systematics of these nominal species, and taking into consideration evidence of hybridization in areas where the distributions of *Cx. pipiens* and *Cx. quinquefasciatus* overlap, Mattingly *et al*. (1951) and Mattingly (1967) concluded that they should be considered members of a single polymorphic species comprised of subspecies *pipiens* and *quinquefasciatus* and several varieties, with *pallens* being one of them. Beginning with Belkin (1962), the recognition of *Cx. quinquefasciatus* as a separate species gradually gained acceptance, resulting in the current recognition of *Cx. pipiens* and *Cx. quinquefasciatus* as closely related sister species and *pallens* as a subspecies of the former species (Smith & Fonseca 2004; Harbach 2012; Fonseca *et al*. 2009; Aardema *et al*. 2020; Wilkerson *et al*. 2021).

Culex pipiens pallens has been regarded as a subspecies since the studies of Japanese mosquitoes by Tanaka *et al*. (1979) and Tanaka (2004). Since then, genetic and molecular studies have shed light on the status of *pallens* in eastern Asia. A multilocus genotype analysis conducted by Fonseca *et al*. (2009) revealed the occurrence of hybridization between *Cx. p. pallens* and *Cx. quinquefasciatus* in China, South Korea and southern Japan, but not in northern Japan. However, Ohashi *et al*. (2014) found that *Cx. p. pallens* and *Cx. pipiens* hybridize in northern Japan, but hybrids have lower fitness than the offspring of either parental taxon. Finally, recent detailed analyses of DNA sequence data conducted by Aardema *et al*. (2020), which included sequence for specimens of *pallens* from China, cogently support the hypothesis that *pallens* is a genetically distinct entity derived from ancestral hybridization between *Cx. pipiens* and *Cx. quinquefasciatus*. The authors note, however, that the "hypothesis warrants further examination." The presence of *pallens* in Mexico and the United States must also be assessed. As indicated by Mattingly *et al*. (1951), some authors have conjectured that the *pallens* form was introduced into California, presumably from Japan. Despite the concerns and implications of hybridization, we feel it is prudent at this time to accept the evidence for the genetic distinction of *pallens* provided by Aardema *et al*. (2020) and hereby re-establish its original species status pending further investigation: ***Culex* (*Culex*) *pallens* Coquillett, 1898**.

It is interesting to note that *Cx. pipiens* and *Cx. quinquefasciatus* are listed as species in the Encyclopedia of Life, but *Cx. pallens* is not included; thus, it needs to be included with the *Culex* species listed therein. Oddly, the *nomen dubium Culex molestus* Kollar, 1832 (in Pohl & Kollar 1832) is listed as a species, probably mistakenly included instead of *Cx. molestus* Forskål, 1775, a recognized synonym and physiological variant (*molestus* form) of *Cx. pipiens*. The list of mosquitoes in the Encyclopedia of Life was not compiled by mosquito taxonomic experts and does not, in many cases, reflect the current taxonomy of various taxa.

Thirty-six nominal taxa (disregarding the name *melanorhinus* Giles, 1900, which was proposed as a replacement name for *Cx. pallipes* Macquart, 1838) are currently recognized as synonyms of *Cx. pipiens*. We consider all synonymous taxa named from localities in Europe (England, France, Germany and Portugal), northern Africa (Algeria, Egypt and Tunisia), Mexico and the United States to be synonyms of *Cx. pipiens*. These include all of the synonyms listed by Harbach (2018) and Wilkerson *et al*. (2021), as well as *Cx. comitatus* Dyar & Knab, 1909a (California) and *Cx. quinquefasciatus* race *dipseticus* Dyar & Knab, 1909a (western Mexico and California), which were listed as synonyms of *Cx. pipiens pallens* Coquillett, 1898. Only a single nominal species, *Cx. osakaensis* Theobald, 1907 (type locality: Osaka, Honshu Island, Japan), is retained as a synonym of *Cx. pallens*.

Culex (*Culex*) *pruina* Theobald

subspecies ***eschirasi*** Galliard, 1931—original combination: *Culex pruina* var. *eschirasi* (subspecific status by Harbach & Howard 2007). Distribution: Burkina Faso, Cameroon, Central African Republic, Gabon, Côte d'Ivoire, Nigeria, Republic of the Congo, Uganda (Wilkerson *et al*. 2021).

subspecies ***pruina*** Theobald, 1901d—original combination: *Culex pruina*. Distribution: Cameroon, Central African Republic, Côte d'Ivoire, Democratic Republic of the Congo, Gabon, Ghana, Liberia, Nigeria, Republic of the Congo, Sierra Leone, South Sudan, Uganda (Wilkerson *et al*. 2021, but not Sudan, see Simsaa *et al*. 2021).

With the exception of Burkina Faso, subspecies *eschirasi* has been recorded from eight of the 12 countries in which the type form has been recorded. The larvae of the two forms, which are apparently sympatric, exhibit significant differences. The larva of the type form was described by Macfie & Ingram (1916), and their description and illustrations of the head and terminal abdominal segments were utilized by Hopkins (1936, 1952), with little additional information. Galliard (1931) illustrated the terminal abdominal segments of *eschirasi* and noted two major distinctions from the type form. Hopkins (1936, 1952) illustrated a longer siphon for *eschirasi* and reiterated the differences between the two forms noted by Galliard (1931). In the type form, the posterior surface of the siphon between the pecten of either side is covered with microtrichium-like spicules (aculeae) whereas in subspecies *eschirasi* the entire surface of the siphon, except narrowly at the base, is covered with aculeae. Both authors indicate that the integument of the thorax and abdominal segments I–VII and part of VIII bears a dense covering of aculeae. Harbach *et al*. (2017) recorded the presence of thoracic and abdominal aculeae in *Cx. pruina*, but they did not indicate which subspecific form was examined. Other differences noted in the descriptions and illustrations of the two forms include the following: Comb scales evenly fringed in *eschirasi* whereas some scales are only fringed at the apex and on one side in the type form; the siphonal setae (seta 1-S) are about 0.6 the diameter of the siphon in the former and about 0.5 the diameter in the latter; seta 1-X is short and single in *eschirasi* and longer with three branches in the type form; and the anal papillae are equally long in *eschirasi*, slightly longer than the length of the saddle, whereas the dorsal and ventral papillae are unequal and the dorsal pair is slightly shorter than the length of the saddle in the type form. The male genitalia of the typical form were partially described and illustrated by Edwards (1914, 1929b, 1941). The genitalia of *eschirasi* have not been illustrated, but Galliard (1931) noted that they look a little different than those of the type form: "appendices chitineux du tube génital (mésosome) sont profondément divisés en deux" [lateral plates of the genital tube (aedeagus + lateral plates) are deeply split in two]. However, Edwards (1941) stated that he could not find any differences between the genitalia of the two forms. That aside, in view of the morphological distinctions of the larvae and the sympatry of the two forms, it is likely that *eschirasi* is genetically distinct and should therefore be afforded specific status: ***Culex* (*Culex*) *eschirasi* Galliard, 1931**. *Culex eschirasi* is currently listed as a species in the Encyclopedia of Life.

Culex pruina has a single synonym, *Cx. pallidothoracis* Theobald, 1909 (type locality: Obuasi, Ashanti Region, Ghana). Until topotypic larvae of this nominal species are available for examination, *Cx. pallidothoracis* should remain a synonym of *Cx. pruina*.

Culex (*Culex*) *shoae* Hamon & Ovazza

subspecies ***shoae*** Hamon & Ovazza, 1954—original combination: *Culex shoae*. Distribution: Ethiopia (Hamon & Ovazza 1954).

subspecies ***ugandae*** van Someren, 1967—original combination: *Culex* (*Culex*) *shoae ugandae*. Distribution: Kenya, Uganda (van Someren 1967).

The type forms of *Cx. shoae* and subspecies *ugandae* are only known from the original descriptions. The type locality of the typical form is an unspecified locality in the Shewa region (Romanized as Shoa) of central Ethiopia. Shewa lies in the Ethiopian Highlands, with elevations mainly above 1,500 m. The type locality of *ugandae* is Ngogwe, Uganda. Ngogwe is a municipality with an elevation of 1,200 m in the Central Region of the country. Van Someren (1967) indicated that larvae of *ugandae* were also found at Kakamega (elevation 1,535 m) in western Kenya. The immature stages of both forms have been found in the axils of wild banana plants, but larvae of *ugandae* have also been found in the axils of *Colocasia*.

Van Someren noted that although subspecies *ugandae* resembles the type form, all life stages exhibit "small but apparently constant differences". The larva of *ugandae* is readily distinguished from the type form by having head seta 4-C with 2–4 branches, comb scales evenly fringed around the apex, the siphonal pecten with 8–10 spines, each with a coarse proximal denticle, and seta 1-X only slightly longer than the saddle. Seta 4-C is unusually large in the type form, with about 13 branches, the comb scales are unique in having lateral spicules that grade distally into blunt denticles and a blunt apex, the pecten consists of about 14 spines, the proximal spines have 1 or 2 denticles and the distal spines are simple, without denticles, and seta 1-X is 3 times as long as the saddle. Differences in the adult and pupa, which van Someren characterized as "only slight and perhaps unreliable", include the following: In adults of subspecies *ugandae* the femora have small and inconspicuous knee spots (produced as narrow bands in the type form); in females the dark dorsal scaling of the hindfemur reaches the base of the femur (it does not reach the base in the type form); in males the outer division of the lateral plate of the phallosome has 6 denticles (3 in the type form) and seta *d* of the subapical lobe of the gonocoxite is stout and bristle-like (fine and hair-like in the type form); in the pupa seta 10-CT has 3 branches (6 branches in the type form), seta 11-CT is single or bifid (with 3 or 4 branches in the type form) and seta 5-VI is usually bifid but sometimes single (bifid in the type form). Differences in the male genitalia which van Someren did not notice include the differently shaped seta *g* of the subapical lobe (narrowed and slightly pointed distally in *ugandae* and broadly rounded apically in the type form), the ventrocaudal process of the outer division of the lateral plate is broad and somewhat duck-head shaped (narrow and more tooth-like in the type form) and the dorsal process of the outer division is broadly triangular in lateral view (more or less digiform in the type form).

There is a wide gap of much lower terrain between the high elevations of Ethiopia and Uganda/Kenya that include the type localities of the typical form and subspecies *ugandae*, respectively, and that area of lower elevation could be a barrier to gene flow and explain the allopatric separation and morphological distinctions exhibited by the two forms. Because the morphological differences between the adults, larvae and pupae of typical *shoae* and subspecies *ugandae*, coupled with their occurrence in separate geographical areas, provide credible evidence for the recognition of *ugandae* as a separate species, it is hereby formally raised to specific status: ***Culex* (*Culex*) *ugandae* van Someren, 1967**. *Culex ugandae* is currently listed as a species in the Encyclopedia of Life.

Culex (*Culex*) *striatipes* Edwards

subspecies ***joanae*** Muspratt, 1955—original combination: *Culex* (*Culex*) *striatipes* ssp. *joanae*. Distribution: Republic of South Africa (Muspratt 1955).

subspecies ***striatipes*** Edwards, 1941—original combination: *Culex* (*Culex*) *striatipes*. Distribution: Burkina Faso, Democratic Republic of the Congo, Ethiopia, Ivory Coast, Kenya, Madagascar, Zambia, Zimbabwe (Wilkerson *et al*. 2021).

Edwards (1941) described and named *Cx. striatipes* based on three adults collected in Kenya, a male and a female from Nairobi and a male from Mt Elgon. The larva and pupa of the species were described by de Meillon *et al*. (1945) from exuviae, derived from two larvae collected at Livingstone, Zambia (as Northern Rhodesia), which were apparently reared to adults that were presumably used to identify the species. Hopkins (1952) repeated verbatim the description of the larva published by de Meillon *et al*. and included illustrations of the head and terminal abdominal segments which were reconstructed from the two larval exuviae used for the original description. The illustrations included details that were not shown in the drawings provided by de Meillon *et al.* (1945). Muspratt (1955) described subspecies *joanae* from six males and six females, one with an associated larval exuviae. The adults were apparently reared from larvae collected "near the Lydenburg to Sabie road over Mount Anderson" in the former Transvaal Province of South Africa. Muspratt stated that the subspecies differed from the typical form "in having no anterior white stripe on the middle femur and the middle tibia either all dark or with at most a faint anterior pale stripe. The hind femur is pale anteriorly only to about half instead of the usual 4/5. The latter character is probably the most reliable distinction as on some otherwise typical specimens from southern Rhodesia [now Zimbabwe] one or more of the white lines on the anterior side of the front and middle femora, and on the middle tibia, are faint or absent. The type series of ssp *joanae* are rather larger and darker than *striatipes* from southern Rhodesia." He stated that the larva "appears to be practically as the typical form". No further morphotaxonomic work has been published on *striatipes*, but interestingly Jupp (1996), who included the species (without *joanae*) in a key to the adult mosquitoes of South Africa, observed that subspecies *joanae* "is indistinguishable from typical *striatipes* in the larva, and probably also in the ♂ genitalia. Adult ♀'s differ in having no anterior white stripe on the midfemur and midtibia, although midtibia sometimes has very faint stripe. Hindfemur is pale anteriorly only to about 0.5 instead of the usual 0.8." As so few specimens have been historically collected and studied, it is difficult to know the degree of morphological variation that exists in populations of the species between Zimbabwe and South Africa, indeed throughout the range of the species, which is also imperfectly known. For the time being, we consider that there is insufficient evidence to retain *joanae* as a subspecies and hereby formally consign it to synonymy: ***joanae* Muspratt, 1955, junior subjective synonym of *Culex* (*Culex*) *striatipes* Edwards, 1941**. Subspecies *joanae* Muspratt, 1955, which is currently listed as a species in the Encyclopedia of Life, should be removed from the list of recognized species of the genus *Culex*.

Culex (*Culex*) *toroensis* Edwards & Gibbins

subspecies ***macrophyllus*** Edwards & Gibbins, 1939—original combination: *Culex vansomereni* spp. *macrophyllus* (subspecific status by Edwards, 1941 concomitant with the elevation of *toroensis* to specific status). Distribution: Cameroon, Uganda (Knight & Stone 1977).

subspecies ***toroensis*** Edwards & Gibbins, 1939—original combination: *Culex vansomereni toroensis* (specific status by Edwards 1941). Distribution: Burundi, Cameroon, Democratic Republic of the Congo, Ethiopia, Kenya, Malawi, Republic of South Africa, Rwanda, South Sudan, Sudan, Uganda (Wilkerson *et al*. 2021).

The typical form and subspecies *macrophyllus* were originally described as subspecies of *Cx. vansomereni* Edwards, 1926a. Edwards (1941) elevated *toroensis* to specific status based on "well-marked larval distinctions from *C. vansomereni*, together with the constant difference in pleural scaling"; consequently, *macrophyllus* became a subspecies of *Cx. toroensis*. Edwards & Gibbins (1939) and Edwards (1941) distinguished the subspecies based solely on features of the male genitalia. In the typical form, foliform seta *g* of the subapical lobe is about as long as seta *f* and more or less pointed, the lateral plate of the phallosome has about five denticles and the gonostylus is long and markedly narrowed distally. In comparison, seta *g* is much larger than seta *f* in subspecies *macrophyllus*, the lateral plate has a slightly different shape with about three denticles and the gonostylus is distinctly shorter and not narrowed distally. The larva of the typical form is known from specimens reared to adults (Edwards 1941; Service 1959). The larva of subspecies *macrophyllus* is not definitely known, but larvae associated with adults collected at the type locality (Edwards & Gibbins 1939) "bore a close resemblance" to the larva of *Cx. andersoni* Edwards, 1914, which is very distinct from the larva of subspecies *toroensis*. The larva of the typical form has not been studied in detail—only features of the head and terminal abdominal structures have been described, with special emphasis on the anterior (dorsal) and posterior (ventral) clusters of spines near the apex of the siphon. As noted by Service (1959), specimens of *toroensis* from Kenya and Sudan examined in the "British Museum" did not exhibit the arrangement of 18 anterior siphonal spines illustrated by Hopkins (1952), and specimens from elsewhere had 0–9 anterior spines. It should be mentioned, however, that a male from Kisomoro, Uganda, the type locality of *toroensis*, was reared from a "larva similar to that figured by Hopkins [1936]… as sp. indet." (Edwards & Gibbins 1939), and was illustrated by Hopkins (1952) as the larva of *Cx. toroensis*. Both Hopkins and Service noted the variable presence of 0–3 posterior spines. In agreement with Service (1959) and Jupp (1996), the variable number of apical siphonal spines makes it impossible to reliably identify the species, *e.g.* to distinguish larvae from those of *Cx. vansomereni*. On the other hand, we feel that such variation may be an indication of a complex of closely related species.

Oddly, Edwards & Gibbins (1939) described *macrophyllus* (p. 31) prior to describing *toroensis* (p. 32); hence, *macrophyllus* could have been taken as the nominotypical species with *toroensis* as a subspecies of *Cx. macrophyllus*. Mattingly (1956) revealed that *macrophyllus* was described from six males, five with dissected genitalia, and four females collected at "Lugezi Camp between Mt. Mgahinga [Mt Gahinga] and Mt. Sabinio [Mt Sabyinyo]" located at the extreme southwestern fringe of Uganda along the border with Rwanda [actually, Mt Sabyinyo, an extinct volcano, is situated at the intersection of present-day Democratic Republic of the Congo, Rwanda and Uganda, and Mt Gahinga, a dormant/extinct volcano, is on the border between Rwanda and Uganda]. Lugezi Camp was apparently located on the Uganda side of the current border with Rwanda. The two mountains were located in the former Kigezi District, which included flanking areas of the two currently neighboring countries. The former Kigezi District now includes the Kabale, Kanungu, Kisoro and Rukungiri Districts and the two mountains are situated at the margins of the Kisoro District. Edwards (1941) indicated that *macrophyllus* was found at the "Saddle between Mts. Mgadinga and Sabinio, 8000 ft. [2,438 m]", but according to Edwards & Gibbins (1939) Lugezi Camp was located at the side of "Mt. Sabinio" at an elevation of "7–8000 ft. [2,135–2,438 m]". Mattingly (1956) observed that *toroensis* was described from five males, two incomplete and three with dissected genitalia, and one female from Kisomoro, Uganda and nine males and nine females from Kararama Camp in the Namwamba Valley, and designated a male with dissected genitalia from Kisomoro as the name-bearing lectotype. Kisomoro (elevation 1,492 m), situated in the Bunyangabu District in the Western Region of Uganda, is located approximately 240 km north of the type locality of *macrophyllus*. It is interesting that the following statement made by Edwards & Gibbins (1939) regarding *toroensis* was apparently overlooked by later workers: "These specimens [from Kararama Camp, Namwamba Valley] have the male hypopygium [genitalia] almost exactly as in the typical form [*vansomereni*], and do not show the enlarged leaf and other slight peculiarities seen in specimens from Kigezi [*i.e.* Lugezi Camp]." The Namwamba Valley is located approximately 37 km southwest of Kisomoro, indicating that *toroensis* is probably widely distributed in the mountainous regions of western Uganda. In view of the differences in structures of the male genitalia of the two forms, especially the very different gonostylus, the extensive variation observed in the anterior siphonal spines of larvae identified as *toroensis* suggesting that it may be a species complex, the likelihood that the larva of *macrophyllus* is similar to the larva of *Cx. andersoni*, and the probability that *toroensis* and *macrophyllus* are likely to occur in sympatry, we feel confident that the latter form is a separate species and hereby formally accord it specific status: ***Culex* (*Culex*) *macrophyllus* Edwards & Gibbins, 1939**. *Culex macrophyllus* is currently listed as a species in the Encyclopedia of Life.

Culex (*Culex*) *trifilatus* Edwards

subspecies ***aenescens*** Edwards, 1941—original combination: *Culex* (*Culex*) *trifilatus* ssp. *aenescens*. Distribution: Eritrea (Mara 1945), Uganda (Edwards 1941).

subspecies ***trifilatus*** Edwards, 1914—original combination: *Culex trifilatus*. Distribution: Angola, Cameroon, Democratic Republic of the Congo, Ethiopia, Gabon, Guinea, Kenya, Madagascar, Malawi, Mozambique, Republic of the Congo, Republic of South Africa, South Sudan, Sudan, Tanzania, Uganda, Zimbabwe, Zambia (Wilkerson *et al*. 2021).

Culex trifilatus was descried by Edwards (1914) based on adult males and females collected in Kabete, Kenya. In 1941, he described subspecies *aenescens* from adults captured in the Toro District of Uganda. Subspecies *aenescens* was distinguished principally from the type form in having seta *c* of the subapical lobe of the male gonocoxite as long as seta *b* (seta *c* is shorter than *b* in the type form), setae *d* and *e* absent (both present in the type form) and seta *f* very slender (broad and flattened in the type form). However, the illustrations of the genitalia provided by Edwards (1941) clearly indicate that the two laterally bent projections of the lateral plate are more slender, the dorsal one is tapered and pointed, and the dorsal arm is narrower and longer in subspecies *aenescens* (the dorsal projection is broadened apically in the nominate subspecies). The larva of subspecies *aenescens* was described by Hopkins (1952) from many specimens collected in the Toro District. The larva of the nominate subspecies was not known until it was described by Ribeiro *et al*. (1982) based on specimens from Angola (Ribeiro & da Cunha Ramos 1980) and Tanzania (V. N. Danilov). As described by these researchers, larvae of subspecies *aenescens* differ from those of the type form as follows: Seta 5-C with 3 branches (4 or more in the type form); siphonal seta 1-S comprised of 3 pairs of alternating setae with 2–5 branches (with 3–9 branches in the type form); seta 1-X single or double (always single in the type form); dorsal pair of anal papillae 1.5 times as long as the ventral pair, which are about as long as the saddle (dorsal pair 3 times as long as the ventral pair in the type form, but the ventral pair are only about half as long as the saddle).

Ribeiro *et al*. (1982) stated that the two subspecies are allopatric based on then present knowledge of their geographical distributions. This is apparently incorrect as both forms are recorded from localities in Uganda and a footnote in Hopkins (1952) provided by P. F. Mattingly indicates that Mara (1945) recorded the presence of subspecies *aenescens* in Eritrea. Stone *et al*. (1959), and later catalogs, indicate that the type form has been found in Ethiopia and Sudan, but without identifying the sources of those records and whether they are based on adult or larval mosquitoes. Assuming the identifications are correct, it seems likely that the two subspecies occur in sympatry in northeastern areas of the Afrotropical Region.

It is an undeniable fact that most species of Afrotropical *Culex* are incompletely (inadequately) described and illustrated or otherwise only superficially known. As a result of critical revisionary studies, it is known that many currently recognized species of the genus are distinguished by a combination of seemingly minor differences in individual life stages, *e.g.* species of the Oriental Vishnui Group (Sirivanakarn 1976), and some nominal species thought to be conspecific have been found to be distinct species with very similar male genitalia that exhibit distinctive minor differences, *e.g. Cx. bidens* Dyar, 1922 and *Cx. interfor* Dyar, 1928 (Harbach *et al*. 1986). It is well known that male genitalia generally provide a better means for distinguishing species than any other morphological characters, especially members of the genus *Culex*. Evolution of genital form is thought to be involved in the origin of species and the reproductive isolation between species. Thus, the differences in the male genitalia noted above would alone provide *prima facie* evidence of separate species; however, those differences coupled with the larval differences and the probable sympatry of the two forms further strengthens the likelihood that *aenescens* is a valid species. For these reasons, we feel justified in formally recognizing this nominal subspecific taxon as a distinct species: ***Culex* (*Culex*) *aenescens* Edwards, 1941**. *Culex aenescens* is currently listed as a species in the Encyclopedia of Life.

***Culex* (*Culex*) *vansomereni* Edwards**

subspecies ***draconis*** Ingram & de Meillon, 1927—original combination: *Culex draconis* (subspecific status by Edwards 1941). Distribution: Republic of South Africa (Ingram & de Meillon 1927).

subspecies ***elgonicus*** Edwards, 1941—original combination: *Culex vansomereni* ssp. *elgonicus*. Distribution: Ethiopia, Uganda (Wilkerson *et al*. 2021).

subspecies ***vansomereni*** Edwards, 1926a—original combination: *Culex vansomereni*. Distribution: Democratic Republic of the Congo, Ethiopia, Kenya, Liberia, Mozambique, Republic of South Africa, South Sudan [but not Sudan (Simsaa *et al*. 2021)], Tanzania, Uganda, Zimbabwe (Wilkerson *et al*. 2021). The record of Lewis (1956) is from Gilo in South Sudan.

Subspecies *draconis* was originally described as a distinct species (Ingram & de Meillon 1927) and interpreted as a subspecies of *vansomereni* by Edwards (1941). This subspecies differs from the type form in having a pair of submedian yellow stripes on the posterior half of the scutum and sometimes an ill-defined pair of curved lines of yellow scales on the anterior half. In males, the lateral plates of the phallosome are of a slightly different shape with more numerous denticles, and more importantly, the subapical lobe of the gonocoxite is not divided, seta *g* is larger, as long as seta *f,* and seta *h* is noticeably flattened. Based on information provided by Jupp (1996), it seems likely that the two forms occurs in sympatry in South Africa.

Subspecies *elgonicus* was described by Edwards (1941) from a female and two males (with dissected genitalia) collected by G. R. L. Hancock (Mattingly 1956) at high elevation (6,500 ft., about 1,980 m) on Mt Elgon in Uganda. Edwards indicated that *elgonicus* resembles the typical form "in nearly all respects" and distinguished it based on differences observed in the male genitalia, including the phallosome with slightly different lateral plates (with a longer and more incurved ventrolateral process and a larger number of marginal denticles), subapical lobe less distinctly divided, seta *d* present, setae *d* and *e* small and slender, seta *f* broader distally and noticeably separated from setae *d* and *e* and seta *g* larger, broader and as long as seta *f*. Catalogers, beginning with Stone *et al*. (1959), indicate that *elgonicus* has been recorded from Ethiopia without providing the source of the record. If *elgonicus* does in fact occur in Ethiopia, then it is more widely distributed and obviously distinguishable from the type form.

Available evidence suggests that *Cx. vansomereni* is a complex of species. Hopkins (1952) observed that "The larvae of this species vary very considerably, particularly in the degree of sclerotization of the head and siphon, the siphonal index, and the number of comb-scales. Examination of a long series of specimens from Nairobi (the type-locality of the species), South Africa (ssp. *draconis* Ingram and de Meillon), and various localities in Uganda (ssp. *vansomereni*) has shown that though the majority of the specimens from South Africa and of those from high elevations in Uganda (6000–7000 ft.) are of the form with strongly-sclerotized and long siphon, and of those from Nairobi and from low elevations (5000 ft. and below) in Uganda of the form with short, weakly-sclerotized siphon, the differences are not constant; in at least one of the Uganda localities specimens of both forms and also intermediates have been found breeding in the same pool. According to Edwards (1941), larvae of *vansomereni draconis* are separable by their longer siphon (index about 6), the fact that the "coronet" of the subapical spines on the siphon is divided into dorsal and ventral groups, and by the subventral tufts of the siphon being double and scarcely longer than the diameter of the siphon." This statement, however, pertains only to larvae, which have not been studied in detail. When other larval features, *e.g.* branching of the dorsal head setae and anal papillae, topographic and distributional data, with indication of sympatry, and particularly differences in structures of the male genitalia are considered, we conclude that the three described forms are likely to be different species; thus, subspecies *draconis* and *elgonicus* are herewith elevated to specific status: ***Culex* (*Culex*) *draconis* Ingram & de Meillon, 1927** and ***Culex* (*Culex*) *elgonicus* Edwards, 1926a**. Both nominal forms are currently listed as species in the Encyclopedia of Life.

***Culex* (*Culex*) *weschei* Edwards**

subspecies ***gediensis*** Edwards, 1941—original combination: *Culex* (*Culex*) *weschei* ssp. *gediensis*. Distribution: Coastal Kenya (Edwards 1941; van Someren *et al*. 1955).

subspecies ***weschei*** Edwards, 1935—original combination: *Culex weschei*. Distribution: Burkina Faso, Cameroon, Democratic Republic of the Congo, Ghana, Guinea, Madagascar, Mali, Mozambique, Nigeria, Senegal, Seychelles, South Sudan, Sudan, Togo (Wilkerson *et al*. 2021), Zimbabwe (Jupp 1996).

As is the case of most species of *Culex* in the Afrotropical Region, knowledge of the morphology and bionomics of *Cx. weschei* is very scanty. The adult female and male and the fourth-instar larva of the type form are known but they have not been studied in detail. The original description was based on the scaling of the legs and abdomen of adults that distinguished them from the adults of *Cx. guiarti* Blanchard, 1905. Subspecies *gediensis* was described as a form that resembles the type form "closely in colouring and in structure of the ♂ terminalia [genitalia], but differs as follows: antenna of ♀ with only 10 instead of 15 hairs [setae] in each whorl; propleura [antepronota] in both sexes with fewer setae (about 10 in ♂ and about 6 in ♀ instead of about 20 and 15 respectively); sternopleura [mesokatepisterna] with fewer scales" (Edwards 1941). The mesokatepisternal scales are numerous in the type form, with the upper and lower patches nearly joined (Edwards 1941). The larva of *gediensis* is unknown. It is interesting to note that the larva of the type form illustrated as "*Culex* sp.?" by Macfie & Ingram (1916) was recognized as the larva of *Cx. weschei* by Edwards (1941), but it was not described until Hopkins (1952) included it, along with the illustrations of Macfie & Ingram, in his treatise on the larvae of the *Mosquitoes of the Ethiopian Region*.

The type form was originally described from Ghana (as Gold Coast) and has been recorded from a number of countries in sub-Saharan Africa. Subspecies *gediensis* was originally described (Edwards 1935) and subsequently recorded (van Someren *et al*. 1955) from the coastal fringe of Kenya. It has not been found elsewhere and the type form has not been recorded from inland areas of Kenya, and except for South Sudan to the northwest, it has not been recorded from the adjoining countries of Ethiopia (north), Somalia (northeast), Tanzania (south) and Uganda (west). In view of its apparent allopatric coastal distribution and the exceptional differences in the vestiture of the antenna, antepronotum and mesokatepisternum compared to the type form, we conclude that *gediensis* is probably a distinct species and therefore formally afford it specific status: ***Culex* (*Culex*) *gediensis* Edwards, 1941**. *Culex gediensis* is currently listed as a species in the Encyclopedia of Life.

***Culex* (*Culiciomyia*) *nebulosus* Theobald**

subspecies ***nebulosus*** Theobald, 1901d—original combination: *Culex nebulosus*. Distribution: Benin, Burkina Faso, Cameroon, Central African Republic, Comoros, Côte d'Ivoire, Democratic Republic of the Congo, Ethiopia, Gabon, Ghana, Kenya, Liberia, Madagascar, Mali, Niger, Nigeria, Republic of the Congo, Republic of South Africa, Saudi Arabia, Senegal, Sierra Leone, Tanzania, Togo, Uganda, Yemen, Zambia (Wilkerson *et al*. 2021, listed in error from Malaysia).

subspecies ***pseudocinereus*** Theobald, 1901c—original combination: *Culex pseudocinereus* (Stone *et al*. 1959 and Knight & Stone 1977 erroneously attributed subspecific status to Edwards 1941, who actually treated the taxon as a variety; however, as explained by Harbach 2018, *pseudocinereus* is deemed to have subspecific rank). Distribution: Botswana, Democratic Republic of the Congo, Lesotho, Malawi, Namibia, Nigeria, Republic of South Africa, Tanzania, Zimbabwe (Wilkerson *et al*. 2021).

Culiciomyia is a very difficult group taxonomically. Females are generally difficult to distinguish, some are indistinguishable, and the identification of species depends mainly on anatomical features of males and fourth-instar larvae. Nineteen species of the subgenus are currently recognized in the Afrotropical Region (Cornel *et al*. 2020). The adults of both sexes and larvae are known for 12 of the species, albeit inadequately or incompletely described, only males are known for six species and one species is only known from the larval stage. As for most species of the subgenus, the adults and larva of *Cx. nebulosus sensu stricto* and subspecies *pseudocinereus* are known but have not been studied and described in detail. Their identification relies on subtle differences in the extent of scaling on areas of the thorax of adults, the development of the maxillary palpal comb scales of males and the form of the pecten spines and spiracular apodeme of larvae. **Note**. The palpal comb (Cornel *et al*. 2020) is a ventral row of long outstanding hair-like scales (Belkin 1962) on the distal half of palpomere 3 (Edwards 1941).

Cornel *et al*. (2020) quoted Edwards (1941) for the development of the palpal comb scales of the typical form, but their photographic illustration differs slightly from Edwards's line drawing. The palpal comb depicted by Edwards consists of a proximal set of 6 long spear-like scales separated by a small gap from a distal set comprised of 7 smaller, distally broader and apically hooked scales. In contrast, the proximal comb set illustrated by Cornel *et al*. consists of 7 scales of two sizes, a proximal group of 4 distinctly longer scales similar to those illustrated by Edwards and a distal group of 3 shorter, broader, apically pointed scales; a gap separates the proximal set from the distal set, which consists of 8 or 9 scales about the same length as the distal scales of the proximal set but developed as illustrated by Edwards. Variation in the composition of the palpal comb of the type form is further illustrated by Jupp (1996): The proximal comb set consists of 7 scales separated by a gap from the distal set comprised of 8 scales, the scales of both sets are as illustrated by Edwards. In summary, the palpal comb of the type form consists of a proximal set of 6 or 7 lanceolate scales separated by a gap from a distal set of 7–9 distally broadened, apically hooked scales. The palpal comb of subspecies *pseudocinereus* has never been illustrated; however, Edwards (1941) noted that "Scales in distal part of palpal comb slightly different in shape from typical *nebulosus*, being bluntly pointed but without strongly hooked tips." During the course of this study, we had an opportunity to examine the holotype male of *pseudocinereus* and noted that the comb scales gradually grade from large scales proximally to smaller scales distally with little change in shape and no apparent gap or clear delimitation of proximal and distal sets. In addition to differences in the palpal comb scales, Edwards also noted that *pseudocinereus* "Closely resembles typical *nebulosus* but differs in both sexes in having much more numerous flat white scales on the mesepimeron; propleura [proepisternum] with a large patch of scales; lower mesepimeral bristle [seta] often accompanied by from one to three short hairs [small setae] (between it and the scales)." Edwards did not find any differences in the male genitalia of the two forms, but this is likely to be due to inattention to delicate structural detail.

Bram (1967) stated that species of *Culiciomyia* are most reliably distinguished in the larval stage; for this reason, it is surprising that Hopkins (1952) did not treat the larva of *pseudocinereus*, the omission of which may have lead Mattingly & Lips (1953) to consider that larvae of *nebulosus* and *pseudocinereus* were indistinguishable. As is the case with most species of Afrotropical *Culex*, the larva of *nebulosus* is superficially and inadequately described. For this reason, it was only possible for Peters (1955) to compare larvae of *pseudocinereus* with the description of the type form provided by Hopkins (1952). In doing so, Peters was only able to determine that the larva of *pseudocinereus* differs from the type form in the development of the pecten spines and the spiracular apodeme ("stirrup-shaped piece"). The pecten spines of the former have a broad base and a single denticle as opposed to a narrower base and usually at least two denticles in the type form. More striking is the development of the spiracular apodeme, which is much broader with the arms of the U-shaped distal end more widely separated and the narrower arm longer and differently shaped than in *pseudocinereus*. As shown for two species of the subgenus *Culex* in Central America (Strickman 1990), the form of the spiracular apodeme is indicative of different species.

Collection records indicate that *nebulosus sensu stricto* probably occurs throughout sub-Saharan Africa. Discounting records of subspecies *pseudocinereus* in Nigeria and the Democratic Republic of the Congo, it appears that this form is prevalent in southeastern and southern countries of the continent where it is probably sympatric with the type form. This is supported by the occurrence of the adults of both forms in Elizabethville, Belgian Congo (Peters 1955), now known as Lubumbashi in the Democratic Republic of the Congo, which is located in the southeast of the country adjacent to the border with Zambia.

Based on the forgoing analysis of morphological and distributional information, it seems highly likely that *nebulosus* and *pseudocinereus* are separate species; hence, the latter form is herewith formally returned to its original specific status: ***Culex* (*Culiciomyia*) *pseudocinereus* Theobald, 1901c**. *Culex pseudocinereus* is currently listed as a species in the Encyclopedia of Life.

Culex nebulosus has a single synonym, *Cx. nigrochaetae* Theobald, 1901c (♀ only of type series; type locality: Lagos, Nigeria) and *Cx. pseudocinereus* has three synonyms, *Cx. freetownensis* Theobald, 1901c (type locality: Freetown, Sierra Leone), *Cx. invenustus* Theobald, 1901d (type locality: Degama, Rivers State, Nigeria) and *Pectinopalpus fuscus* Theobald, 1909 (type locality: Obuasi, Ashanti Region, Ghana). These four nominal forms are based on superficial descriptions of adults: The type specimens of the first three are females and the type of *fuscus* is a male. Until reared specimens from the type localities of these nominal species are available for critical comparative study, they must remain synonyms of their senior synonyms.

Culex (*Eumelanomyia*) *hayashii* Yamada

subspecies ***hayashii*** Yamada, 1917—original combination: *Culex hayashii*. Distribution: Japan, People's Republic of China, Russia, South Korea, Taiwan (Wilkerson *et al*. 2021).

subspecies ***ryukyuanus*** Tanaka, Mizusawa & Saugstad, 1979—original combination: *Culex* (*Eumelanomyia*) *hayashii ryukyuanus*. Distribution: Japan (Ryukyu Archipelago) (Tanaka *et al*. 1979).

Sirivanakarn (1972), in his revisionary study of the subgenus *Eumelanomyia* in Southeast Asia and adjacent areas, stated that "The adults of *C. hayashii* show a great deal of variation in size, color, texture of scutal scales and in the length of male palpus. The specimens from the Ryukyu Islands differ from the specimens from Japan and Korea in smaller size, darker coloration, finer scutal scales and shorter male pulpus [*sic*]. However, these differences are not correlated with any differentiation in the male terminalia [genitalia], indicating that there is in all probability only one species involved." Tanaka *et al*. (1979) interpreted *ryukyuanus* to be a subspecies distinct from the type form based on the following characteristics: Generally smaller body size, wing with a smaller ratio of the length of cell R_2 to the length of vein R_{2+3}, a slight difference in the ratio of the length of hindtarsomere 1 to the length of the hindtibia (0.98–1.11 as opposed to 0.85–1.03 in the type form), male with shorter maxillary palpus (palpomere 2 shorter than it is in the type form). They stated that the larva of *ryukyuanus* did not appear to be significantly different from *hayashii sensu stricto* on Japan's main island (Honshu).

The Ryukyu Archipelago comprises an arc of 55 islands and islets that extend about 1,000 km southwestward from 40 km south of Kyushu, the southernmost of Japan's main islands, to 100 km east of northern Taiwan. The chain of islands is divided by two large gaps, a northern gap of about 270 km between Yakushima Island and the Amami island group, and a southern gap of about 280 km between the islands of Okinawa and Miyako. The flora and fauna tend to be very different on either side of these gaps, and forms that occur on islands of the Archipelago that have been regarded as subspecies are proving to be genetically distinct (Toma *et al*. 2019; Somboon *et al*. 2020a; Wilkerson *et al*. 2022). For example, Toma *et al*. (2019) clearly showed that *Tripteroides bambusa yaeyamensis* Tanaka, Mizusawa & Saugstad, 1979 in the central and southern regions of the archipelago is molecularly and genetically distinct from *Tp. bambusa* (Yamada, 1917) in the northern Palaearctic region of Japan. Based on the results of their study and similar findings regarding the specific status of *Aedes* (*Hulecoeteomyia*) *yaeyamensis* Tanaka, Mizusawa & Saugstad, 1979 (Somboon *et al*. 2020a; Wilkerson *et al*. 2022), despite the morphological similarity observed by Sirivanakarn (1972) and Tanaka *et al*. (1979), we believe it is likely molecular study will reveal that *ryukyuanus* and *hayashii sensu stricto* are separate species. Therefore, unless genetic evidence proves otherwise, we hereby formally elevate *ryukyuanus* to specific rank: ***Culex* (*Eumelanomyia*) *ryukyuanus* Tanaka, Mizusawa & Saugstad, 1979**. *Culex ryukyuanus* is currently listed as a species in the Encyclopedia of Life.

For comparison, see the analogous treatments of the subspecies of *Toxorhynchites manicatus* (Edwards, 1921a) and *Uranotaenia novobscura* Barraud, 1934 presented below.

Culex (*Eumelanomyia*) *horridus* Edwards

subspecies ***horridus*** Edwards, 1922—original combination: *Culex horridus*. Distribution: Angola, Benin, Burkina Faso, Cameroon, Central African Republic, Comoros, Côte d'Ivoire, Democratic Republic of the Congo, Ghana, Kenya, Liberia, Madagascar, Mali, Mozambique, Nigeria, Republic of the Congo, Republic of South Africa, South Sudan [but not Sudan (Simsaa *et al*. 2021)], Tanzania, Togo, Uganda, Zambia, Zimbabwe (Wilkerson *et al*. 2021).

subspecies ***rageaui*** (Hamon & Rickenbach, 1955)—original combination: *Neoculex horridus* var. *rageaui* (subspecific status by Harbach & Howard 2007). Distribution: Cameroon (Hamon & Rickenbach 1955). These authors considered specimens from Benin and Burkina Faso that they compared with subspecies *rageaui* to be specimens of the nominotypical form (see below); thus, those two countries were erroneously included in the distribution of *rageaui* in the catalogs of Knight & Stone (1977) and Wilkerson *et al*. (2021).

Edwards (1922) proposed *horridus* as a replacement name for *Protomelanoconion fusca* Theobald, 1909, type locality Accra in present-day Ghana, which was preoccupied by *Taeniorhynchus fuscus* Theobald, 1905d, a synonym of *Culex* (*Culiciomyia*) *fragilis* Ludlow, 1903. Unfortunately, Edwards (1922, 1941) only briefly described (with lack of detail) and did not illustrate the male genitalia of *horridus*. Hamon & Rickenbach (1955) examined two series of specimens, one consisting of three males, one from Benin and two from Burkina Faso, and the other consisting of six males from Cameroon. They provided two illustrations of the subapical lobe of the gonocoxite, one drawn from a male from Burkina Faso labelled as *horridus* and the other drawn from the holotype of *rageaui* from Cameroon. The two illustrations are similar except in the former there is only one seemingly flexible simple seta (*d* or *e*) in group *d–f* and the three rod-like setae *a–c* are closely aligned parallel to each other with *c* inserted slightly distal to *a* and *b*. Subspecies *rageaui* has two straight (stiff?) setae (*d* and *e*) in group *d–f* and seta *c* projects at a 90-degree angle from setae *a* and *b*, which is very unusual and could be due to distortion. Except for setae *d* and *e*, the characteristics (shapes) of the other setae (*a–c* and *f–h*) are otherwise the same. Jupp (1996) also illustrated the subapical lobe of *horridus*, but setae *d–g* are very different than those illustrated by Hamon & Rickenbach. Whereas group *d–f* of the males from Burkina Faso and Cameroon consists of one or two simple setae (*d* and *e*) and four blades (*f*) with rounded tips and three or four apical barbs, group *d–f* of the specimen illustrated by Jupp consists of setae *d* and *e* and a single seta *f* with a bifid tip (which Jupp indicated may be an artefact). Whereas seta *g* is distinctly asymmetrical and as long as or slightly longer than seta *f* in the specimens illustrated by Hamon & Rickenbach, it is symmetrical and shorter than seta *f* in the specimen illustrated by Jupp. Obviously the species illustrated by Jupp is not conspecific with the species examined by Hamon & Rickenbach.

Hamon & Rickenbach stated that the genitalia of their two series of specimens are identical, and noted that they differed from Edwards's description of *horridus* as follows: "the three rods (rods or blades) [setae *a–c*] are pointed at their apex, and at least two are curved into a hook; the four strong setae (blunt tipped setae) [seta *f*] are in fact narrow blades, rounded at their apex, and each bearing 3 to 4 subapical barbs; they are accompanied by one or two setae [*d* and *e*] thinner and shorter than themselves; the leaf [seta *g*], apparently unstriated, is very asymmetrical in shape and is accompanied by a strong seta [*h*] as long or longer than it…" (translated from the French). However, whereas the scutal scales are dark brown in the specimens of *horridus* from Benin and Burkina Faso, as described by Edwards for the typical form, the scutum of *rageaui* is "uniformly covered with yellowish-white scales" (translated from the French), whence the characteristic that distinguishes subspecies *rageaui* from the description of the type form provided by Edwards. The nature of the differences, especially the major difference in the color of the scutal scaling, prompted one of us (REH) to examine the syntype males of *Protomelanoconion fusca* Theobald, 1909 (for which Edwards replaced with the name *horridus*) in the Natural History Museum (NHM), London. This resulted in an unexpected discovery. The subapical lobe shown in the two drawings of Hamon & Rickenbach (1955) is very different than the subapical lobe of the syntypes, and also different than the drawing of Jupp (1996). Out of curiosity, drawings of subapical lobes in Edwards (1941) were scanned to see if any of the other species he treated was similar to the syntypes of *fusca* (= *horridus*). Edwards classified most species currently in the subgenera *Eumelanomyia* and *Maillotia* as species of the subgenus *Neoculex*. Astonishingly, the illustration of the subapical lobe he provided for *Cx. salisburiensis* Theobald, 1901c, a species of the subgenus *Maillotia*, agrees with that of *fusca*, particularly the shape of setae *d–f* and the distinctive foliform seta *g* with an elongate stem. Consequently, it seemed necessary to look at other treatments of *salisburiensis*, which resulted in another unexpected discovery. Knight (1953), in his paper on the mosquitoes of Yemen, consulted Peter Mattingly at the British Museum (Natural History) (now the NHM), concerning differences between the male genitalia of specimens they identified as *salisburiensis* and the genitalia of the species illustrated by Edwards (1941). Mattingly responded with the following.

> I am afraid almost all of the differences you noted are due to errors in Edwards' description. The only difference of any significance is that, while the Nairobi males have terminalia [genitalia] identical with the Yemen form, those from further south lack the longest of three accessory bristles [seta *f*] on the subapical lobe and one of the two small setae on the dististyle [gonostylus]. It is clear therefore that we have a northern and a southern form but it is impossible to say which is the type form since I have no males from Salisbury [Harare, Zimbabwe]…. It may be possible eventually to distinguish two subspecies. The southern forms are certainly much darker than yours, especially with respect to the scutal scaling but the Nairobi specimens are intermediate and, I should think, would probably intergrade in Eritrea. Also the two specimens from Chilanga [Zambia] suggest that there is considerable seasonal variation since one, collected in January, is very dark, while the other collected in November, is as pale as the Nairobi form. Edwards' figure for the length of the female palps [maxillary palpi] seems to have been based on a single aberrant or shrunken specimen; and the tergal bands are variable, even in the same locality. The other differences are just errors in description.

It appears that the figure of the subapical lobe that Edwards's attributed to *Cx. salisburiensis* is that of *Cx. horridus* (*i.e. P. fusca*). His descriptions of the genitalia of both species are brief, but the description given for

Cx. horridus and the illustration attributed to *Cx. salisburiensis* clearly correspond with the syntypes of *P. fusca*. Therefore, there is little doubt that the species illustrated by Hamon & Rickenbach, and also Jupp, are not *Cx. horridus* and are separate species. The only problem that remains is the question about the color of the scutal scaling. Hamon & Rickenbach cite Edwards's description of *Cx. horridus*, which says the scutal scales are dark. The scutal scales of the syntypes of *P. fusca* definitely are not dark, but are golden and those on the anterior margin are white. Examination of specimens in the NHM from several East African countries all have golden scutal scales with white scales on the anterior margin. This would suggest an error in the description, or perhaps Edwards's interpretation of dark scutal scaling due the optics and light sources that were available at the time. However, as the genitalia of the males with dark and yellowish white scutal scales are the same, it would seem possible that this is due to seasonal or geographical variation within a single species, or they may be two different closely related species. In any case, the subspecific form described by Hamon & Rickenbach must be considered to be a distinct species, ***Culex* (*Eumelanomyia*) *rageaui* Hamon & Rickenbach, 1955**, and the question of whether or not the form with dark scutal scaling is the same or a different species must await further study. *Culex rageaui* is currently listed as a species in the Encyclopedia of Life.

Culex (*Lophoceraomyia*) *curtipalpis* (Edwards)

subspecies ***curtipalpis*** (Edwards, 1914c)—original combination: *Lophoceratomyia curtipalpis*. Distribution: Cambodia, Indonesia, Malaysia, Singapore, Thailand, Vietnam (Wilkerson *et al*. 2021).

subspecies ***sumatranus*** Brug, 1931—original combination: *Culex* (*Culex*) *sumatranus* (subspecific status by Meng & Chen 1980). Distribution: Cambodia, Indonesia, Macau, People's Republic of China, Vietnam (Wilkerson *et al*. 2021).

Edwards (1914c) described *curtipalpis* from five males collected at Kuching Reservoir in Sarawak, Malaysia. His description did not mention or include an illustration of the male genitalia. Edwards (1928) added some details to his previous description, including a brief description of the genitalia and an illustration of the gonostylus. The larva and pupa were described by Edwards & Given (1928) based on association with reared adults. The male and larva were later described and illustrated in more detail by Colless (1965), Bram (1967) and Sirivanakarn (1977), and the pupa was described by the last author.

Subspecies *sumatranus* was originally described by Brug (1931) as a species of the subgenus *Culex*, described from a single male reared from a larva taken from a pitcher plant in the vicinity of Dermajoe, Benkoelen, Sumatra. Brug illustrated the male genitalia and the head and terminal abdominal segments of the larval exuviae. The species was transferred to the subgenus *Neoculex* by Brug & Edwards (1931), and this was accepted (see Stone *et al*. 1959) until Sirivanakarn (1971) recognized it as a species of the subgenus *Lophoceraomyia*. It was later regarded as a subspecies of *Cx. curtipalpis* by Meng & Chen (1980).

As revealed by Barraud (1934), in a footnote on page 351, and discussed by Sirivanakarn (1977), the larva described and illustrated by Brug (1931) was wrongly associated with the adult male, and adults reared from larvae collected in Hong Kong and elsewhere are identical with the larva of *curtipalpis* described by Edwards & Given (1928). Sirivanakarn treated *sumatranus* as a distinct species, but noted that "All stages of *sumatranus* are exceedingly similar to and indistinguishable from *curtipalpis* except for the male which differs from the latter rather strikingly in the absence of the modified tufts of the male antenna." For clarity, unlike *curtipalpis*, the flagellar whorls of *sumatranus* are weakly verticillate or comprised of relatively fewer long setae and tufts of modified setae/scales are absent on flagellomeres 5–9 or a rudimentary or inconspicuous tuft of four very short setae may be present on the mesal surface of flagellomere 7. Contrary to Sirivanakarn (1977), Meng & Chen (1980) considered this striking difference to be nothing more than interspecific variation.

In view of the poor illustration of the male genitalia of *sumatranus* provided by Brug (1931), we decided it was important to examine the holotype in the Natural History Museum, London. The dissected genitalia of the holotype are poorly mounted on a microscope slide. The left gonocoxite seems to be positioned differently than indicated in Brug's illustration, and the gonostylus, which is tapered to the apex in the illustration, is expanded and strongly modified as illustrated by Colless (1965: fig. 29d), Bram (1967: fig. 22) and Sirivanakarn (1977: fig. 69). The setae of the subapical lobe are inaccurately drawn, but the two setae proximal to setae *a–c* are clearly present. Setae *a–c* are more tapered and pointed than illustrated, and also tapered more distally than illustrated by Colless, Bram and Sirivanakarn for *curtipalpis*. Foliform seta *g* is not shown in the drawing, but it probably was not seen by Brug because it is very faint and difficult to see even under differential interference contrast microscopy, which we used to examine the genitalia. Surprisingly, it is much longer and narrower than seta *g* shown in the illustrations of the genitalia of *curtipalpis* provided by Colless, Bram and Sirivanakarn, which is short and very broad, about as broad as long. It is likely that Sirivanakarn (1977) also did not see seta *g* when he examined the holotype of *sumatranus* (he undoubtedly used traditional bright-field microscopy), otherwise he would have noted this obvious difference in his description of the species. These differences, along with the absence of modified tufts of setae or scales on the antennal flagellum, are a clear indication that *sumatranus* is a species distinct from *curtipalpis*. Based solely on the antennal characteristics, both forms have been found in areas of Cambodia, Indonesia (Sumatra) and Vietnam. Considering this apparent sympatry and the morphological distinctions exhibited by the adult male, we believe *curtipalpis* and *sumatranus* are genetically distinct species and hereby reinstate the latter to its original specific status: ***Culex* (*Lophoceraomyia*) *sumatranus* Brug, 1931**. *Culex sumatranus* is currently listed as a species in the Encyclopedia of Life.

Culex sumatranus has a single synonym, *Cx. gudouensis* Chang, Zhao, Hang & Chen, 1975 (type locality: Xin-hui Shien, Kwangtung Province, People's Republic of China), which was synonymized with *sumatranus* by Meng & Chen (1980). The illustration of the subapical lobe of *Cx. gudouensis* provided by Chang *et al*. (1975) is very poor. There is no indication of seta *g*, but Meng & Chen examined the type specimens and noted the presence of a "broad leaf" that was "ignored in the original description" (translated from the Chinese). This does not clearly indicate, however, whether seta *g* is like that of *Cx. curtipalpis* or *Cx. sumatranus*, but Meng & Chen also noted that a tuft of specialized short setae was present only on the seventh flagellomere of the antenna, and used this as the primary character to support the synonymy of *Cx. gudouensis*. Unless other information becomes available to indicate otherwise, *Cx. gudouensis* should continue to be recognized as junior synonym of *Cx. sumatranus*.

***Culex* (*Maillotia*) *hortensis* Ficalbi**

subspecies ***hortensis*** Ficalbi, 1889—original combination: *Culex hortensis*. Distribution: Afghanistan, Albania, Algeria, Andorra, Armenia, Austria, Azerbaijan, Belgium, Bosnia and Herzegovina, Bulgaria, Crimean Peninsula, Cyprus, Czech Republic, France, FYRO Macedonia, Georgia, Germany, Greece, Hungary, India, Iran, Iraq, Israel, Italy, Kosovo, Lebanon, Liechtenstein, Malta, Morocco, Poland, Portugal (includes Madeira), Romania, Russia, Serbia, Slovakia, Slovenia, Spain, Switzerland, Tajikistan, Tunisia, Turkey, Ukraine (Wilkerson *et al*. 2021).

subspecies ***maderensis*** Mattingly, 1955—original combination: *Culex* (*Neoculex*) *hortensis* ssp. *maderensis*. Distribution: Madeira Islands (Portugal) (Mattingly 1955a; Ribeiro *et al*. 1988).

Culex hortensis, originally described and named from specimens collected at locations in Tuscany, Italy (Ficalbi 1889), is widely distributed in western areas of the Palaearctic Region. Mattingly (1955) described and named subspecies *maderensis* for a population on Madeira Island of Portugal for which the adults have "scarcely any apical banding of the abdominal segments" (Christophers 1929). Mattingly stated "In my opinion, its color very clearly different from that of all the other forms of *C. hortensis* that I have been able to examine, as well as the clear presumption that it is characteristic for a determined geographical area, give me the right to re-describe it as a separate subspecies" (translated from the French). Christophers and Mattingly both noted that the genitalia of the two forms are identical. Schaffner *et al*. (2001) suspected that *maderensis* also occurs in the Canary Islands, but the presence of *hortensis* in the Canaries was confirmed by F. M. Edwards, as indicated in a footnote in Christophers (1929): "Specimens from the Canaries have been very kindly examined by Mr. Edwards who very kindly informs me that the hypopygeal [genitalic] characters are, as I suspected, identical." More recently, Rogozi *et al*. (2012) identified *maderensis* in Albania, presumably based on reduced apical pale banding of the abdominal terga; thus, indicating sympatric variation with regard to this anatomical feature. It seems likely that *Cx. hortensis* was transported to Madeira Island in historical times and has not evolved into a separate species, and is, as suggested by Christophers (1929), nothing more than a "locally less banded variety". Henceforth, unless molecular data show otherwise, which seems unlikely, the nominal subspecies *maderensis* must be formally recognized as a synonymous name: ***maderensis* Mattingly, 1955, junior subjective synonym of *Culex* (*Maillotia*) *hortensis* Ficalbi, 1889**. The nominal *maderensis*, which is listed as a species in the Encyclopedia of Life, must be removed from the list of valid species of *Culex*.

With the synonymy of *maderensis*, *Cx. hortensis* now includes three junior synonyms. The previously recognized synonyms include *Maillotia pilifera* Theobald, 1907 (type locality: Bornand, Haute Savoie, France) and *Cx. lavieri* Larrousse, 1925 (type locality: Algeria). These are undoubtedly conspecific with *Cx. hortensis*.

Culex (*Maillotia*) *salisburiensis* Theobald

subspecies ***capensis*** de Meillon, 1935—original combination: *Culex* (*Neoculex*) *salisburiensis* var. *capensis* (subspecific status by White 1975). Distribution: South Africa (de Meillon 1935).

subspecies ***coursi*** Doucet, 1949—original combination: *Culex coursi* (subspecific status by White 1975). Distribution: Madagascar (Doucet 1949).

subspecies ***salisburiensis*** Theobald, 1901b 1901c—original combination: *Culex salisburiensis*. Distribution: Democratic Republic of the Congo, Kenya, Lesotho, Madagascar, Nigeria, Saudi Arabia, South Africa, South Sudan [but not Sudan (Simsaa *et al*. 2021)], Uganda, Yemen, Zambia, Zimbabwe (Wilkerson *et al*. 2021).

This is another of the many Afrotropical species of *Culex* that have been poorly collected, little studied and are imperfectly known taxonomically. Many nominal species placed in the genus have been reduced to subspecies or synonyms when they were not studied as part of revisionary works. This applies to White (1975), who recognized variety *capensis* de Meillon, 1935 and the species *coursi* Doucet, 1949 as subspecies of *salisburiensis*. The concept of *capensis* is clouded by the loss of the type material, the original description based only on the adult female and its synonymy with *salisburiensis* by Edwards (1941). The issue is further complicated by the description of *Cx. salisburiensis naudeanus* Muspratt, 1961 from Cape Province of South Africa, which includes the type locality of *capensis*. As surmized by White (1975), Muspratt "dismissed the availability of the name *capensis* because of the lack of type-material. He might also have wanted to allow for it being a species distinct from *salisburiensis*, since its identity cannot be completely resolved until further topotypic material is obtained. However, the published description of *capensis* quite supports its inclusion as a form [subspecies] of *salisburiensis*." But how the description supports Mattingly's conclusion is questionable as it only states that *capensis* is similar to *salisburiensis* but is darker and the proboscis is slightly longer than the forefemur. It is interesting to note that de Meillon (1935) questioned the recognition of *capensis* as a mere variety of *salisburiensis*: "Unfortunately, we did not collect any males, so for the present we have given this insect varietal rank only." Unlike *capensis*, Muspratt described *naudeanus* from a series of males and females with associated larval and pupal exuviae and fourth-instar larvae, and found that "This form appears to differ chiefly from *C. salisburiensis* *) in the larval comb and pecten spines… which are quite distinct."—the asterisk and parenthesis refer to a footnote that says "The variety *capensis* De Meill. could not be compared owing to lack of type specimens." As for the male genitalia, Muspratt stated that "no differences [were] found from [the] *salisburiensis* typical form."

Knight (1953) identified a male and two females with associated larval and pupal exuviae collected in Yemen as specimens of *Cx. salisburiensis*, but questioned the identification because of many differences noted between the Yemen adults and the description of *salisburiensis* provided by Edwards (1941). To confirm the identification, Knight sent a full description of the specimens and a drawing of the male genitalia (fig. 2 in Knight 1953) to Peter Mattingly for comparison with specimens of *salisburiensis* deposited in the museum in London known at the time as the British Museum (Natural History). Comparisons were made with specimens from [South] Sudan, Kenya, Zambia (as N. Rhodesia), Zimbabwe (as S. Rhodesia) and many locations in South Africa, including Cape Province. Mattingly responded with the following assessment.

> I am afraid almost all of the differences you noted are due to errors in Edwards' description. The only difference of any significance is that, while the Nairobi males have terminalia [genitalia] identical with the Yemen form, those from further south lack the longest of three accessory bristles [seta *f*] on the subapical lobe and one of the two small setae on the dististyle [gonostylus]. It is clear therefore that we have a northern and a southern form but it is impossible to say which is the type form since I have no males from Salisbury [Harare, Zimbabwe]…. It may be possible eventually to distinguish two subspecies. The southern forms are certainly much darker than yours, especially with respect to the scutal scaling but the Nairobi specimens are intermediate and, I should think, would probably intergrade in Eritrea. Also the two specimens from Chilanga [Zambia] suggest that there is considerable seasonal variation since one, collected in January, is very dark, while the other collected in November, is as pale as the Nairobi form. Edwards' figure for the length of the female palps [maxillary palpi] seems to have been based on a single aberrant or shrunken specimen; and the tergal bands are variable, even in the same locality. The other differences are just errors in description.

As confirmation of the errors in Edwards's description, we note that seta *g* of the subapical lobe of the gonocoxite illustrated by Knight as having "a distinctive angular and serrate margin and with a distinctive median pigmented area" bears no resemblance to the simple leaf illustrated by Edwards (fig. 83a).

Although White (1975) synonymized *naudeanus* with *capensis*, this was apparently unknown to or ignored by Jupp (1996), who treated *naudeanus* as a subspecies of *salisburiensis*. He distinguished the larva of *naudeanus* from the larva of the typical form in a key and an illustration of the terminal abdominal segments, and illustrated the gonocoxite and phallosome of the male genitalia. His study was based on specimens collected in southern Africa that were housed in the former National Institute for Virology and the South African Institute for Medical Research, which were united in the year 2000 to form the South Africa National Institute for Communicable Diseases. The two forms in southern Africa are clearly easily distinguished by the form of the comb scales and pecten spines, as originally noted by Muspratt (1961). Subspecies *naudeanus* differs from the typical form in having mostly spine-like comb scales with saw tooth-like lateral margins and simple curved darkly pigmented pecten spines. In the typical form, the comb scales are evenly fringed and the pecten spines have a row of proximal denticles. It should also be noted that head seta 5-C is about as long and thick as seta 6-C in larvae of *naudeanus*, as opposed to being about half as long and thinner in the type form (Muspratt 1961). A comparison of the drawings of the gonocoxite provided by Knight (1953) and Jupp (1996) indicates that setal group *d–f* of *naudeanus* (= *capensis*) consists of fewer setae and seta *g* has a more globose head and a narrower stem. One can only imagine how many other differences would be found to distinguish *capensis* from the typical form if the adults, larvae and pupae were subjected to a comprehensive comparative anatomical study. Based on the distinctive differences in structures of the larvae and male genitalia, and also because *capensis* and the type form occur in the same geographical areas, we believe that further study will reveal that the former is a genetically separate species; thus, we believe that *capensis* should be formally afforded species status: ***Culex* (*Maillotia*) *capensis* de Meillon, 1935**. *Culex capensis* needs to be added to the list of *Culex* species recognized in the Encyclopedia of Life.

Subspecies *coursi* was described as a full species based on larvae collected at the edge of a rice field on the road between Bejofo and Amparafaravola in the Alaotra-Mangoro Region of Madagascar (Doucet 1949). The adults are unknown. White (1975) dismissed the specific status of *coursi* based on his perception that "the published description differs insufficiently from that of [the] *salisburiensis* type-form to warrant maintaining *coursi* above subspecific rank." We have carefully examined the description (in French, translated into English by Hopkins 1952) and illustrations of *coursi* provided by Doucet and it seems obvious that White completely misjudged the degree of morphological distinction from *salisburiensis*. The larva of *coursi* bears the following exceptional differences from the larva of *salisburiensis*: Dorsomentum differently shaped, resembling an equilateral triangle with six acute lateral teeth (more convex with four or five larger blunter lateral teeth in *salisburiensis*); comb comprised of about 35 rather broad scales with a fringe of rather coarse spicules (about 40–50 narrower scales with an even fringe of slender spicules in *salisburiensis*); siphon relatively short, broad at the base and tapered to the apex, index about 5 (siphon longer, more or less cylindrical, index about 7 in *salisburiensis*); three pairs of seta 1-S, each seta with 2–4 branches and distinctly shorter than the diameter of the siphon (four to six pairs of seta 1-S, each seta with 5–8 branches and distinctly longer that the diameter of the siphon in *salisburiensis*); siphon with two anterolateral setae, each with 2 or 3 branches (siphon with three anterolateral setae, each with 1 or 2 branches in *salisburiensis*); anal papillae about as long as the saddle, dorsal pair about the same length as the ventral pair (anal papillae shorter than the saddle, dorsal pair distinctly shorter than the ventral pair in *salisburiensis*). Based on these striking differences, we agree with Doucet (1949) and Hopkins (1952) that *coursi* is unlikely to be conspecific with *salisburiensis*, which it does not resemble as closely as was perceived by White (1975). Additionally, *coursi* is apparently sympatric with *salisburiensis* in the Lake Alaotra region on the eastern slopes of the central highlands of Madagascar (Doucet 1949; Tantely *et al*. 2016). Obviously, it is necessary for *coursi* to be reinstated to its original status as a distinct species: ***Culex* (*Maillotia*) *coursi* Doucet (1949)**. *Culex coursi* is currently listed as a species in the Encyclopedia of Life.

Two nominal species are recognized as junior synonyms of *Cx. salisburiensis*: *Cx. bostocki* Theobald, 1905c (type locality: Transvaal Province, South Africa) and *Cx. salisburiensis* var. *amboannulatus* Theobald, 1913a (type locality: Hout Bay, Pinelands and Palmiet River, Cape Province, South Africa). These nominal forms are based on descriptions of adult specimens—the type specimen of *bostocki* is a female and the type of *amboannulatus* is a male (genitalia not described or illustrated). In the absence of information about the larvae and male genitalia, it is not possible to know whether the two nominal forms might be conspecific with *Cx. capensis* rather than *Cx. salisburiensis*; consequently, for the time being they should remain as synonyms of the latter species.

***Culex* (*Microculex*) *imitator* Theobald**

subspecies ***imitator*** Theobald, 1903a—original combination: *Culex imitator*. Distribution: Argentina, Brazil, Colombia, Ecuador, French Guiana, Guyana, Honduras, Lesser Antilles (includes Trinidad and Tobago), Mexico, Panama, Suriname, Uruguay, Venezuela (Wilkerson *et al*. 2021).

subspecies ***retrosus*** Lane & Whitman, 1951—original combination: *Culex* (*Microculex*) *imitator retrosus*. Distribution: Brazil (Lane & Whitman 1951).

Despite being included in many taxonomic studies, *Cx. imitator* has only been superficially described, especially the larval and pupal stages. This also applies to subspecies *retrosus*, which has only been described once (Lane & Whitman 1951; summarized by Lane 1953). However, Lane & Whitman provided distinctions, some unmentioned but illustrated, which seem to indicate that *retrosus* is a separate species. The differences include the following. In the male genitalia, ninth tergal lobe (as illustrated) short with relatively weak apical setae only slightly longer than the lobe (lobe elongate with strong apical setae about as long as the lobe in *imitator*); subapical lobe of the gonocoxite (as illustrated) relatively long, setae *a* and *b* equally broad with narrow hooked apices, proximal side of lobe with a row of relatively long setae (lobe shorter, setae *a* and *b* constricted before short somewhat leaf-like apical segment, seta *b* distinctly stouter than seta *a*, proximal side of lobe with a row of relatively short setae in *imitator*); basal hook of the lateral plate of the phallosome strongly curved/sharply bent (slightly curved, not bent in *imitator*). In the larva, based on the "prothoracic hair formula", seta 4-P 3-branched and setae 6,8-P 2-branched (seta 4-P 2-branched and setae 6,8-P single in *imitator*). This, coupled with molecular evidence that *Cx. imitator* is a species complex in Brazil (Demari-Silva *et al*. 2011), based on high intraspecific divergence (3.5%) in the mitochondrial *COI* gene and associated morphological differences in the pupal stage, we believe it is likely that further study will reveal *retrosus* is a separate species. Thus, *retrosus* is hereby elevated to specific status: ***Culex* (*Microculex*) *retrosus* Lane & Whitman, 1961**. *Culex retrosus* is currently listed as a species in the Encyclopedia of Life.

Three nominal species are currently considered to be synonyms of *Cx. imitator*: *Cx. daumasturus* Dyar & Knab, 1906b (type locality: Trinidad and Tobago), *Cx. vector* Dyar & Knab, 1906b (type locality: Trinidad and Tobago) and *Microculex argenteoumbrosus* Theobald, 1907 (type locality: Rio de Janeiro, Brazil). It is possible the first two nominal forms represent a distinct species and the last one may be conspecific with *Cx. retrosus*, but we believe it is prudent to retain them as synonyms of *Cx. imitator* for the time being.

***Culex* (*Microculex*) *inimitabilis* Dyar & Knab**

subspecies ***fuscatus*** Lane & Whitman, 1951—original combination: *Culex* (*Microculex*) *inimitabilis fuscatus*. Distribution: Brazil, State of Rio de Janeiro (Lane & Whitman 1951; Lane 1953).

subspecies ***inimitabilis*** Dyar & Knab, 1906b—original combination: *Culex inimitabilis*. Distribution: Brazil [(Middle Coastal States, São Paulo, Rio de Janeiro, Pará (Lane 1953)], Colombia, Ecuador, French Guiana, Guyana, Lesser Antilles (includes Grenada, Trinidad and Tobago), Panama, Suriname, Venezuela (Wilkerson *et al*. 2021).

The subgenus *Microculex* has not been dealt with since Lane & Whitman (1951) and Lane (1953), and the species are generally very poorly known. *Culex inimitabilis* was described from larvae, apparently lost (Stone & Knight 1957a), that were collected in Trinidad. Howard *et al*. (1915) reproduced the very brief original description of the larva, provided a more detailed description of the larva and described the adult male and female, which established the currently accepted morphological concept of the species. They did not describe the pupa. Dyar (1928) provided a less detailed description of the female, male and larva, but he also did not describe the pupa

Lane & Whitman (1951) established *fuscatus* as a subspecies of *inimitabilis* based on specimens reared from larvae collected in Rio de Janeiro, Brazil. The authors, and also Lane (1953), provided brief descriptions of the female, male, pupa and larva of both forms and distinguished *fuscatus* based on the following differences: Abdominal terga of the adult female without basolateral white spots (present in the type form), siphon 10–12 times longer than the basal width (8–10 times longer in the type form), abdominal terga II–IV of the pupa with somewhat triangular area of dark pigmentation, the broad areas on terga each with a pair of unpigmented spots (dark area of pigmentation on terga III and IV and a pair of unpigmented spots on III in the type form), pupal seta 5-II nearly twice as long as the tergum (slightly shorter than the tergum in the type form). It is interesting that Howard *et al*. (1915) described the siphon of the larva of *inimitabilis* as being about 14 times longer than the basal width, and yet, in agreement with Lane & Whitman, Dyar (1928) indicated that the siphon of the type form is 10 times longer than the basal width, which brings into question the value of the siphon index for distinguishing the two forms. That aside, the differences exhibited by adult females and pupae, coupled with the recorded occurrence of both forms in Rio de Janeiro State, suggests that *fuscatus* and *inimitabilis* are separate species that exist in sympatry. Therefore, until additional observations may prove otherwise, we believe it is prudent to recognize *fuscatus* as a separate species: ***Culex* (*Microculex*) *fuscatus* Lane & Whitman, 1951**. *Culex fuscatus* is currently listed as a species in the Encyclopedia of Life.

***Culex* (*Oculeomyia*) *annulioris* Theobald**

subspecies ***annulioris*** Theobald, 1901a—original combination: *Culex annulioris*. Distribution: Angola, Benin, Burkina Faso, Cameroon, Central African Republic, Côte d'Ivoire, Democratic Republic of the Congo, Ethiopia, Ghana, Guinea, Kenya, Liberia, Madagascar, Malawi, Mali, Nigeria, Republic of the Congo, São Tomé and Príncipe, Senegal, Seychelles, South Africa, South Sudan, Sudan, Tanzania, Uganda, Zimbabwe (Wilkerson *et al*. 2021).

subspecies ***consimilis*** Newstead, 1907 (in Newstead *et al*. 1907)—original combination: *Culex tigripes* var. *consimilis* (subspecific status by Edwards 1941). Distribution: Cameroon, Democratic Republic of the Congo, Gabon, Ghana, Kenya, Liberia, Mozambique, Nigeria, Sierra Leone, South Sudan (Lewis 1956, but not Sudan, see Simsaa *et al*. 2021), Tanzania, Uganda (Wilkerson *et al*. 2021).

Culex annulioris was described from a single female collected in Salisbury, Southern Rhodesia (present-day Harare, Zimbabwe), "distinguished by the abdominal ornamentation, which is very marked and peculiar", "each segment with a triangular basal patch of creamy yellow scales, and with apical lateral patches of yellow scales" (Theobald 1901a).

Subspecies *consimilis*, originally proposed as a variety of *Lutzia tigripes* (de Grandpré & de Charmoy, 1901) and subsequently recognized as a subspecies of *annulioris* by Edwards (1941), was described from females collected at several localities in the Belgium Congo (present-day Democratic Republic of the Congo). The abdomen of the female was described by Newstead (in Newstead *et al*. 1907) as having "narrow basal bands; basal segment with two median black apical spots; sixth and seventh segments with two lateral apical pale spots." As pointed out in a footnote, Edwards (1941) observed that "in the lectotype the slight appearance of banding is merely due to the pale marginal hairs [setae] and not to pale scales." He also noted that "only small apical lateral spots, if any…" were present on segments VI and VII. Oddly, except for Edwards, there is no mention of a lectotype of *consimilis* in the catalogs of Stone *et al*. (1959), Knight & Stone (1977) and Wilkerson *et al*. (2021); however, Townson (1990) indicated the presence of two syntype females in the British Museum (Natural History) (now the Natural History Museum, London), one from Kasongo, Zaire (present day Democratic Republic of the Congo) and the other one with no locality. As confirmation of the lectotype, Hamon & Ovazza (1956) stated that *consimilis* was "described from a female from Kasongo, Belgium Congo," which "differs from the type form by: the absence of basal pale markings on the terga 1–7, the apicolateral pale triangular spots being reduced and not appearing clearly as on segments 6 and 7" (translated from the French).

Edwards (1911b) treated *consimilis* as a species of *Culex*, distinct from *Cx. annulioris*, and recognized *Cx. pseudoannulioris* Theobald, 1909, described from three females captured at Obuasi, Gold Coast (present-day Ghana), as its junior synonym. Theobald recognized *pseudoannulioris* as "A very pronounced, banded proboscis species, coming near *C. annulioris*, Theobald", differing in having the "Abdomen unbanded, deep blackish brown with lateral creamy scales, which to some extent form apical spots above". In addition to *pseudoannulioris*, Edwards (1941) recognized *Cx. annulioris* var. *congolensis* Evans, 1923 and *Cx. bitaeniorhynchus* var. *mayumbae* Galliard, 1931 as synonyms of subspecies *consimilis*. The former was described from two males collected at Leopoldville, Belgian Congo (present-day Kinshasa, Democratic Republic of the Congo), characterized as having the "*abdomen entirely dark scaled above* [*sic*], the median basal and lateral apical white markings characteristic of *annulioris* being entirely absent." The variety *mayumbae* was based on features of the phallosome of males reared from larvae collected in Tchibanga and Mouila, Gabon.

Two other nominal forms, *Cx. annulioris* var. *gambiensis* Theobald, 1903b and *Cx. annulioris* var. *major* Edwards, 1935, are presently considered to be junior synonyms. The former, listed as a synonym of the type form by Edwards (1932a), was described from a single female reared from a larva collected at [Bathurst, renamed Banjul in 1973], Gambia as having the abdomen "like the type, but the triangular basal white spots are very indistinct, but can be detected on each segment by a few white scales". The variety *major*, subsequently raised to subspecific rank by Edwards (1941) and synonymized with subspecies *consimilis* by Hamon & Ovazza (1956), was described from a series of specimens, including the type male, from Nairobi, Kenya, which differed from the type form in being larger and having "abdominal tergites [terga] with distinct basal pale bands which are somewhat widened in the middle; apical lateral pale spots very small or even absent." Although Edwards (1935) mentioned that the male genitalia of *major* were not obviously different from those of the typical form, he later (Edwards 1941) noted that the phallosome differed "slightly from both the typical form and from ssp. *consimilis*." Actually, the lateral plate of *major* is more than slightly different than those of the type form and subspecies *consimilis* (see below). In addition to the specimens from Nairobi, Edwards also identified specimens of *major* from localities in the Democratic Republic of the Congo (as the Belgian Congo) and Uganda.

Based on the examination of type material and specimens from Benin (as Dahomey), Cameroon, Côte d'Ivoire, Ethiopia, Kenya, Republic of Upper Volta (as Haute-Volta) and Senegal, Hamon & Ovazza (1956) concluded "that [in] *Culex annulioris* there are very many variations in colouring which do not correspond at all to variations in the structure of the phallosome, the same structure of the phallosome being able according to the regions to correspond to very dark forms or to very pale forms. The systematic value of the types of *C. annulioris* and *C. annulioris consimilis* is therefore almost zero since they are females. For the sake of simplicity, we propose to continue to call *C. annulioris sensu stricto* the specimens with smooth phallosome [*i.e.* lateral plate, see below] and *C. annulioris* var. *consimilis* those with phallosome bearing numerous and long spicules. Although an almost pure population is generally observed at a given point, there are some forms of passage between the two types of phallosome; given the variations recorded here both in the exterior colouring and in the structure of the phallosome, it does not seem appropriate to continue to regard *C. annulioris major* as a different variety from *C. annulioris consimilis* and we propose to treat it as a synonym [translated from the French]."

Cutting to the chase, we find that the conclusions reached by Hamon & Ovazza (1956) are not convincing because they are based on presumed probability that features of the lateral plates of the male genitalia are not correlated with observed differences in the ornamentation of the adult females, principally the absence or presence and development of pale scaling on the abdominal terga. For the most part, neither the quantity nor quality of material available for study was adequate for resolving the taxonomy of the nominal forms. The study of Hamon & Ovazza was based entirely on adult mosquitoes, and characteristics of the immature stages were not considered. Indeed, the larval and pupal stages for all of the nominal forms are unknown, except the type form, which has not been definitely associated with topotypic material. As communicated by Macfie & Ingram (1923), "The larva of this mosquito [*Cx. annulioris*] has been figured by Edwards [1912d]… and included in his key to the larvae of African CULICIDAE; it is therefore unnecessary for us to do more than mention a few additional characters." As usual, Edwards only illustrated the head (dorsal view) and abdominal segments VIII and X (lateral view). Macfie & Ingram also provided a description of the pupa, based on a single exuviae, and an illustration of the trumpet. The descriptions were based on specimens found in pools at Accra, Ghana. The authors did not indicate how the specimens were identified to species, but they were presumably associated with reared adults that were identifiable as the type form of *Cx. annulioris*. Hopkins (1936, 1952) also described and illustrated the head and terminal abdominal segments of the *annulioris* larva, with notable differences from the illustrations of Edwards (1912d): Antenna slightly curved and slightly more slender distal to seta 1A, with more numerous branches; comb with fewer large spine-like scales; siphon shorter (index about 6.0 as opposed to about 8.4); pecten short, on approximately the basal 0.06 of the siphon (on approximately the basal 0.15 of the siphon illustrated by Edwards).

With regard to the male genitalia, it is disappointing that attention has only been given to the structure of the lateral plate of the phallosome, which, in the case of the nominal taxa considered here, has been referred to inaccurately as the "hypopygium" (Galliard 1931; Edwards 1935), "mesosome" (Galliard 1931) and "phallosome" (Edwards 1941; Hamon & Ovazza 1956). Jupp (1996) correctly referred to it, for the most part, as the "lateral plate of phallosome". More specifically, distinctions between the nominal forms for which the male genitalia are known (*i.e. annulioris*, *consimilis* and *major*) have focused on the curved ventrocaudal surface of the inner division of the lateral plate (the "posterior margin of the inner division" of Edwards 1941). In the type form, that surface of the inner division bears numerous very minute spicules (characterized as "smooth" by Hamon & Ovazza 1956) whereas in *consimilis* and *major* it bears many semi-recumbent thorn-like projections. However, the lateral plate is a complicated structure that exhibits differences in the shape and development of the dorsocaudal angle and its dorsally projecting recurved teeth, differences which seem to have been overlooked but are readily apparent in the illustrations provided by Galliard (1931), Edwards (1941), Hamon & Ovazza (1956) and Jupp (1996). Although the lateral plates of *consimilis* and *major* both have thorn-like projections on the ventrocaudal surface, the contour and development of the surface between the projections and the dorsally projecting teeth is very different, as shown in figures 101f (*major*) and 101g (*consimilis*) of Edwards (1941). As illustrated by Edwards, and also Hamon & Ovazza (1956), in *consimilis* the region of the plate bearing the thorn-like projects is more or less evenly rounded and a distinct group of small dorsally directed denticles is present at the base of the recurved teeth whereas in *major* the region bearing the thorn-like processes is more angular and there are no denticles at the base of the recurved teeth. Surprisingly, none of the illustrations of the lateral plates which Hamon & Ovazza illustrated as those of *consimilis* are similar to the lateral plate of *major* illustrated by Edwards. We anticipate that other differences in structures of the male genitalia, *e.g.* the development of the subapical lobe of the gonocoxite and its specialized setae, will be found that further indicate the existence of a number of closely related species.

In addition to overlooking information about larvae and pupae, Hamon & Ovazza (1956) also failed to consider the descriptions and illustrations of structures of the female genitalia of *annulioris* and *consimilis* (as separate species) provided by Macfie & Ingram (1922). Differences were noted as follows: In *annulioris*, the postgenital lobe (their tenth segment) bears four or five small setae on each side of the ventral surface and the posterior margin is emarginate; the spermathecal capsules are "sub-equal, oval; length 99 μ, breadth 68 μ, the chitinised portion of the ducts very short, about 2 μ." In contrast, the postgenital lobe of *consimilis* "bears about nine small setae on each side on its ventral aspect" and the posterior margin is not emarginate; the spermathecal capsules are larger, "the middle one measured 137 μ in length by 84 μ in breadth, and the chitinised portion of its duct was about 7 μ long, and in the other two spermathecae the corresponding measurements were 129 μ, 80 μ, and 4μ respectively." The authors did not mention how the specimens were identified to species or where they were collected, but the observed differences clearly indicate potential specific distinctions.

A look at the collection records for the type form and subspecies *consimilis* and *major* reveals that the three forms occur in sympatry throughout central (sub-Saharan) and eastern Africa. It is interesting to note that the type localities of all nominal forms currently regarded as junior synonyms are in countries of central and western Africa, far north of the type locality of *annulioris sensu stricto* in Zimbabwe. It is particularly interesting to note that the type locality of *gambiensis*, the sole synonym of the type form, is located more than 6,500 km (by land) from Zimbabwe. Considering the ecological and topographical differences over the very wide distribution of *Cx. annulioris sensu lato*, it is surprising that Hamon & Ovazza found no correlation of the marked variation in the coloration of the adults with geographical distribution. This is very puzzling because such variation is often suggestive of a species complex.

Whereas Hamon & Ovazza (1956) interpreted *Cx. annulioris* as an extremely variable species, we believe that the available morphological and distributional data provide evidence of a species complex. In the absence of a comprehensive study of topotypic material, the nominal forms remain poorly and inadequately known, particularly because the immature stages have never been used to help define them—the complete larval and pupal chaetotaxy has not been studied even for the two currently recognized subspecies. As in the case of several species of the Vishnui Subgroup of the subgenus *Culex*, whose lateral plates are very similar to those of *Cx. annulioris* and which exhibit marked similarities in the adult stage (see Colless 1957 and Sirivanakarn 1976), we anticipate that larvae of reared specimens collected in the type localities are likely to show that *annulioris*, *consimilis* and *major* are clearly differentiated species.

In addition to morphology, bionomical and molecular data are needed to resolve the composition of the Annulioris Complex. For the time being, we believe it is prudent to recognize the following nominal taxa as separate species of the complex: ***Culex* (*Oculeomyia*) *annulioris* Theobald, 1901a**, ***Culex* (*Oculeomyia*) *consimilis* Newstead, 1907** and ***Culex* (*Oculeomyia*) *major* Edwards, 1935**. *Culex consimilis* and *Cx. major* need to be added to the list of *Culex* species recognized in the Encyclopedia of Life. The following nominal forms are provisionally retained as junior synonyms: *Cx. annulioris* var. *gambiensis* Theobald, 1903b (synonym of *Cx. annulioris* Theobald, 1901a); *Cx. pseudoannulioris* Theobald, 1909, *Cx. annulioris* var. *congolensis* Evans, 1923 and *Cx. bitaeniorhynchus* var. *mayumbae* Galliard, 1931 (synonyms of *Cx. consimilis* Newstead, 1907).

Culex (*Oculeomyia*) *aurantapex* Edwards

subspecies ***aurantapex*** Edwards, 1914—original combination: *Culex aurantapex*. Distribution: Democratic Republic of the Congo, Kenya, Madagascar, Mozambique, South Africa, Zambia (Wilkerson *et al*. 2021), also Zimbabwe (Jupp 1996).

subspecies ***ellinorae*** Ovazza, Hamon & Neri, 1956—original combination: *Culex* (*Culex*) *aurantapex* var. *ellinorae* (although originally designated a variety, *ellinorae* is a replacement name for a recognized subspecies (*abyssinicus* van Someren, 1945) and has been recognized as a subspecies of *aurantapex* since Stone *et al*. 1959). Distribution: Ethiopia (Ovazza *et al*. 1956).

subspecies ***jinjaensis*** Edwards**,** 1941—original combination: *Culex* (*Culex*) *aurantapex* var. *jinjaensis* (subspecific status by Harbach & Howard 2007). Distribution: Uganda, Zambia (Wilkerson *et al*. 2021).

Culex aurantapex was described from a single female collected in Nairobi, Kenya (Edwards 1914), a black species with distinctive abdominal scaling—"segments 2–4 black-scaled (dorsally), with a few scattered orange scales; segments 5–8 almost entirely orange-scaled both above and below [terga and sterna]." Edwards (1941) described *jinjaensis* (as a variety) from a series of seven males and seven females from Jinja, Uganda and a male from Kampala (Mattingly 1956), characterized as being blacker than the type form with "the abdomen lacking the conspicuous orange tip; tergites 5–8 [terga V–VIII] in both sexes with apical lateral yellow patches, which tend to unite to form rather irregular lateral yellow stripes on distal half of abdomen." Jinja is located on the shore of Lake Victoria in southern Uganda. Edwards stated that the male genitalia of *jinjaensis* differ "little if at all from those of the typical form", the genitalia of which Edwards described from specimens collected in Nairobi.

Subspecies *ellinorae*, described by van Someren (1945), under the preoccupied name of *abyssinicus*, from females collected at Sciasciamanna and Lake Awasa in present-day Ethiopia that differ "from the type form by having more extensive orange markings on the abdominal tergites [terga]"—"2 with narrow black lateral borders and 2 large triangular orange spots the bases of which usually meet on the apical border of the segment to form a narrow orange band; 3 sometimes like 2 and sometimes the same as 4 which is mainly orange with narrow black lateral borders and 2 small median black triangles; 5 orange with narrow black lateral borders; 6–8 all orange. The black markings have a few scattered orange scales. Sternites 6–8 [sterna VI–VIII] all orange; 5 black with a few scattered orange scales and a narrow orange apical band; remainder black with scattered orange scales."

Culex aurantapex is very poorly known morphologically and taxonomically. The larva of the type form and that of subspecies *jinjaensis* are both only known from a single exuviae from their type localities (Hopkins 1952). Hopkins did not describe or illustrate these larvae because he was unable to find any differences between the exuviae and the larva of *Cx. annulioris* (see above). The pupa was described by Ingram & de Meillon (1927), which was apparently (not explicitly stated) identified from adults reared from larvae collected from a large swamp east of forest at Empangeni KwaZulu-Natal (as Zululand), South Africa. Edwards (1941) acknowledged the description but pointed out that "confirmation of the identity of this is desirable, but the paedotype pelt [exuviae] from Nairobi is similar in most respects." Obviously, the immature stages of the nominal forms are essentially unknown.

It is unfortunate that the male genitalia of the nominal forms have not been fully described and illustrated, and the immature stages have not been unequivocally associated with the type form. Because the variation observed in adults is suggestive of a species complex, with respect for the intuitive interpretation of morphological observations of the authors of the nominal forms, we are compelled to regard them as separate species pending morphological and molecular confirmation: ***Culex*** **(*Oculeomyia*) *ellinorae* Ovazza, Hamon & Neri, 1956** and ***Culex*** **(*Oculeomyia*) *jinjaensis* Edwards, 1941**. *Culex ellinorae* and *Cx. jinjaensis* are both currently listed as species in the Encyclopedia of Life.

Culiseta (*Culicella*) *ochroptera* (Peus)

subspecies ***amurensis*** Maslov, 1964—original combination: *Culiseta silvestris amurensis* (status as subspecies of *ochroptera* by Berlov & Kuberskaya 2023). Distribution: Central Amur region, Ussuri Basin, Southern Maritime Province, Northeast China (Maslov 1964); Primorye (Primorsky Krai, far East Region), Russia (Maslov 1964).

subspecies ***minnesotae*** Barr, 1957—original combination: *Culiseta minnesotae* (status as subspecies of *ochroptera* by Berlov & Kuberskaya 2023). Distribution: Canada, United States (Alaska, continental) (Wilkerson *et al*. 2021).

subspecies ***nipponica*** La Casse & Yamaguti, 1950—original combination: *Culiseta* (*Culicella*) *nipponica* (status as subspecies of *ochroptera* by Berlov & Kuberskaya 2023). Distribution: Japan, South Korea (Wilkerson *et al*. 2021).

subspecies ***ochroptera*** (Peus, 1935)—original combination: *Theobaldia* (*Culicella*) *ochroptera*. Distribution: Belarus, Belgium, Czech Republic, Estonia, Finland, Germany, Hungary, Lithuania, Netherlands, People's Republic of China, Poland, Romania, Russia, Slovakia, Sweden, Ukraine (Wilkerson *et al*. 2021).

Soon after submission of this monograph for review, Berlov & Kuberskaya (2023) published a paper titled "Additions and corrections to the catalog of blood-sucking mosquitoes of the world (Insecta: Diptera, Culicidae) by Wilkerson *et al.* (2021)" [verbatim translation from the Russian]. The authors inferred that *Culiseta amurensis* Maslov, 1964, *Cs*. *minnesotae* Barr, 1957, *Cs*. *nipponica* LaCasse & Yamaguti, 1950 and *Cs*. *ochroptera* (Peus, 1935) were incorrectly listed in the catalog as valid species. They pointed out that Maslov (1964, 1967, 1989) classified them as subspecies of *Cs. silvestris* Shingarev, 1928. However, because *Cs. silvestris* has been treated as a doubtful species since Dahl & White (1978) listed it, without explanation, as a *nomen dubium* in a footnote to a table of European mosquito species, Berlov & Kuberskaya proposed that *amurensis*, *minnesotae* and *nipponica* should be recognized as subspecies of *ochroptera*, the oldest of the four nominal taxa. To gain a better understanding of this taxonomic conundrum, we examined Maslov's (1964) treatment of *Cs. silvestris*. The reasoning behind his recognition of *Cs. silvestris* and its purported subspecies is revealed in the following passages (translated from the Russian).

> …*C. silvestris* Sching. – was described very unsuccessfully, too fragmentary and general, so much so that it was difficult to extract anything significant from the description (Shingarev, 1928). Not surprisingly, Peus (1935) later described the same species under the name *C. ochroptera* Peus. It is under this name that he [Peus] now appears in the literature. Unfortunately, the holotype and allotype of *C. silvestris* have not been preserved, but in the year of description (1928) N. I. Shingarev [the author of *silvestris*] gave me one male, one female, and them as paratypes. Later from the Moscow region, in the area where *C. silvestris* was first found, I also managed to obtain larvae of this species. Thus, at present, it seems to me necessary in the revision of the Eurasian representatives of the subgenus *Culicella* to establish the following taxonomic divisions: the species name *C. silvestris* with three subspecies[1] *C. silvestris silvestris* Sching. – Eastern Europe, the Urals, Western Siberia; *C. silvestris ochroptera* Peus – Central Europe and the Baltics; *C. silvestris amurensis* Masl. (subsp. n.) (Maslov, 1949, 1963) – the extreme east of the species range – Piamurye and Primorye. Below is a redescription of the species with a differential diagnosis of all subspecies and a description of *C. silvestris amurensis*, subsp. n.
>
> [1] It is possible that when analyzing more extensive European material, the first two forms [*silvestris sensu stricto* and *ochroptera*] will turn out to be one and the same subtype.
>
> In Japan, another species was described (La Casse a. Yamaguti, 1950), assigned by the authors to the subgenus *Culicella*, *C. nipponica*. Unfortunately, adult females and males of this species remain unknown; as for the larva of the 4th stage, then differentiating *C. nipponica* from *C. silvestris amurensis* n. is not possible (Maslov, 1963). It is probable that there are not two species here, even sub-indigenous, but one form, and then the Far Eastern *C. silvestris amurensis* n. would prove to be synonymous with Japanese *C. nipponica*, which would need to be considered as a subspecies, *C. silvestris nipponica*. However, at the present time, due to the lack of descriptions of the male and female already indicated, both forms have to be preserved.
>
> Recently, another species of *Culicella* – *C. minnesotae* Barr, was described in the USA (Barr, 1957, 1959; Price, 1958). Among the mosquitoes I received from the USA (Wisconsin) from prof. R. Matheson, turned out to be one male matching the description (Barr, 1957), especially in the structure of the phallus. Comparison of American *C. minnesotae* with other representatives of the subgenus *Culicella* confirmed significant differences in all developmental stages from *C. morsitans morsitans* and *C. morsitans dyari*. However, an amazing similarity between *C. minnesotae* and *C. silvestris* mosquitoes was unexpectedly revealed: the most characteristic imaginal signs of one (spotted wing, the presence of not only basal but also apical bands on the abdominal tergites [terga], etc.) coincided with those of the other. Of particular interest was the similarity in the structure of the phallus [genitalia] of *C. minnesotae* and *C. silvestris silvestris* (Fig. 9, A, B). A comparison of the larval morphological structures also does not support the species independence of *C. minnesotae* Barr. The same is shown by the details of pupal chaetotaxy (Maslov, 1963). Thus, *C. minnesotae* should not be considered as an independent species, but only as a subspecies – *C. silvestris minnesotae* Barr.

Following the above, Maslov (1964) distinguished the females, males and fourth-instar larvae of subspecies *amurensis*, *minnesotae*, *ochroptera* and *silvestris* in separate keys, accompanied by descriptions of *silvestris sensu lato* and the new subspecies *amurensis*. Maslov (1967, 1989) incorporated the keys into keys for distinguishing the females, males and fourth-instar larvae of all known species of *Culiseta* and provided descriptions for *silvestris sensu stricto* and each of the four subspecies.

Because Maslov (1964) had examined paratypes and topotypic specimens of *silvestris*, and recognized *ochroptera* as the same species, we were inclined to consider *ochroptera* as a synonym of *silvestris* until we noticed that Gutsevich *et al*. (1971, 1974) justified the retention of *ochroptera*: "A. V. Maslov (1964) considered *C. ochroptera* as a synonym of *C. silvestris* Shingarev, 1928, but to judge from Shingarev's incomplete description, 'it is certain that the two species are not identical' (Shtakel'berg, 1937 [Stackelberg 1937]). The holotype of *C. silvestris* is lost and Maslov examined only paratypes. Because of the incomplete original description of *C. silvestris*, it seems advisable to retain the name *C. ochroptera* [translated from the Russian]." It is important to note here that Stackelberg (1937) treated *ochroptera* and *silvestris* as separate species (of *Theobaldia* Neveu-Lemaire, 1902) [the map in Maslov (1967, 1989: fig. 82) indicates they may have allopatric distributions], and distinguished them in a key for the identification of males. It seems likely that Dhal & White (1978) listed *silvestris* as a *nomen dubium* based on the explanatory note and recommendation proffered by Gutsevich *et al*. (1971, 1974). Until the identity of *silvestris* is resolved, we concur with Dahl & White that it should remain a *nomen dubium*.

Wood *et al*. (1979) provided a cogent summary of the *silvestris-ochroptera* conundrum and decided to continue to recognize *minnesotae* as a separate species "Until Russian workers concur in choosing between *ochroptera* and *silvestris*". We agree with this rationale and reaffirm the specific rank of *minnesotae* established by Wood *et al*. (1979), and accepted by later workers (*e.g.* Darsie & Ward 1981, 2005; Belton 1983; Harrison *et al*. 2016): ***Culiseta* (*Culicella*) *minnesotae* Barr, 1957**. *Culiseta minnesotae* is currently listed as a species in the Encyclopedia of Life.

Berlov & Kuberskaya (2023) incorrectly asserted that Maslov (1967, 1989) had considered *nipponica* to be a subspecies of *silvestris*. All prior authors (Maslov (1964, 1967, 1989; Gutsevich *et al*. 1971, 1974; Tanaka *et al*. 1979; Lu *et al*. 1997) recognized *nipponica* as a distinct species. As there is no justification or precedence for treating *nipponica* as a subspecies, the specific rank of this nominal species must be retained: ***Culiseta* (*Culicella*) *nipponica* La Casse & Yamaguti, 1950**, as listed in the Encyclopedia of Life.

We have not been able to find a source for the recognition of *amurensis* as a species; consequently, its listing as a species by Harbach (2018) was apparently in error; it should have been listed as a subspecies of *ochroptera*. The error was repeated in Wilkerson *et al*. (2021). Although *amurensis* is recorded from the extreme northeast of China (Knight & Stone 1977; Wilkerson *et al*. 2021), it is not treated or even mentioned by Lu *et al*. (1997) in their monograph on the culicine mosquitoes of China (however, they do recognize and describe *Cs. nipponica*). As noted above, Maslov (1964) thought it "probable" that *amurensis* was the same as *nipponica*, in which case the apparent morphological similarity of the two nominal forms may explain why Lu *et al*. only recognized the presence of *nipponica* in China. In agreement with Maslov (1964), we also believe *amurensis* is likely to be synonymous with *nipponica*; hence, until proven otherwise, it is herewith consigned to synonymy: ***amurensis* Maslov, 1964, junior subjective synonym of *Culiseta* (*Culicella*) *ochroptera* (Peus, 1935)**. The nominal subspecies *amurensis*, which is listed as a species in the Encyclopedia of Life, must be removed from the list of valid species of *Culiseta*.

Culiseta (*Culiseta*) *alaskaensis* (Ludlow)

subspecies ***alaskaensis*** (Ludlow, 1906)—original combination: *Theobaldia alaskaensis*. Distribution: Armenia, Austria, Belarus, Canada, Crimean Peninsula, Czech Republic, Denmark, Estonia, Finland, France, Georgia, Germany, Hungary, Iran, Ireland, Latvia, Lithuania, Moldova, Mongolia, Netherlands, Norway, Poland, Romania, Russia, Slovakia, Slovenia, Sweden, Switzerland, Turkey, Ukraine, United Kingdom, United States (Wilkerson *et al*. 2021).

subspecies ***indica*** (Edwards, 1920)—original combination: *Theobaldia indica* (subspecific status by Maslov 1964). Distribution: Armenia, Azerbaijan, Georgia, India, Kazakhstan, Kyrgyzstan, Pakistan, Russia, Tajikistan, Turkmenistan, Ukraine, Uzbekistan (Wilkerson *et al*. 2021).

Culiseta alaskaensis was described from five females and one male collected at Fort Egbert, Alaska (Ludlow 1906). According to published works, *Cs. alaskaensis sensu stricto* is a Holarctic species. In the Nearctic Region, it is found in western North America from Colorado to Alaska and across Canada to Newfoundland. In the Palaearctic Region, it occurs in northern Europe southward to the northern slopes of the Alps and eastward to the far east of Siberia. Subspecies *indica* was originally described as a species based on specimens collected in the hilly and mountainous areas of Haryana State (Ambala) and Himachal Pradesh State (Bakloh and Dalhousie) in the far north of India (Edwards 1920) and was reclassified as a subspecies of *alaskaensis* by Maslov (1964). Both subspecies are recorded from localities in Armenia, Georgia, Russia and Ukraine. If the identifications are correct, it would appear that the distributions of the two forms overlap, indicating that they may occur in sympatry. However, those countries lie far north of the type locality of *indica*, which is located on the south side of the Himalaya Mountains, and they are thus likely to be based on misidentified specimens of the typical form. This agrees with the allopatric distributions of the two forms depicted by Maslov (1967, 1989: map, fig. 60). According to Maslov, individuals of the typical form are "Mostly forest mosquitoes found as frequently in the hills as in the plains" whereas individuals of *indica* "are mosquitoes of the plains in forest-free regions". Wood *et al*. (1979) confirmed that the type form "is widely distributed in the boreal forest across northern Europe, the USSR, and northern Canada."

Maslov (1967, 1989) and Gutsevich *et al*. (1971, 1974) distinguished the two subspecies as follows. *Culiseta alaskaensis sensu stricto* is a dark mosquito, integument and scales dark brown or black; dark and pale scaling of tarsi and abdominal terga in strong contrast; wing entirely dark-scaled or with few pale scales on anterior veins, clusters of dark scales distinct; posterior half of abdominal terga entirely dark-scaled. In general, *indica* is a paler mosquito, integument light brown or ochreous brown, scutum covered with golden-yellowish scales; dark and pale scales of tarsi and abdominal terga not well contrasted; most veins of wing with scattered pale scales, clusters of dark scales indistinct; posterior half of abdominal terga with few scattered pale scales. Maslov (1967, 1989) is the only researcher to distinguish the male genitalia and larvae of the two forms. In the type form, 2 large setae on basal mesal lobe of gonocoxite bent in distal one-third; larva with seta 4-C (postclypeal) 3-branched, very rarely with 4 branches; head and siphon very dark, often almost black. In *indica*, 2 large setae of basal mesal lobe of gonocoxite bent just beyond mid-length; larval seta 4-C with 3–7 (usually 5 or 6) branches; head and siphon light brown, sometimes yellowish brown.

Qutubuddin (1952) purportedly described and illustrated the larva of *indica* from Pakistan. Although he received comments on his manuscript from Peter Mattingly in London, there is no doubt the larva he described is that of an undescribed species of the subgenus *Allotheobaldia* Brolemann, 1919. The larva is very similar to the larva of *Cs. longiareolata* (Macquart, 1838), the only currently recognized species of the subgenus, but it bears some distinct differences. The following characteristics place the larva in *Allotheobaldia*: Antenna short, seta 1-A weakly developed; siphon short and stout, not sclerotized at base, siphon index 1.5, pecten comprised of simple spines (one bifid spine is illustrated), setae 1a-S and 2a-S absent; saddle incomplete ventrally, covering dorsal half of segment X; seta 2-X multi-branched, seta 3-X double; ventral brush (seta 4-X) extended anteriorly on ventral midline of segment, with about 9 pairs of setae. The larva was described from exuviae associated with three reared females. Unlike larvae of *alaskaensis*, the exuviae examined by Qutubuddin were those of larvae collected "from foul-smelling water in an unused masonry well". "Several adults were, later on, taken from the same place." It seems that the adults were misidentified and Peter Mattingly, if he saw the illustrations, did not notice that the larva could not be the larva of *indica*, which does "not differ [substantially] from those of the nominate subspecies" (Gutsevich *et al*. 1971, 1974). The larva illustrated by Qutubuddin (1952) differs distinctly from the larva of *Cs. longiareolata* (based on the description of Hopkins 1952) in having setae 5- and 6-C with multiple branches (single in *longiareolata*), 5-C more or less pectinate with branches arising from a short stout stem; dorsomentum shorter, less acute distally (a straight-sided triangle in *longiareolata*); some comb scales distinctly asymmetrical (spicules on one side) (evenly fringed in *longiareolata*); siphon shorter (index about 2 in *longiareolata*); pecten comprised of 5–7 spines born entirely on the siphon (pecten with 3 or 4 small spines proximal to the base of the siphon and about 9 on the siphon in *longiareolata*). In contrast, as described and illustrated by Carpenter & LaCasse (1955), Maslov (1967, 1989), Gutsevich *et al*. (1971, 1974), Wood *et al*. (1979) and Becker *et al.* (2020), the larva of *alaskaensis* bears the following comparable traits: Setae 5- and 6-C fan-like with multiple aciculate branches; dorsomentum short, edges not exactly straight; comb scales elongate and evenly fringed; siphon longer, index 2.5–3.5; pecten comprised of numerous short spines on proximal 0.2 followed by a row of 16–18 filamentous spines extending to about distal 0.25 of the siphon.

Two nominal species, *Theobaldia arctica* Edwards, 1920 and *Culiseta siberiensis* Ludlow, 1920, are currently recognized as synonyms of the nominotypical subspecies, and the nominal *Theobaldia wassilievi* Shingarev, 1927 is a synonym of subspecies *indica*. *Theobaldia arctica* was described from a single male collected at Arkhangel (English for Arkhangelsk), located far north of Moscow on the Northern Dvina River where it empties into the White Sea, and *Cs. siberiensis* was described from 24 females collected at three places, including Verkhne-Udinsk (former name of present-day Ulan-Ude), located southeast of Lake Baikal in south-central Siberia. The type localities of both nominal forms reside within the distribution of *alaskaensis sensu stricto* (Maslov 1967, 1989), and both have been listed as synonyms of the type form since Edwards (1921d). In fact, when Edwards (1920) described *arctica*, he stated that "In coloration and genital structure this insect agrees almost entirely with *T. alaskaensis*, Ludlow, and may in fact be the same."

Theobaldia wassilievi was recognized as a distinct species until Martini (1930) treated it as a variety of *alaskaensis* and Stackelberg (1937) later treated it as a subspecies. Contrary to Knight & Stone (1977), Harbach (2018) and Wilkerson *et al*. (2021), *wassilievi* was placed in synonymy with *indica* (when it was still recognized as a species) by Edwards (1932a), not by Maslov (1967, 1989). *Theobaldia wassilievi* was originally described as a species from Turkestan, a city in the Kazakh Desert in the southernmost region of Kazakhstan. Turkestan lies at the northern limit of the distribution of *indica* mapped by Maslov (1967, 1989). *Theobaldia wassilievi* should therefore remain a synonym of *indica*.

Based on the available morphological, ecological and distributional information, it seems prudent to recognize *indica* as a separate species: ***Culiseta* (*Culiseta*) *indica* (Edwards, 1920)**. *Culiseta indica* is currently listed as a species in the Encyclopedia of Life. Based on the wide distribution of *Cx. alaskaensis*, we think it is likely that molecular data will show it is a complex of species.

***Culiseta* (*Neotheobaldia*) *frenchii* (Theobald)**

subspecies ***atritarsalis*** (Dobrotworsky, 1954)—original combination: *Theobaldia frenchi* [*sic*] *atritarsalis*. Distribution: Australia (Victoria) (Lee *et al*. 1988a).

subspecies ***frenchii*** (Theobald, 1901c)—original combination: *Culex frenchii*. Distribution: Australia (South Gippsland, Victoria) (Lee *et al*. 1988a).

It is surprising that *Cs. frenchii* has received comparatively little taxonomic attention. According to Dobrotworsky (1965) and Lee *et al*. (1988a), this species is only known with certainty from Victoria State of Australia—the Eastern Highlands (Great Dividing Range or Great Divide) and Gippsland (a region in the southeast), with the northwestern limit of its distribution being roughly defined by the isohyet of 100 cm of annual rainfall. Ironically, subspecies *atritarsalis* is only known from the highlands of South Gippsland (Lee *et al*. 1988a), a region of rolling hills extending from Latrobe Valley in the north to the southernmost point of Victoria State. Larvae of the type form are found in the tunnels of terrestrial crayfish. In the absence of specific information, larvae of subspecies *atritarsalis* presumably occupy the same habitat (Lee *et al*. 1988a).

When Dobrotworsky (1954) described subspecies *atritarsalis*, he stated that the male genitalia, pupa, larva and eggs are identical with those of the type form. This was reiterated by Dobrotworsky (1965), and Maslov (1967, 1989) also noted that "The distribution and ecology of these two subspecies are identical." In his original description of *frenchii*, based on adult females, Theobald (1901c) provided illustrations of the head and wing. Edwards (1926a) described the male, but did so without illustrations. The male genitalia were later illustrated by Dobrotworsky (1954, 1965) and Maslov (1967, 1989), and the head and terminal abdominal segments of the larva were illustrated by Dobrotworsky (1965). The descriptions associated with the illustrations indicate the male genitalia and larvae were not studied in detail and were only superficially examined. None of the life stages of subspecies *atritarsalis* have been illustrated, and the immature stages have not been fully described for either subspecies.

Dobrotworsky (1954) briefly described the adults of subspecies *atritarsalis* as follows: "This subspecies is clearly distinguished from the type by its general darker colour; the thorax is brown, the proboscis, the palps [maxillary palpi] and the legs are clothed with almost black scales; the legs also are dark apically [in the type form "the last three segments of the tarsi are pale"]. The male palpi are even more hairy than those of the type, and the shaft apically has about thirty long hairs." Maslov (1967, 1989) more succinctly stated that the "two subspecies differ in the following way: in the former [type form], the first 3 distal tarsal segments of all legs are completely light while, in the later [*atritarsalis*], the tarsi are entirely dark." In the absence of detailed comparative anatomical data for all life stages of the two nominal forms, the entirely dark-scaled tarsi of *atritarsalis*, as opposed to the pale-scaled distal three tarsomeres of the type form, is sufficiently diagnostic to warrant recognition of the two forms as distinct, separate, seemingly sympatric species. Consequently, *atritarsalis* is hereby formally elevated to the rank of species: ***Culiseta* (*Neotheobaldia*) *atritarsalis* (Dobrotworsky, 1954)**. *Culiseta atritarsalis* is currently listed as a species in the Encyclopedia of Life.

Eretmapodites silvestris Ingram & de Meillon

subspecies ***conchobius*** Edwards, 1941—original combination*:* *Eretmapodites silvestris* ssp. *conchobius*. Distribution: Ethiopia, Kenya, Nigeria (Wilkerson *et al*. 2021, excluding South Sudan and Sudan).

subspecies ***silvestris*** Ingram & de Meillon, 1927—original combination: *Eretmapodites plioleucus*. Distribution: Ethiopia, Kenya, Nigeria, Republic of South Africa, South Sudan, Tanzania (Wilkerson *et al*. 2021, excluding Sudan).

Eretmapodites has never been the subject of a thorough revisionary study. The genus currently includes 49 formally recognized species (Harbach 2022b), many of which are poorly known (Service 1990). The species treated here, and the one that follows, are the only two species of the genus for which subspecies are recognized.

All species of the genus are characterized principally on diagnostic features of the male genitalia. The females are known for 24 species, larvae for 19 species and pupae for 17 species (Service 1990; Wilkerson *et al*. 2021). The majority of species are incompletely described and some known life stages have not been illustrated, or only partially.

Eretmapodites silvestris is a member of the Plioleucus Group (Rickenbach & Eouzan 1970), which includes six other species: *brevis* Edwards, 1941, *ferrarai* Rickenbach & Eouzan, 1970, *germaini* Rickenbach & Eouzan, 1970, *lacani* Rickenbach & Eouzan, 1970, *ravissei* Rickenbach & Eouzan, 1970 and *tendeiroi* da Cunha Ramos, Ribeiro & de Barros Machado, 1992. By odd coincidence, *silvestris sensu stricto* and subspecies *conchobius* are the only forms of the group for which the male, female, larva and pupa are known. Only the male is known for the other species, with the exception that the female of *Er. tendeiroi* is also known (Service 1990; Wilkerson *et al.* 2021).

Although the male, female, larva and pupa are known for *silvestris sensu stricto* and subspecies *conchobius*, they are incompletely described and illustrated. Ingram & de Meillon (1927) described the female, larva and pupa of *silvestris* based on specimens reared from larvae taken from leaf axils of a succulent shrub of the genus *Dracaena* Linnaeus while conducting surveys at Eshowe in present-day KwaZulu-Natal Province of South Africa. In contrast to *silvestris*, Edwards (1941) described *conchobius* based on specimens from the coastal area of Kenya: A male from Malindi and "specimens from Simba Hills and Tiwi (near Mombasa)… reared from larvae found in snail-shells in forest, this being a notably different habitat from that of the type form". Edwards characterized *conchobius* as differing from *silvestris sensu stricto* as follows: "Integument of thorax clearer yellow, no darkening even in middle of pleurae beneath the silvery stripe. Median line of yellow scales on scutum either entirely lacking or represented by a short stripe in front of scutellum and a narrow line extending a short distance only from front margin; scales covering most of scutum brownish rather than black and less irregularly distributed. Hind femur with the antero-ventral yellow area less extensive, reaching little if at all beyond middle of femur instead of about ¾ of its length."

A decade later, Hoogstraal & Knight (1951) described specimens they identified as *conchobius* that were reared from larvae found in the leaf axils of *Sansevieria nilotica* Baker growing in the vicinity of Torit, a city in present-day South Sudan. They described the adult as being "intermediate between the typical species, *silvestris* Ingram and de Meillon, and *conchobius* as described by Edwards (7) [Edwards 1941, number 7 in the list of References] in that it possesses the medial transverse dark brown pleural (integumental) stripe of the former, and the scutal and hind femoral coloration of the latter. The male genitalia are as in the typical form (7, fig. 73c). The Torit specimens go to the subspecies *conchobius* in Haddow's keys (10) [Haddow 1946], and in van Someren's (11) [van Someren 1949] more recent keys."

Hoogstraal & Knight illustrated the head, thorax and terminal abdominal segments of the presumed larva of *conchobius*. Ingram & de Meillon (1927) described but did not illustrate the head and thorax of the type specimen of *silvestris*, making it difficult to draw comparisons with the description provided by Hoogstraal & Knight. From the poor illustrations of the dorsomentum and siphon provided by Ingram & de Meillon, the only clear-cut difference is the length of the siphon, which is "about as broad as it is long" compared to having an index of "1.7–2.0" in specimens examined by Hoogstraal & Knight. Hopkins (1952) reconstructed and illustrated the terminal abdominal segments of the larval exuviae of the type specimen, and noted: "Siphon crushed… (index 1, perhaps about 1½ before crushing)”. In a footnote that followed the brief description of the larva of *silvestris* provided by Hopkins, P. F. Mattingly made the following observations.

> A pelt [exuviae] of ssp. *conchobius* from Taveta, Kenya, has been sent me by Mrs. E. C. C. van Someren, and Knight and Hoogstraal have a description of further larvae of this sub-species, from Torit, Sudan, in the press (*Amer. J. Trop. Med.*). I am indebted to Lt.-Cdr. Knight for permission to quote from their MS. The Kenya pelt differs from the only available pelt of the type form in the shape of the comb spines which resemble Haddow’s type 16 of *chrysogaster* (Fig. 133). The figure of *silvestris* (Fig. 134) is misleading in this respect since it shows the basal denticles more strongly developed than in fact they are. The Kenya pelt also differs from that of the type form in having more strongly developed secondary denticles on the pecten spines and in having the subventral tuft [seta 1-S] of the siphon trifid instead of bifid. The comb spines of the Sudan form appear to resemble those of the Kenya form fairly closely though with a higher proportion having the median denticle relatively exaggerated. It is not thought that this difference is significant. The pecten spines, as figured, are much simpler than in the Kenya pelt in which they have very numerous secondary denticles both dorsally and ventrally. The subventral seta [1-S] of the siphon is shown as trifid.—P. F. M.

A comparison of the illustration provided by Hopkins with the one provided by Hoogstraal & Knight reveals the following additional differences, which were not noted by Mattingly. In the type of *silvestris*: Seta 1-VIII long and single (short and multi-branched in “*conchobius*”); seta 5-VIII branched at midlength (single in “*conchobius*”); saddle of segment X large, covering about dorsal half of the segment (small, covering about dorsal third of the segment in “*conchobius*”); anterior seta 4a-X (of ventral brush) long, double (very short, triple in “*conchobius*”); seta 4c-X double, shorter than 4b,d-X (single, probably as long as 4b,d-X in “*conchobius*”); anal papillae distinctly longer than segment X (about as long as segment X in “*conchobius*”).

Edwards (1941) illustrated the male genitalia of *silvestris*, and provided the following brief description: “Coxite [gonocoxite] with thumb-like basal lobe bearing a few long hairs [setae]; apical lobe unmodified, but bearing three distally-flattened hairs; no scale-tufts. Style [gonostylus] [strongly bent] with one long hair and two short ones, no scales. Proximal claspette bearing a few long simple hairs; distal claspette stout and moderately long, bearing two bent [strongly sigmoid] hairs at its tip and a few simple ones.” Curiously, Jupp’s (1996) illustration of the male genitalia of *silvestris* from South Africa differs from Edwards’s illustration as follows: Thumb-like lobe of the gonocoxite with four relatively shorter setae; apical lobe without flattened setae; gonostylus only very slightly bent, with four long setae; distal claspette with two relatively smaller wavy setae at the tip.

Edwards (1941) stated that the male genitalia of *conchobius* (Kenya) were “exactly as in typical *silvestris*”, and Hoogstraal & Knight (1951) also stated that the male genitalia of “*conchobius*” in South Sudan “are as in the typical form”. In view of the differences between the illustrations of Edwards and Jupp (1996) noted above, we suspect the statements of those authors are based on superficial resemblance.

Despite the lack of detailed, comparative anatomical data for all life stages, we believe the morphological and ecological (larval habitat) differences noted above are indicators of a species complex, consisting of at least three or four species, one of which is *conchobius*. For this reason, we are compelled hereby to elevate *conchobius* to species rank: ***Eretmapodites conchobius*** **Edwards, 1941**. *Eretmapodites conchobius* is currently listed as a species in the Encyclopedia of Life.

Eretmapodites wansoni Edwards

subspecies ***douceti*** Adam & Hamon, 1959—original combination: *Eretmapodites oedipodius* [*oedipodeios*] ssp. *douceti*. Distribution: Burkina Faso, Côte d’Ivoire (Wilkerson *et al*. 2021).

subspecies ***wansoni*** Edwards, 1941—original combination: *Eretmapodites oedipodius* [*oedipodeios* (*sic*)] ssp. *wansoni* (specific status by Hamon 1961). Distribution: Burkina Faso, Cameroon, Central African Republic, Côte d’Ivoire, Democratic Republic of the Congo, Republic of the Congo, Togo (Wilkerson *et al*. 2021).

Prior to Hamon (1961), the species known as *Er. oedipodius* Edwards, 1912b consisted of six subspecies: The nominotypical subspecies, *douceti* Adam & Hamon, 1959, *marcelleae* Adam & Hamon, 1959 (incorrectly spelled *marcellei*, emended by White 1975), *parvipluma* Edwards, 1941, *stanleyi* Edwards, 1941 and *wansoni* Edwards, 1941. Hamon (1961) synonymized *stanleyi* with *oedipodius*, raised *marcelleae*, *parvipluma* and *wansoni* to specific rank, and recognized *douceti* as a subspecies of *wansoni*, based mainly on characters of the genitalia and the ornamentation of the mid- and hindtarsi of males. He proffered the following taxonomic assessment (translated from the French).

> The subspecies *oedipodius*, *parvipluma*, *wansoni*, *marcellae* [*sic*] and *douceti* are very clearly distinguished from each other by the male genitalia and can be classified into two groups depending on whether the simple claw of the midleg is flattened (*oedipodius* and *marcellae*) or not (*parvipluma*, *wansoni* and *douceti*). The simultaneous presence of *marcellae* and *oedipodius* in the same region and the great differences that exist in the structure of the apical leaf of the proximal claspette make it necessary to treat them as distinct species. Although the ranges do not coincide (within the limits of our current knowledge), it also seems logical to treat *parvipluma* and *wansoni* as separate species, given the differences in the structure of the proximal claspette which, in *parvipluma*, bears in its apical part two long fine setae and a spiculate leaf while, in *wansoni*, this claspette has half a dozen long fine setae and ribbed leaves with un-spiculate edges. The status of *douceti* is less clear and we propose to maintain it as a subspecies of *wansoni*, given the affinities found both in the structure of the male genitalia and the claw of the midleg and in the ornamentation of the posterior tarsus [hindtarsus]. It seems that *wansoni* is confined to the lower Guinean forest district and *douceti* exists only in the upper Guinean savannah district, but there are still very large gaps in collecting in these areas.

Subspecies *douceti* was described from three males, two reared from larvae collected from water held in a fallen leaf in the Nasso forest of present-day Burkina Faso and one captured while flying in undergrowth of oil palms at Katiola, Ivory Coast (Adams & Hamon 1959). In addition to those specimens, Hamon (1961) also examined a male from Togo, which only differed from the type specimens of *douceti* in the apical leaf of the proximal claspette being bifid at the apex.

Adam & Hamon (1959) described the male of *douceti* as follows (translated from the French).

> The posterior tarsus [hindtarsus] is similar to that of *Eretmapodites oedipodius wansoni* Edwards: the 3rd tarsomere bears neither erect scales nor long setae; the 4th and 5th tarsomeres are enlarged and pinnate, each forming a pronounced angle with the preceding tarsomere.
>
> The 5th tarsomere of the midleg does not bear an abnormally enlarged claw (fig. 3 B).
>
> The male genitalia (fig. 2) are characterized by the proximal claspette which is short, quite thick in its basal 2/3, then sharply narrows and bears half a dozen setae at the point of narrowing, but none are inserted close to the leaf as in *E. oe. wansoni*; the terminal leaf is quite broad, tapering at its apex and barbed laterally. The distal claspette is long, curved, with a rounded apex bearing a long lateral seta, six small joined leaves thinning into a filament at their end and 12 to 14 strong setae curved in the form of a hook.

Based on these differences, and the fact that *douceti* is known only from localities in savannah, as opposed to *wansoni* being known only from forest sites, it is surprising that Haman (1961) preferred to recognize *douceti* as a subspecies of *wansoni*. We believe that when the larval and pupal stages of *wansoni* are known and compared with those of *douceti*, and molecular data become available for both forms, it will be apparent that *douceti* and *wansoni* are separate species. Until proven otherwise, we hereby formally elevate *douceti* to species rank: ***Eretmapodites douceti*** **Adam & Hamon, 1959**. *Eretmapodites douceti* is currently listed as a species in the Encyclopedia of Life, however the date of authorship needs to be corrected from 1958 to 1959. The issue of the journal (no. 4) intended for publication in 1958 was not published until 1959.

Mansonia (*Mansonioides*) *africana* Theobald

subspecies ***africana*** (Theobald, 1901c)—original combination: *Panoplites africanus*. Distribution: Angola, Benin, Botswana, Burkina Faso, Cameroon, Central African Republic, Côte d'Ivoire, Democratic Republic of the Congo, Equatorial Guinea, Ethiopia, Gabon, Ghana, Kenya, Liberia, Mali, Mozambique, Nigeria, Senegal, Sierra Leone, South Africa, South Sudan, Sudan, Tanzania, Gambia, Uganda, Zambia (Wilkerson *et al*. 2021).

subspecies ***nigerrima*** Theobald, 1910—original combination: *Mansonia nigerrima* (varietal status by Edwards 1913a; subspecific status by Harbach & Howard 2007). Distribution: Senegal, Tanzania, Uganda (Wilkerson *et al*. 2021).

Mansonia africana is a well-known African species of the subgenus *Mansonioides* Theobald, 1907; however, like most Afrotropical species of Culicidae, the larval and pupal stages of this species have not been fully described and illustrated. Descriptions of the adults of subspecies *nigerrima* lack illustrations and are brief and superficial, and the immature stages are unknown.

Theobald (1901c) described *Mn. africana* (as *Panoplites africanus*) from "Quite a number of this species in the collection from Asaba", a city in southern Nigeria. He added that "The specimens collected at Asaba differ in no respects from those in the other parts of West and Central Africa." According to Townsend (1990), two syntypes are present in the Natural History Museum, London—"Malawi: 2 female [head only of 1, on slide], Zomba, Chiromo, Lower Shire.… This is one of the syntypes from 'West and Central Africa' referred to generally in the description and listed more fully in Theobald (1901c: 188)." It is not clear to which of the two females this applies, but we assume it is not the one represented by the slide-mounted head. In either case, the localities listed by Theobald (1901c) for his (second) description of *Panoplites africanus* do not include Asaba [they include Chiromo, Fort Johnstone (now called Mangochi) and Lower Shire (Shire River) in former British Central Africa (present-day Malawi), and Lagos and Old Calabar (contemporary Duke Town) in Nigeria]. It is unfortunate that Stone *et al*. (1959) and Knight & Stone (1977) did not arrange Theobald's early publications in strict chronological order. Theobald (1901c) [??/09/1901] predates Theobald (1901c) [12/11/1901] by two months; consequently, it seems that the specimens from Asada, Nigeria are non-extant and the two "syntype" females have no taxonomic status.

Theobald (1910) described *Mansonia nigerrima* based on a single female from Mpuma, Uganda (Mpuma, now known as Mpuma-Luga, is a city in the Mukono District, Central Region, located about 28 km east of Kampala). Edwards (1913a) placed *Ma. major* Theobald, 1903a and *Mn. nigerrima* in synonymy with *Mn. africana* (as *Mansonioides africanus*) but then, seemingly reluctantly, treated *nigerrima* as a variety, saying: "*M. nigerrima* may perhaps rank as a good variety; it is much darker than the type: the thorax is darker, with hardly a trace of pale markings; the dark scales of the wings are much more numerous than the light, and the white rings at the bases of the hind tarsal joints are much narrower than in typical *M. africanus*. The male genitalia, however, do not differ in any way. This form has up to the present only been found in Uganda." Edwards (1932a, 1941) was the only taxonomist post-Theobald (1901c, 1901d) to recognize and treat *nigerrima* as a separate form. Later workers, Hopkins (1936, 1952), da Cunha Ramos & Ribeiro (1975), Service (1990), Jupp (1996) and Becker *et al*. (2020), only recognized the nominotypical form, perhaps because they considered *nigerrima* to merely be a morphological variant. These authors were, of course, with the possible exception of Becker *et al*., unaware that Harbach & Howard (2007) had raised *nigerrima* to subspecific rank based on provisions of the *International Code of Zoological Nomenclature*: "Despite Edwards' (1913a) apparent reluctance to treat *nigerrima* as a variety, implying that it should perhaps be regarded as an infrasubspecific entity, it is deemed to have subspecific rank because it was adopted (originally) as the valid name of a species before 1985 (Article 45.6.4.1)." In the absence of concrete morphological differentiation and evidence of geographical isolation, we believe that the action taken by Harbach & Howard, based merely on provisions of the *Code*, was ill-considered. Of course *nigerrima* could possibly be a separate species, but until this is conclusively proven, based on comparative morphological study of all life stages and molecular assessment, we believe it is prudent to consign *nigerrima* to synonymy: ***nigerrima* Theobald, 1910, junior subjective synonym of *Mansonia* (*Mansonioides*) *africana* (Theobald, 1901c)**. Consequently, *Mansonia nigerrima* should be removed from the species of *Mansonia* listed in the Encyclopedia of Life.

As indicated above, contrary to Wilkerson *et al*. (2021), *Mn. major* Theobald, 1903a was synonymized with *Mn. africana* by Edwards (1913a), not Edwards (1932a), who stated that "*M. major* was described from a flattened, but typical female specimen [of *Mansonioides africanus*]." There is no reason to doubt this synonymy, and it is retained, along with *Mn. nigerrima*, as a synonym of *Mn. africana*.

Mimomyia (*Mimomyia*) *chamberlaini* Ludlow

subspecies ***chamberlaini*** Ludlow, 1904b—original combination: *Mimomyia chamberlaini*. Distribution: Australia, Bangladesh, Cambodia, India, Indonesia, Malaysia, Myanmar, Nepal, Papua New Guinea, People's Republic of China, Philippines, Sri Lanka, Thailand, Vietnam (Wilkerson *et al*. 2021).

subspecies ***clavipalpus*** (Theobald, 1908)—original combination: *Radioculex clavipalpus* (subspecific status by Mattingly 1957a). Distribution: India, Pakistan, Sri Lanka (Wilkerson *et al*. 2021).

subspecies ***metallica*** (Leicester, 1908)—original combination: *Conopomyia metallica* (subspecific status by Rattanarithikul

> *et al*. 2006a). Distribution: Australia, Cambodia, Indonesia, Laos, Malaysia, Papua New Guinea, Philippines, Singapore, Taiwan, Thailand, Vietnam (Wilkerson *et al*. 2021).

As the most recent reviser of *Mimomyia* (as a subgenus of *Ficalbia*), Mattingly (1957a) recognized *clavipalpus* as a subspecies and treated *metallica* as a variety of *chamberlaini*. Curiously, Mattingly included *chamberlaini sensu stricto* and var. *metallica* in keys for the identification of adult females and males (separate keys), and included only *chamberlaini sensu stricto* in keys to larvae and pupae. He did not include subspecies *clavipalpus* in any of the keys. Mattingly & Grjebine (1958), who also recognized *Mimomyia* as a subgenus of *Ficalbia*, treated *metallica* as a species, but explicitly noted that "*F. metallica* is probably only a color variety of *F. chamberlaini* [translated from the French]." It is interesting that Mattingly & Grjebine did not mention *clavipalpus*, perhaps because their paper was in press when Mattingly (1957a) was published and they also recognized it as a subspecies of *chamberlaini*. Without comment, Rattanarithikul *et al*. (2006a) included *metallica* as a subspecies of *chamberlaini* in keys to the adults and larvae of the mosquitoes known to occur in Thailand. Prior to these actions, *clavipalpus* was recognized as a synonym of *chamberlaini* and *metallica* was regarded as a separate species (Edwards 1932a).

Mimomyia chamberlaini was described from a single male collected at Bayamban, Pangasinan, Luzon Island, Philippines (Ludlow 1904b). Ludlow did not provide illustrations and did not describe the genitalia of the specimen. Four years later, Theobald (1908) described *Radioculex clavipalpus* from a series of females and males captured at Calcutta, West Bengal, India, but the description did not include illustrations. In the same year, Leicester (1908) described the female and male of *Conopomyia metallica* from specimens collected at Barrack Pool, Kuala Lumpur, Malaysia. Leicester also did not provide illustrations of the nominal species.

Published records indicate that *Mi. chamberlaini sensu stricto* occurs in most areas of the Oriental Region and tropical areas of the Australasian Region. As pointed out by Mattingly (1957a), available morphological evidence suggests that *chamberlaini sensu stricto* and *metallica* are variants of a single species. His assessment is as follows.

> The classical diagnostic character has been the occurrence in *F. metallica* of median pale markings on the abdominal tergites [terga] and the absence of such markings in *F. chamberlaini*. In Malaya complete inter-gradation between these conditions has been found to occur. I have specimens with a more or less continuous pale median line on the abdomen, others with this line reduced to one or two small spots on posterior tergites and one with abdomen completely dark above. As already noted… this last specimen is associated with a larval skin [exuviae] having the distal part of the antenna pale while all my other Malayan larvae have the antenna entirely dark. This is another traditional distinction between *F. chamberlaini* and *F. metallica* and were no other evidence available one would be inclined to attribute the one specimen to the first species and the remainder to the second. As against this, however, Philippines specimens with all dark abdomen have larvae with all dark antenna. Other larval differences noted by Edwards & Given… will be seen that at best they are partial differences and they seem to represent differences between the Indian and Indomalayan forms rather than between *F. chamberlaini* and *F. metallica* as such. The only significant larval variation within the Indomalayan area appears to be the occurrence of an unusually small number of branches in head seta B [seta 6-C] of the Philippines form (3–5, not less than 4 elsewhere) and a tendency for Malayan larvae to approximate to the Indian form [*clavipalpus*] in the reduced number of teeth [scales] in the distal row(s) of the comb (1–8, 3–10 elsewhere) and rather less strongly developed spiculation of the saddle edge. In the adult the only notable colour variation concerns the scaling of the prescutellar area. In most cases this is quite extensively pale scaled. Malayan forms, however, tend to have the pale scaling greatly reduced or even absent and my one New Guinea specimen has this area wholly or largely dark. Australian specimens appear regularly to have this area very extensively pale scaled but I have seen individual specimens with it equally pale from Sumatra, Java and Tonkin [Vietnam]. I do not think this variation is taxonomically significant.
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> In view of the striking difference in appearance between well marked specimens of *F. chamberlaini* and *F. metallica* it has seemed to me desirable to distinguish the latter as var. *metallica*, using the term "var." in the same sense as Edwards (1941: 2) as indicating "bridged variation in one area" as against the geographically representative variation associated with subspecies.

In view of the observations and arguments put forward by Mattingly (1957a), until more evidence becomes available, we believe that *metallica* should be recognized as a synonymous name; therefore, it is here formally placed in synonymy with that species: ***metallica*** **(Leicester, 1908), junior subjective synonym of *Mimomyia***

(*Mimomyia*) *chamberlaini* Ludlow, 1904b. We should add, however, that it would seem likely that *Mi. chamberlaini* is a complex of species, but as Mattingly aptly stated, "Very much more material is however needed before this can be put forward as more than a most tenuous hypothesis." For the record, Edwards & Given (1928, Singapore), Galliard & Ngu (1949, Vietnam) and Chen & Lien (1956, Taiwan) treated *metallica* as a separate species based principally on the characters which Mattingly (1957a) found to be attributable to variation. In agreement here, *metallica* is not listed as a species in the Encyclopedia of Life.

Mattingly (1957a) had the following to say about *clavipalpus*.

> The Indian form of *F. chamberlaini* (=*Radioculex clavipalpus* Theobald) differs from other forms, so far as can be judged from the limited material available to me, in a number of interesting partial characters of the larva. Thus the antenna is constantly pale on the distal segments in Indian larvae… while in most Indomalayan specimens it is wholly dark. However, I have one larval skin [exuviae] with the Indian type of antenna from Malaya and it may be presumed that the larvae from Tonkin [Vietnam] provisionally assigned to *F. chamberlaini* by Galliard & Ngu (1949: 497) also had antennae of this type. It is interesting to find that the Malayan skin is associated with the only adult which I have from that territory with complete suppression of median pale markings on the abdominal tergites [terga]. This is, however, of doubtful significance since the U.S. National Museum has adults from the Philippines with complete suppression of these markings associated with larval skins having wholly dark antennae. Other differences between the Indian form and those occurring in the Indomalayan and Australian areas… [include (in general, using up-to-date terminology) setae 5- and 6-C with more branches, scales in distal row(s) of the comb fewer in number, saddle generally with fewer spicules on the posterior margin and pecten with more spines]. …The number of long spicules on the distal edge of the saddle is to some extent a matter of subjective estimate since some spicules are of intermediate length. However, the difference seems quite clear and constant. …It may be felt that these differences justify distinguishing the Indian form as a separate subspecies.

Based on the adult and larval distinctions exhibited by *clavipalpus*, and because it has only been found in areas of India, Pakistan and Sri Lanka where *chamberlaini* and *metallica* have not been recorded, we feel that this nominal form should be returned to its original specific rank, at least provisionally: ***Mimomyia* (*Mimomyia*) *clavipalpus* (Theobald, 1908b)**. *Mimomyia clavipalpus* is currently listed as a species in the Encyclopedia of Life.

Toxorhynchites (*Afrorhynchus*) *viridibasis* (Edwards)

subspecies ***viridibasis*** (Edwards, 1935)—original combination: *Megarhinus aeneus* var. *viridibasis* (specific status by Edwards 1941). Distribution: Burkina Faso, Central African Republic, Côte d'Ivoire, Mali, Nigeria, South Sudan, Sudan, Uganda (Wilkerson *et al*. 2021); also the Democratic Republic of the Congo (see below).

subspecies ***voltaicus*** Ribeiro, 2005—original combination: *Toxorhynchites* (*Afrorhynchus*) *viridibasis voltaicus*. Distribution: Burkina Faso (Ribeiro 2005).

Edwards (1935) described *viridibasis* (as a variety of *Megarhinus aeneus* Evans, 1926) from two adult females collected in Uganda, the type specimen from Kampala and the second female from Soroti. The description was very brief and did not include illustrations. In addition to a slightly more detailed description of the two females, Edwards (1941) provided a very brief description of a dubious adult male, stating: "Although the male is damaged I think it must belong to the same species as the females: it is clearly quite different from the male of *erythrurus*, but it is quite possible that both *viridibasis* and *aeneus* should be regarded as subspecies of *lutescens*; the available material is too scanty for any conclusion to be formed of the point."

Ribeiro (2005) based the description of subspecies *voltaicus* on a single adult male captured on 18.7.54 at Banankélédage (Banankeledaga), cercle (circle, area) Bobo-Dioulasso, Haute-Volta (now Burkina Faso)—Banankeledaga is a village located near the city of Bobo-Dioulasso, the capital of Houet Province. Ribeiro did not mention how he identified the specimen as being conspecific with the female of the nominate form, but he distinguished the two subspecies in a key for the identification of males of species of the subgenus *Afrorhynchus* Ribeiro, 1992. Oddly, the two subspecies keyed out in different couplets, with the nominate subspecies keying out in a couplet with *Tx. ruwenzori* (van Someren, 1948) and subspecies *voltaicus* keying out in a couple in which the alternate character state leads to two consecutive couplets that identify *Tx. capelai* Ribeiro, 1992b, *Tx. lutescens*

(Theobald, 1901a) and *Tx. zairensis* Ribeiro, 2005. Scaling on the mesokatepisternum was used to distinguish subspecies *viridibasis* from subspecies *voltaicus* and the other three species: In the nominate subspecies, "Golden scales on mesokatepisternum restricted to the lower portion of the sclerite [sternum]"; in subspecies *voltaicus*, "A patch of golden scales present on the upper portion of the mesokatepisternum, at base of prealar knob". According to Edwards (1941), the female of the nominate form has "much of the pre-alar area (except the knob) clothed with white scales." It is uncertain whether the prealar area of the male also has white scaling as Edwards only mentioned that the male "resembles ♀ in colouring of body and legs (thorax much denuded)."

In the diagnosis of *voltaicus*, Ribeiro mentioned that the male also differed from the male of the type form in having "a purple third tergum" and the coloration of the maxillary palpus, which is "extensively golden" in the nominate form and "mainly purplish golden with violet reflections" in *voltaicus*. He noted that "No significant differences were found between the male genitalia of *Tx. v. voltaicus* and those of the male *Tx. v. viridibasis* from Coquilhatville, Congo" [Coquilhatville is the former name of present-day Mbandaka, a city on the Congo River in the Democratic Republic of the Congo]. For clarity, Edwards (1941) stated that the maxillary palpus of the questionable male of the nominate form that he examined was "as in *lutescens*", which he described as having the "shaft and penultimate segment golden beneath, only tip of latter dark, and with some golden scales above, terminal segment all dark".

In the original description of *viridibasis*, Edwards (1935) characterized the female as having the "First three abdominal segments almost entirely green-scaled, contrasting with the remainder, which are purple." In 1941, he more precisely described the abdominal terga: "Abdomen with first three tergites [terga I–III] clothed with metallic green scales, a slight admixture of purple scales on the third, rest purple." Although this pertains to females, it suggests that the third tergum may not always be entirely green-scaled and could prove to be predominately or entirely purple on inspection of a much larger number of specimens; perhaps more so in males.

The larva and pupa of *Tx. viridibasis* were described by Lewis (1945, southern Sudan) and Wolfs (1947, Democratic Republic of the Congo), and minor details of the larva were provided by Hamon (1954, Burkina Faso). In each case, larvae were reared to adults, which were used to identify the species. Wolfs apparently described the larva from exuviae associated with two individually reared males.

It is noteworthy that the holotype male of *voltaicus* designated by Ribeiro (2005) was collected and identified as *Tx. viridibasis* by J. Hamon, who recorded the following: "we obtained an *ex larva* [from a larval rearing] specimen which allows us to add the following indications to the descriptions of Lewis and Wolfs: head seta B [seta 6-C] has 5 branches; the subventral bristle of the siphon [seta 1-S] is bifid on one side and simple [single] on the other [translated from the French]." For comparison, Wolfs (1947) indicted that setae 6-C and 1-S are both 4-branched in larvae from the Democratic Republic of the Congo, whereas Lewis (1945) indicated that specimens from Sudan have seta 6-C with 2 or 3 branches "near the tip" and seta 1-S single, but "may have 1 or 2 branches near its tip." It was not obvious until now that the holotype male of *voltaicus* is one of the two males which Hamon (1954) reared from larvae collected in an area that "forms approximately a circle with a radius of 50 kilometers and is entirely included in the administrative subdivision of Bobo Dioulasso [translated from the French]." Therefore, one of the larval exuviae examined by Hamon (1954) is the larval exuviae of the holotype of *voltaicus*.

Based on the scant morphological data listed above, it would seem that subspecies *voltaicus* differs from the nominate form principally in features of the adults—abdominal tergum III entirely with purple scales (entirely green or with a few intermixed purple scales in the type form), upper mesokatepisternal scale-patch comprised of golden scales (these scales white in the type form), maxillary palpus of the male mainly clothed in purplish golden scales with violet reflections (mainly clothed in golden scales in the type form). Because the interpretation of color is subjective and dependent on lighting, and may be variable within a species, we consider such differences to be of questionable value in recognizing species-group taxa. With regard to the larva, the paucity of information shows that the larva of *voltaicus* shares the single or bifid seta 1-S with the type form in Sudan, and both differ from the form in the Democratic Republic of the Congo in which this seta is 4-branched. There seems to be a greater difference in the branching of seta 6-C, which has two or three apical branches in Sudanese larvae and is four- and five-branched in larvae from the Democratic Republic of the Congo and the type locality of subspecies *voltaicus*, respectively. It is impossible to know whether these differences are attributable to variation across the range of a single species or an indication of a potential species complex. In the absence of firm evidence, we feel it is prudent at this time to formally consider *voltaicus* as nothing more than a local morphological variant of the nominotypical form: ***voltaicus*** **Ribeiro, 2005, junior subjective synonym of *Toxorhynchites* (*Afrorhynchus*) *viridibasis* (Edwards, 1935)**. Consequently, *voltaicus* should be removed from the species of *Toxorhynchites* listed in the Encyclopedia of Life.

***Toxorhynchites* (*Lynchiella*) *haemorrhoidalis* (Fabricius)**

subspecies ***haemorrhoidalis*** (Fabricius, 1787)—original combination: *Culex haemorrhoidalis*. Distribution: Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru, Suriname, Trinidad and Tobago, Venezuela (updated from Knight & Stone 1977).

subspecies ***separatus*** (Lynch Arribálzaga, 1891b)—original combination: *Megarhina* [*sic*] *separata* (subspecific status by Lane 1951). Distribution: Argentina, Bolivia, Brazil, Paraguay (Wilkerson *et al*. 2021, Nicaragua deleted).

subspecies ***superbus*** (Dyar & Knab, 1906a)—original combination: *Megarhinus superbus* (subspecific status by Lane 1951). Distribution: Belize, Colombia, Costa Rica, Cuba, Ecuador, French Guiana, Guatemala, Honduras, Mexico, Nicaragua, Panama, Suriname, Trinidad and Tobago, Venezuela (Wilkerson *et al*. 2021).

The taxonomic history of *Tx*. *haemorrhoidalis* involves four nominal species: *Culex haemorrhoidalis* Fabricius, 1787, *Megarhina separata* Lynch Arribálzaga, 1891b, *Megarhinus lynchi* Dyar & Knab, 1906a and *Megarhinus superbus* Dyar & Knab, 1906a. *Megarhina separata* was considered a synonym of *haemorrhoidalis* as early as Lutz & Neiva (1913). Dyar (1928) followed earlier workers in recognizing *Megarhinus lynchi* as a valid species; it was regarded as a questionable synonym of *haemorrhoidalis* by Edwards (1932a) and formally synonymized with *separatus* by Lane (1939). Five years later, Lane (1944) treated *haemorrhoidalis*, *separatus* and *superbus* as separate species; however, he distinguished the last two based only on distribution: *superbus* in Central America and *separatus* in Argentina. It seems Lane (1951), without explanation, was unable to further support the specific rank of *separatus* and *superbus* and reduced them to subspecies of *haemorrhoidalis*. Lane (1953), in accordance with his earlier interpretation, distinguished the two subspecies based only on distribution, and stated in a note that “We have placed *T. superbus* and *T. separatus* as subspecies of *T. haemorrhoidalis*. Such a course taken by us is strengthened by the fact that the zoogeographical distribution of the three forms is quite distinct.” This is not clear, but we believe Lane intended to say that the distributions of each of the three forms are distinct from one another. Except for Vargas (1953), who either disagreed with or was unaware of Lane (1951, 1953) and recognized *superbus* as a species in Central America, *separatus* and *superbus* have continued to be recognized as subspecies to this day.

Dyar & Knab (1906a), in a discussion explaining why they gave the new name *lynchi* to the species in Argentina previously identified as *haemorrhoidalis* by Lynch Arribálzaga (1891b), Theobald (1901a), Giles (1902) and Blanchard (1905), stated that “Great confusion has been caused by basing the diagnosis on the tarsal markings without reference to sex. We find that when the sexual differences are considered the tarsal markings are a useful guide in the diagnosis of the species and are a much more constant character than has been supposed.” It is noteworthy that Dyar & Knab treated *separatus*, also originally described from Argentina, as a synonym of *haemorrhoidalis*, and described *superbus* as a new species based on specimens from Trinidad and Mexico. Their concept of *superbus* also included the identification of *haemorrhoidalis* by Williston (1900) based on specimens from Cuba, French Guiana and Mexico, as well as the identification of *Megarhinus violaceus* by Dyar & Knab (1906a) and Coquillett (1906) based on specimens collected in Central America. Dyar (1928) subsequently separated *lynchi* and *superbus* from *haemorrhoidalis* based on the presence or absence of a basal pale band on hindtarsomere 2, present in *haemorrhoidalis* and absent in the other two. He distinguished *lynchi* and *superbus* based on environmental location: *superbus* “From the northern edge of the tropics” and *lynchi* “From the southern edge of the tropics”. These distinctions were restated, using slightly different terminology, by Lane (1944, 1953), an indication that he either accepted the observations of Dyar without further study or he was unable to find additional characters to distinguish the three nominal forms.

In his treatment of the *Toxorhynchites* (as *Megarhinus*) of “Brasil Meridional” (southern Brazil), Lane (1944) stated the following (translated from the Portuguese).

> It is very interesting to note that, while this species [*haemorrhoidalis*] occurs in the Guianas and the Amazon Valley, the two related species are found, one in the North (*superbus*) and the other in the South (*separatus*). The distinguishing characteristics of these three species reside in the development of the abdominal tufts of the males and in the marking of the tarsi of the females.
>
> We think it very likely that they represent a single species and that both *superbus* and *separatus* are just geographic forms. A definitive solution of this case is impossible for us due to lack of material.

The available descriptions of the leg markings of both sexes are confusing and lack explicit detail, but it appears that they are the same in all four nominal forms except for hindtarsomere 2 of females, which is pale basally in *haemorrhoidalis* and completely dark-scaled in *lynchi*, *separatus* and *superbus*. The lateral tufts on the posterior abdominal segments of males are said to be more strongly developed in *haemorrhoidalis* than they are in the other three nominal forms, but the degree of development has not been made explicit. Dyar & Knab (1906a) indicated that strictly red tufts are only present on abdominal segment VII in *superbus* but are present on segments VI and VII in *haemorrhoidalis* and *lynchi*. In contrast, Dyar (1928) stated that the male of *haemorrhoidalis* has "Abdominal red tufts on the last four segments", and this is quoted verbatim by Lane (1953). In their identification keys, Dyar (1928) and Lane (1953) merely indicated that the "abdominal red tufts [are] well developed" in *haemorrhoidalis* and are "less developed" in *lynchi* (*separatus* of Lane) and *superbus*. It is interesting to note that Dyar & Knab (1906a) distinguished the males of *haemorrhoidalis* and *lynchi* based on the length of "segments 3 and 4" [palpomeres 3 and 4] of the maxillary palpus—equal in length in *haemorrhoidalis* and 3 longer than 4 in *lynchi*. Considering what is now known about the development of the maxillary palpus of mosquitoes (Harbach & Kitching 1998), "segments 3 and 4" are actually palpomeres 4 and 5. Oddly, this character was not mentioned in later works, and the descriptions of the maxillary palpi provided by Dyar (1928) and Lane (1953) are ambiguous. Dyar stated that *haemorrhoidalis* has "Palpi with the third joint long and pointed" (quoted verbatim by Lane), which surely must refer to the terminal palpomere, and Lane added that *superbus* has the "Last palpal segment long and acuminate" and *separatus* is "Similar to *T. haemorrhoidalis superbus*."

As revealed by da Costa Lima (1931), Dyar (1928) failed to notice that Goeldi (1905) had described the egg, larva and pupa of *separatus*, and provided a color illustration of the adult male. It is interesting to note that hindtarsomere 2 is pale basally in the male illustrated by Goeldi, indicating that the species he described is not *separatus*, nor any of the other three nominal forms under discussion here, all of which have hindtarsomere 2 completely dark-scaled. Séguy (1950) provided a similar color illustration, which seems to correctly depict the male of *haemorrhoidalis*.

The larva and pupa of *separatus* were briefly described by Forattini & Lane (1952) based on a single larva captured in the Serra do Diabo region in the western area of São Paulo State in southern Brazil that was reared to an adult. The sex of the adult was not mentioned, but it is presumed to have been a female otherwise the specimen could not have been identified as *separatus*. The descriptions (in Portuguese) were repeated (in English) by Lane (1953). Dyar (1928) and Lane (1953) provided brief descriptions of the larva of *separatus*. Their descriptions lack comparable information except the former author reported that the siphon is "over four times as long as wide" whereas the latter author described the siphon as being "three and a half times basal width." Lane (1953) also provided brief descriptions of the larva and pupa of the nominotypical form. He unintelligibly characterized the larval siphon as "slightly more than one time as broad as wide." However, judging from his illustration of the terminal abdominal segments, he obviously meant to say the siphon is slightly longer than broad. Vargas (1953), in a key for the identification of larvae of species of *Toxorhynchites* (as *Megarhinus*) known to occur in Venezuela, characterized the larval siphon of *superbus* as being twice as long as the saddle of segment X (transliterated from the Spanish). In comparison, Lane (1953) described the length of the siphon of *superbus* as being "two and a half times greatest width." Although these authors expressed siphon length in different ways, the degree of actual difference seems to be greater than expected for individuals of the same species.

The subgenus *Lynchiella* Lahille, 1904, to which *haemorrhoidalis* and 16 other species belong, is predominantly Neotropical, with an extension into eastern areas of the United States and southeastern Canada represented by *Tx. rutilus* (Coquillett, 1896) (see below). For the most part, the current taxonomy of *Lynchiella* dates back to Lane (1953) and Vargas (1953). Their studies were based almost entirely on adult mosquitoes, and the immature stages, as noted above, were described very superficially. With the exception of *Tx. gerbergi* Belkin, 1977, *Tx. guadeloupensis* (Dyar & Knab, 1906a) and *Tx. portoricensis* (von Röder, 1885), the larva and pupa of which were fully described and illustrated by Belkin (1977), Augier *et al.* (2003) and Belkin *et al.* (1970), respectively, the complete larval and pupal chaetotaxy has not been studied for any other species of the subgenus. As noted by Belkin *et al*., *Toxorhynchites* "is amazingly similar in all [life] stages throughout its nearly worldwide distribution and great difficulty is experienced in identifying species. New World species have been diagnosed largely on the basis of light markings of the tarsi, which frequently differ in the 2 sexes and are not always reliable. The metallic coloration of the thoracic scales shows considerable differences among species but is subject to some variation and is difficult to describe accurately owing to marked changes in color depending on the angle of observation. Few specific differences have been noted in the male genitalia. To date no reliable characters have been found to separate any of the species of a group in the larval and pupal stages….", which is obviously due to the fact that they have not been studied in comparative detail. It is worth noting that Belkin *et al*. provisionally applied the name *superbus* to the species in Cuba. Likewise, Belkin and his colleagues applied the name *superbus* to specimens reared from collections made in Colombia (Heinemann & Belkin 1978c); Costa Rica (Heinemann & Belkin 1977a); Guatemala, Honduras and Nicaragua (Heinemann & Belkin 1977b); Mexico (Heinemann & Belkin 1977c); Panama (Heinemann & Belkin 1978a); Trinidad (the type locality of *superbus*) (Heinemann *et al*. 1980); and Venezuela (Heinemann & Belkin 1978b; Navarro 1996). Those researchers identified *haemorrhoidalis sensu stricto* in collections made in northern Brazil and Ecuador (Heinemann & Belkin 1979); Colombia (Heinemann & Belkin 1978c); and also French Guiana, Guyana and Surinam (Heinemann & Belkin 1978b). It is certain that *haemorrhoidalis sensu stricto* and *superbus* are sympatric in at least Venezuela (Navarro *et al*. 2007). It is interesting to note that the collections made in Colombia, French Guiana, Guyana and Surinam also included a species identified as sp. D, near *superbus*.

From the foregoing, it should be evident that the three subspecific forms may prove to be morphologically distinct, particularly in the larval stage; there is evidence that the distributions of *haemorrhoidalis sensu stricto* and *superbus* overlap in northern countries of South America; and available information indicates that *separatus* may be geographically separated from *haemorrhoidalis sensu stricto* and is restricted to areas southward of approximately latitude 20° south. In view of these indicators, we believe it is likely that *haemorrhoidalis*, *separatus* and *superbus* are separate species; thus, we here formally return *separatus* and *superbus* to their original specific status: ***Toxorhynchites* (*Lynchiella*) *separatus* (Lynch Arribálzaga, 1891b)** and ***Toxorhynchites* (*Lynchiella*) *superbus* (Dyar & Knab, 1906a)**. We anticipate that molecular data will confirm these two forms and *haemorrhoidalis* are three separate species. *Toxorhynchites separatus* and *Tx. superbus* are currently listed as species in the Encyclopedia of Life. Based on available morphological data and having type localities in Argentina, *Megarhinus lynchi* Dyar & Knab, 1906a is retained as a synonym of *Tx. separatus* (Lynch Arribálzaga, 1891b).

***Toxorhynchites* (*Lynchiella*) *rutilus* (Coquillett)**

subspecies ***rutilus*** (Coquillett, 1896)—original combination: *Megarhinus rutila* [*sic*]. Distribution: Extreme southeastern United States—Florida, Georgia (mainly coastal), North Carolina (Harrison *et al*. 2016), South Carolina (coastal) (Jenkins 1949; Darsie & Ward 2005).

subspecies ***septentrionalis*** (Dyar & Knab, 1906a)—original combination: *Megarhinus septentrionalis* (subspecific status by Jenkins & Carpenter 1946). Distribution: Eastern North America, northward from northern Florida to Canada (southwestern Ontario) and westward to Kansas, Oklahoma and Texas (Jenkins 1949; Wood *et al*. 1979; Darsie & Ward 2005).

Coquillett (1896) indicated that *Tx. rutilus*, as *Megarhinus rutila*, was described and named based on three males and five females from North Carolina and Georgiana, Florida. According to Stone & Knight (1957c), the original collection included two specimens from Georgiana, Florida and seven from undisclosed localities in Florida, but none from North Carolina. They selected a male from Georgiana bearing a type label to be the lectotype. Georgiana is located on Merritt Island of Brevard County on the eastern side of central Florida.

Dyar & Knab (1906a) described and named *Tx. septentrionalis*, also as a species of *Megarhinus* Robineau-Desvoidy, 1827, from a collection of 13 males and 11 females from localities in the District of Columbia, Louisiana, Maryland, Mississippi, Missouri, North Carolina, Virginia and West Virginia. Stone & Knight (1957c) considered a male from Woodstock, Virginia bearing a type label to be the holotype.

The subspecific status of *septentrionalis* was established by Jenkins & Carpenter (1946), and reinforced by Jenkins (1949) based on conclusions drawn from a study that included specimens form a narrow zone of overlap and apparent integration with the type form. Jenkins described the evidence for integration as follows.

> In the zone of overlap of ranges of the two subspecies, all types of integrations occur. In the northern part of the zone in Georgia and South Carolina, the male intergrades have segments [tarsomeres] 2 and 3 of the fore tarsi with white areas or with isolated white scales surrounded by purple. Two typical intergrades from Myrtle Beach, South Carolina, Carpenter and Jenkins (1945) [*i.e.* 1946], have the following markings on the fore tarsi: Specimen 1.-2nd segment [foretarsomere 2] with basal three-fourths silvery white; 3rd segment [foretarsomere 3] with three white scales. Specimen 2.- 2nd segment, (left) with six white scales, (right) with 4 white scales; 3rd segment, (left) with 3 white scales, (right) entirely purple. In the southern part of the zone of overlap in Florida, the fore tarsi of the intergrade males are usually typical *T. r. rutilus* with the second and basal two-thirds of the third segment silvery white, but interspersed with several dark purple scales. The intergrades were observed from Jacksonville, Tallahassee, and Bushnell, Florida.
>
> The amount of white on the fifth segment [tarsomere 5] of the hind tarsi of the males is variable. There is a decided tendency for this segment to be mostly white in Florida *T. r. rutilus* specimens, and mostly dark purple in the main part

> of the range of *T. r. septentrionalis*. This is quite variable and a specimen of the subspecies from Falls Church, Virginia has this segment almost entirely white. The type of intergradation described for the fore tarsi and often observed on the fifth hind tarsal segment [hindtarsomere 5]. An unusual amount of white was observed on the fore tarsi of males from Duval Co., Leon Co., and Orange Co., Florida that had the 2nd, 3rd and about half of the 4th segments [foretarsomeres 2, 3 and 4] silvery white. A few specimens exhibited white scales on the apical tip of the tibiae.

Jenkins summarized his findings and previous observations (Jenkins & Carpenter 1946) in the form of conclusions:

> The tropical genus *Toxorhynchites* is represented in the United States by two closely related forms which are considered to be subspecies for the following reasons.
>
> 1. The distributions of the two forms overlap in part of their ranges.
> 2. A complete series of intergrades between the two forms occurs throughout the zone of overlap in ranges.
> 3. The only known character separating the two forms is a color difference of the males which is subject to variation.
> 4. No significant differences have been found to separate the two forms in the male genitalia, larvae, pupae, or females.
> 5. The life histories, habitats, and breeding habits of the two forms have been found to be similar.

It is important to note that conclusions 3 and 4 have been repeated, apparently without further detailed morphological study, by later authors (Carpenter & LaCasse 1955; Wood *et al*. 1979; Harrison *et al*. 2016). Conclusion 5 is meaningless as it applies to species of *Toxorhynchites* in general.

It is surprising to find that the subspecific status of *septentrionalis* has been accepted by taxonomists without question since the studies of Jenkins & Carpenter (1946) and Jenkins (1949), and has not since been re-examined using genetic and molecular tools. There are four records of DNA sequences in GenBank: 28S rRNA, *MT-CYB* and *MT-ND5*, Colony, Florida Medical Entomology Laboratory, recorded as *Tx. rutilus* (Krzywinski *et al*. 2001a); mt-*COI* (partial), mt-*COII* and tRNA-*Leu*, York County, Pennsylvania, recorded as *Tx. rutilus* (Mitchell *et al*. 2002); mt-*COI*, Ontario, Canada, recorded as *Tx. rutilus* (Cywinska *et al*. 2006); and 18S rDNA, Stonington, Connecticut, recorded as *Tx. r. septentrionalis* (Shepard *et al*. 2006). Unfortunately, because the researchers did not produce the same molecular sequences, it is not possible to conduct a meaningful analysis of relationships. That aside, the identity of the records attributable to *Tx. rutilus* are problematic. The records from Canada and Pennsylvania must certainly be based on specimens of *septentrionalis*, and it is not possible to know whether the Florida colony was derived from specimens of *rutilus sensu stricto* or intergrades. It should be noted, however, that researchers who conducted ecological studies of treehole mosquitoes in eastern North America (Bradshaw & Holzapfel 1975, 1977; Chambers 1985) did not recognize *septentrionalis*.

As there is no indication of intermediates in the geographically separated populations, there is little doubt that specific traits are being maintained outside the zone of introgression. This is evidence for independent species cohesion, and we believe that molecular systematic studies will reveal that the two forms are separate species that hybridize in a narrow zone where the two species overlap. This supports the taxonomic conclusion that the type form and *septentrionalis* are distinct species; therefore, we hereby formally return *septentrionalis* to its original rank as a species: ***Toxorhynchites* (*Lynchiella*) *septentrionalis* (Dyar & Knab, 1906a)**, which is currently listed as a species in the Encyclopedia of Life.

Toxorhynchites septentrionalis has a single synonym, *Megarhinus herrickii* Theobald, 1906 (type locality: Mississippi State, USA), synonymy by Howard *et al*. (1917). As noted by Belkin (1968), Theobald based the description of *herrickii* on Herrick's (1905) description of *Megarrhinus portoricensis*, apparently without having seen any specimens—probably the ultimate reason for naming the species after Herrick. *Megarhinus herrickii* remains a junior subjective synonym of *Tx. septentrionalis*.

***Toxorhynchites* (*Toxorhynchites*) *brevipalpis* Theobald**

subspecies ***abyssinicus*** Ribeiro, 1991—original combination: *Toxorhynchites* (*Toxorhynchites*) *brevipalpis abyssinicus*. Distribution: Ethiopia (Ribeiro 1991).

subspecies ***brevipalpis*** Theobald, 1901a—original combination: *Toxorhynchites brevipalpis*. Distribution: Angola, Benin, Burkina Faso, Cameroon, Central African Republic, Côte d'Ivoire, Democratic Republic of the Congo, Ghana, Kenya, Liberia, Malawi, Mozambique, Nigeria, Senegal, South Africa, Tanzania, Uganda, Zambia, Zimbabwe (Wilkerson *et al*. 2021).

subspecies ***conradti*** Grünberg, 1907—original combination: *Toxorhynchites conradti* (subspecific status by Hopkins 1936). Distribution: Burkina Faso, Cameroon, Côte d'Ivoire, Democratic Republic of the Congo, Equatorial Guinea, Gabon, Ghana, Gambia, Liberia, Mali, Nigeria, Republic of the Congo, Sierra Leone, South Sudan, Sudan, Uganda (Wilkerson *et al*. 2021).

Theobald (1901a) described *brevipalpis* from two females collected in "Natal", now known as KwaZulu-Natal, a coastal province of South Africa. Steffan & White (1981) noted that the two specimens were originally "in Walker's collection", but "Since only one of the ♀♀ mentioned by Theobald is now in the BM Collection [Natural History Museum, London], it is designated as the lectotype." This is the specimen Edwards (1941) indicated was from Durban, which is considered to be the type locality even though the name of the city does not appear on the labels that accompany the specimen (Steffan & White 1981). Edwards apparently gleaned the locality from other information associated with Walker's collection.

Subspecies *conradti* was originally described as a distinct species by Grünberg (1907) based on a female and a male captured on different dates at the Johan-Albrecht-Höhe station on the crater rim of Lake Barombi near Kumba in the Southwest Region of Cameroon. The species was listed as a synonym of *brevipalpis*, without explanation, by Edwards (1912b, 1932a) and remained so until Hopkins (1936) described the larva of "*brevipalpis*" (as a species of *Megarhinus*) and inadvertently referred to *conradti* as a variety: "The description and figures are of var. *conradti* Grünberg." The figures that Hopkins ascribed to *conradti* were reproduced from Macfie & Ingram (1923), who described and illustrated the larva of "*Megarhinus* (*Toxorhynchites*) *brevipalpis*" from specimens collected at localities in present-day Ghana: Nsawam and Sekondi (the twin city of Sekondi-Takoradi). They prefaced their description as follows: "A figure showing the paddles and the last three abdominal segments of the pupa of this mosquito has been published, together with a few words of explanation, by Bacot (Yellow Fever Commission, West Africa, Reports, iii, p. 145); and a larva, presumed to be that of *M. brevipalpis*, has been briefly described by Edwards (Bull. Ent. Res. iii, p. 375). Neither of these authors, however, has given sufficient details to distinguish the species, and indeed it seems not unlikely that the characters mentioned by them are mainly generic. As we have in our possession specimens of both larvae and pupae of *M. brevipalpis*, we have taken the opportunity of examining them in detail." The specimens were apparently identified to species, in the absence of associated adults, with the help of G. A. K. Marshall, Imperial Bureau of Entomology, and F. W. Edwards, British Museum. The *Toxorhynchites* of Africa were so very poorly known at the time that the identification of the specimens as *conradti* by Macfie & Ingram (1923) was probably presumptive, based on its known distribution in West Africa. Incidentally, we note that Hopkins (1936) is wrongly credited with the recognition of *conradti* as a subspecies in all subsequently published mosquito catalogs (Stone *et al*. 1959; Knight & Stone 1977; Wilkerson *et al*. 2021) when in fact the author clearly referred to it as a variety of *brevipalpis*. It appears that *conradti* was first formally recognized as a subspecies by Edwards (1941).

Removal of the records listed for the presence of subspecies *conradti* in Benin and Senegal, which were not corroborated in the study of Ribeiro (1991), and discounting the separate contradictory records for the presence of *conradti* and the type form in the Central African Republic, Kenya and Nigeria, it would appear that the two forms are largely sympatric in the tropical rain forest region of central Africa, mainly in the Democratic Republic of the Congo. It must be borne in mind that all country records for both forms are based solely on differences in the amount of white scaling in the caudolateral tufts of abdominal tergum VI of females (nearly or completely white in the type form; all black or with a few anterior white setae in *conradti*) and the presence or absence of basal white scaling on foretarsomere 2 of males and females (present in the type form; absent in *conradti*). It must also be noted that Ribeiro (1991) found "intermediate forms" (sex not mentioned) in Angola, Burkina Faso, Nigeria and Uganda with black and white scale-tufts on abdominal tergum VI, which he considered to be *brevipalpis* x *conradti* hybrids. Because the two forms are otherwise distinct throughout their ranges, we believe the "intermediate forms" may be morphological variants of one or the other form or, perhaps more likely, a currently unrecognized species.

In the same paper, Ribeiro (1991) described subspecies *abyssinicus* based on a single male collected in the former Keffa (or Kaffa) Province of Ethiopia, which is now a Zone in the South West Region of the country. Ribeiro distinguished *abyssinicus* from *brevipalpis sensu stricto* by the absence of white scales on foretarsomere 2 (also entirely dark-scaled in *conradti*), from *conradti* by the white-scaled tufts of abdominal tergum VI (as in the type form) and from both *brevipalpis sensu stricto* and *conradti* by the presence of fewer (8 and 10) setae on the ninth tergal lobes of the male genitalia (15–20 setae on each lobe in the other forms).

Hopkins (1936), after revealing he used the illustrations of the larva of *conradti* published by Macfie & Ingram (1923) to represent the larva of *brevipalpis*, stated that "The larva of the typical form has not been distinguished, but is known to be very similar and probably indistinguishable." He did not indicate the source of this knowledge. Hopkins (1952) repeated verbatim his 1936 treatment of *brevipalpis*, except for the sentences from the last paragraph quoted above, which he changed to read "The descriptions and figures are of ssp. *conradti* Grünberg, but the larva of the typical form is not distinguishable (E. C. C. van Someren, 1946b)." This is a delusive statement because van Someren (1946b) actually stated that the larva of the type form is "Indistinguishable from that of *M. brevipalpis* subsp. *conradti* as described by Macfie and Ingram (1922 [1923]) and Hopkins (1936)." Obviously this chain of presuppositions obscures the fact that the larva of *brevipalpis sensu stricto* is essentially unknown and has not been the subject of detailed comparative morphological study.

If it is not obvious from the analyses of the previous three species of *Toxorhynchites*, it should be noted that species of *Toxorhynchites* are generally very poorly known taxonomically, extremely similar in all life stages and troublesome to identify. Most species have been distinguished based on pale scaling of the tarsi, which is often different in males and females of the same species, and the color of scales on areas of the thorax and abdomen, which may be variable or dependent on lighting and interpretation. Additionally, as pointed out by Steffan & Evenhuis (1985), "Species that are easily distinguishable in one stage may be entirely indistinguishable, or separable by only a single character, in another stage. …Because of the subtleties involved in distinguishing among the different species of *Toxorhynchites* in various stages, accurate identification necessitates well-preserved and prepared specimens of both sexes in each stage. Adults with associated pupal and larval skins [exuviae]… provide the most useful taxonomic information." Unfortunately, individually reared adults with associated larval and pupal exuviae are lacking for *Tx. brevipalpis* and its currently recognized subspecies. Nevertheless, we believe that the available morphological and distributional information is sufficient to formally recognize the three nominal forms as separate species: The nominotypical species and ***Toxorhynchites* (*Toxorhynchites*) *conradti* Grünberg, 1907**, which have largely allopatric distributions that overlap in central Africa, without demonstrable evidence of introgression, and ***Toxorhynchites* (*Toxorhynchites*) *abyssinicus* Ribeiro, 1991**, which is diagnosed by a unique combination of characters and appears to be isolated from populations of *Tx. conradti*. *Toxorhynchites conradti* and *Tx. abyssinicus* are both currently listed as species in the Encyclopedia of Life.

Toxorhynchites brevipalpis has a single synonym, *Tx. marshallii* Theobald, 1903a, described from an adult male from Salisbury, Mashonaland, a region in northern Zimbabwe which today is divided into four provinces. The type locality of *marshallii* is within the allopatric range of *Tx. brevipalpis*, and should be retained as a synonym of that species. *Toxorhynchites conradti* has two synonyms, *Tx. schultzei* Enderlein, 1931 (type locality: "Französisch Äquatorial-Afrika, Mongumba am Ubangi-Fluß"—Mongoumba is a town on the Ugangi River in the Central African Republic), and *Tx. tessmanni* Enderlein, 1931 (type locality: "Spanisch-Guinea. Uam-Gebiet: Alen Benito"—Alen Benito [?Benito River; Alen is a mountain], Uam area [Rio Muni mainland], Equatorial Africa). These two nominal forms are each based on a single adult female. Their type localities are located in the allopatric range of *conradti*, and they should be retained as synonyms of that species.

***Toxorhynchites* (*Toxorhynchites*) *christophi* (Portschinsky)**

subspecies ***aurifluus*** (Edwards, 1921a)—original combination: *Megarhinus aurifluus* (subspecific status by Danilov 1987). Distribution: Taiwan (Wilkerson *et al*. 2021, not Indonesia, see below).

subspecies ***christophi*** (Portschinsky, 1884)—original combination: *Megarhina* [*sic*] *christophi*. Distribution: Japan, Russia, South Korea (Wilkerson *et al*. 2021), China (Danilov 1987; Lu *et al*. 1997).

Portschinsky (1884) described *Toxorhynchites christophi* (as *Megarhina christophi*) from an unspecified number of adult females from "Amur", the present-day Amur Oblast, located in the south of the Russian Far East region on the border with Heilongjiang Province of China. Subspecies *aurifluus* was originally described as a species of *Megarhinus* based on four males and a single female collected at several localities on the island of Formosa, present-day Taiwan (Edwards 1921a). The adults (both sexes), larva and pupa are known for both forms and have been described and partially or fully illustrated and treated as separate species by various researchers: *Tx. aurifluus*—Lien (1965), Lu *et al*. (1997); *Tx. christophi*—Tanaka *et al*. (1979), Lu *et al*. (1997).

Tanaka *et al*. (1979) provided the following assessment, which serves as a prelude to an understanding of the taxonomic status of the two nominal species.

> *Toxorhynchites christophi* appears to be very closely allied to *aurifluus* (Edwards) from Taiwan. The male genitalia are apparently identical. The aedeagus has no sclerotized tergomedian band in specimens studied (2 Korean *christophi* and 2 *aurifluus*); Lien (1965) does not show any band on the aedeagus of *aurifluus*; it appears the same in Siberian *christophi*.* [Footnote: "*Danilov 1977, personal communication."]
>
> Korean specimens of *christophi* are identical with *aurifluus* (3 males and 4 females from Taiwan were examined) in the presence of a yellowish brown median area on the mid- and hindtibiae, but different from it in the existence of a pale median band on the proboscis, the golden color of the scutal marginal metallic scales (bluish green in *aurifluus*), the more developed white scaling of the tarsi, the lack of the sublateral patches on female abdominal tergum IV (occasionally a few white scales present) (*aurifluus* has sublateral patches sub-equal to those of III in size), and in that the lateral tufted bristles [setae] on female abdominal tergum VI are all dark (anterior 0.33–0.40 of lateral bristles are yellow in *aurifluus*). In the larvae, only minor differences are detected (Table 40).
>
> The metallic coloration in insects in general is quite variable, it easily changes within a species between green, blue, purple, coppery golden, etc. Such variability must be considered. White scaling of the tarsi was found to be more developed in the northern populations of *towadensis* [*Tx. towadensis* (Matsumara, 1916)] than in the southern ones. Differences in the tarsal white scaling between Korean *christophi* and Formosan *aurifluus* appear to be a similar case. All the differences in the larvae are in the branching of minor setae, and their significance may not be very great. Thus, important characters will be: (1) the pale median band of the proboscis, (2) the yellowish brown median area of the mid- and hindtibiae, (3) the sublateral patches of female abdominal tergum IV and (4) the lateral tufted bristles of female abdominal tergum VI. Korean *christophi* differs from *aurifluus* in (l), (3) and (4). They are, however, consistent in other essential characters, the tergomedian band of the aedeagus, the lateral tufted bristles of abdominal terga VII–VIII, and larval seta 11-II. On the basis of present knowledge, they appear allopatric. Thus, there might be 2 possible interpretations, they are either 2 distinct species, or local forms (subspecies) of a single species. For a final decision of their taxonomic statuses, much more material must be studied.

Danilov (1987) examined more material of *Tx. christophi* and reportedly observed longitudinal clinal variation in the average lengths of several larval setae, which he interpreted as "grounds to consider *Tx. aurifluus* not an independent species, but a subspecies of *Tx. christophi — Tx. ch. aurifluus* Eds. (comb. n.), common only on Taiwan, where the type locality is located, i.e., no longer in the Palearctic, like *Tx. ch. christophi*, but in the north of the Oriental Zoogeographic Region [translated from the Russian]."

Ten years later, Lu *et al*. (1997) published a monumental treatise on the mosquito fauna of China in which both *aurifluus* and *christophi* are treated as species. The authors recorded *Tx. christophi* from Jilin Province in northeastern China, bordering North Korea and Russia, and stated that *Tx. aurifluus* is found in Taiwan, Hubei and Hainan. Hubei is a landlocked province in east-central China approximately 700 km northwest of the Taiwan Strait and Hainan is an island province located off the southernmost point of mainland China. Assuming that specimens from Hubei and Hainan Provinces were correctly identified, *aurifluus* is distributed south of approximately latitude 42° N and *christophi* north of approximately latitude 44° N. There are no records of the two forms between these latitudes. We note that *aurifluus* was most recently treated as a species by Lin *et al*. (2016).

Based on available records, the distribution of *christophi* includes the Primorye and Khabarovsk regions of far eastern Russia, northeastern China and the Korean Peninsula, whereas *aurifluus* occurs in eastern China from Hubei Province to Taiwan and southward to Hainan Island. As noted by Danilov (1987), the distribution of *christophi* lies in the Palaearctic Region and that of *aurifluus* is in the Oriental Region. Based on the morphological differences recorded by Tanaka *et al*. (1979) and Lu *et al*. (1997), and the apparent allopatric distributions of the two forms, we agree with Lien (1965), Lu *et al*. (1997) and Lin *et al*. (2016) that *aurifluus* should be recognized as a separate species: ***Toxorhynchites* (*Toxorhynchites*) *aurifluus* (Edwards, 1921a)**. *Toxorhynchites aurifluus* is currently listed as a species in the Encyclopedia of Life.

Wilkerson *et al*. (2021) list two synonyms for *Tx. aurifluus*: *Megarhinus aurifluus* variety *formosaensis* Ogasawara, 1939 and *Toxorhynchites changbaiensis* Su & Wang, 1981. The former, synonymized by Lien (1962), is correct, *i.e. formosaensis* is undoubtedly conspecific with *aurifluus*. The latter, however, credited to Danilov (1987), is incorrect. *Toxorhynchites changbaiensis* was described from specimens collected in the Huang-Song-Pu forest area of Jilin Province in northeastern China. As explicitly noted by Danilov (1987), and correctly listed by Lu *et al*. (1997), *changbaiensis* is a synonym of *Tx. christophi*, not *Tx. aurifluus*.

A note needs to be added here to address the record of *aurifluus* in Indonesia, which was first addressed by Danilov (1987), who suggested "it is possible that another subspecies of *Tx. christophi*, which has not yet been described, occurs there, since, for example, the pupa from Sumatra described as *Tx. aurifluus* [by] (Brug, 1932) differs in the shape of the paddles from the pupae of *Tx. ch. aurifluus* from Taiwan [translated from the Russian]." The records of *aurifluus* in Indonesia listed in the catalogs of Stone *et al*. (1959), Knight & Stone (1977) and Wilkerson *et al*. (2021) should be disregarded because they are certainly based on misidentifications. The record by Brug (1932) is based on the identification of an adult (sex not indicated) reared from a pupa collected from a pitcher plant in Sumatra, a habitat that is highly unlikely to be utilized by larvae of *aurifluus*, which thrive in bamboo stumps, tree holes and artificial containers (Lien 1965); the record of *aurifluus* in Sulawesi (as Celebes) by Brug (1939) is based on an undisclosed number of females, but the identification was regarded as uncertain because *aurifluus* was originally described from a male and the female was unknown at the time. As revealed by Lane (1992), the new species from Sulawesi which he described as *Tx. auranticauda* was confused in previous literature with *aurifluus* from Taiwan. Consequently, Indonesia should be deleted from the distribution of *Tx. aurifluus*.

***Toxorhynchites* (*Toxorhynchites*) *inornatus* (Walker)**

subspecies ***albitarsis*** (Brug, 1939)—original combination: *Megarhinus inornatus* var. *albitarsis* (subspecific status by Stone *et al*. 1959). Distribution: Indonesia (Sulawesi) (Brug 1939).

subspecies ***inornatus*** (Walker, 1865)—original combination: *Megarhina inornata*. Distribution: Australia, Fiji, Indonesia, Papua New Guinea (Wilkerson *et al*. 2021), including the Islands Region (Bismarck Archipelago) of Papua New Guinea and tentatively Buru Island of Indonesia (Lee *et al*. 1988b).

Walker (1865) described *Tx. inornatus* (as *Megarhina inornata*) from an undisclosed number of adult males from New Guinea. Theobald (1901a) redescribed *inornatus* "from two specimens in the British Museum, one presumably Walker's type of the ♂ described in Proc. Linn. Soc. Lond. viii. p. 102. A female is placed with it with broadly banded tarsi, the bands of white being basal. They both come from New Guinea, and are evidently a ♂ and ♀ of the same species. The caudal tuft is clearly yellow and black, although no mention is made of it in Walker's short description." Surprisingly, despite the existence of the "type" specimen denoted by Theobald (1901a) and Edwards (1923b), and its recognition as the holotype ♂ by Belkin (1962), Steffan & White (1981) found it necessary to designate a lectotype from "Walker's series" to represent the species. Although inexplicable, we must assume that Steffan & White had good reasons for designating a lectotype, and it should be regarded as the type specimen.

Brug (1939) described *albitarsis* as a variety of *Megarhinus inornatus* from four males "reared from larvae found in leaf-axillae of Colocasia in Kalawara (Celebes)", a town in present-day Central Sulawesi, Indonesia [*albitarsis* was raised to subspecific status by Stone *et al*. (1959) without explanation]. Brug noted that *albitarsis* is distinguished from the type form "by the scales of the vertex being bluish green instead of bronzy green; by most of the scales on the posterior pronotal lobe [postpronotum] being white instead of green. The white parties [bands] on the mid and hind tarsus are more extensive, in the typical form those on the second and mid and hind tarsal joint occupying half the length at most. However, the typical form has a white patch on the first hind tarsal [hindtarsomere 1], which *var. albitarsis* has not. In the former there are well defined white lateral patches on the abdominal tergites [terga], in the latter at most some scattered white scales." Unfortunately, the adult female, larva and pupa of *albitarsis* are unknown, and it is not possible to make comparisons with published descriptions of the female (Theobald 1901a; Edwards 1923b; Belkin 1962), larva and pupa (Belkin 1962) of the type form. For the time being, it is only possible to compare features of the male of *albitarsis* described by Brug (1939) with those described for the male of the type form (Brug 1939; Edwards 1923b; Belkin 1962), as shown in Table 6.

TABLE 6. Differences between the males of the subspecies of *Toxorhynchites inornatus*.

Character (♂)	***albitarsis***	***inornatus***
Maxillary palpus, length	About as long as proboscis	Distinctly longer than proboscis
Postpronotum, scaling	*Mostly white-scaled	Mostly green-scaled
Scutum, scaling	Dusky green, pale green at sides	Strongly metallic, greenish, particularly at sides
Abdomen, dorsal	Tergum I pale blue in middle, white at sides; other terga dark blue, shining pale blue at sides	Shades of green at base to shades of blue towards tip, or terga bluish, purplish caudad
Abdomen, ventral	Purple with some golden scales laterally on sterna V and VI	Board median purple stripe, broadened on sternum IV and at bases of sterna II, V, VI and VII
Lateral scale-tufts of segment VI	*Black	About half white and half black
Midtarsomere 2	*Almost entirely white, few black scales at apex	With basal white band
Hindtarsomere 1	Dark-scaled	Basal white band sometimes present
Hindtarsomere 2	*Almost entirely white, few black scales at base and apex	With basal band at most 0.5 length of tarsomere

Characters marked with an asterisk (*) appear to be diagnostic for *albitarsis*. The other characters are liable to variation or subjective perception. Although anatomical data for the female and immature stages of *albitarsis* are not available for comparison with those of the type form, we believe that the characters of the male identified with asterisks are sufficiently diagnostic to warrant recognition of *albitarsis* as separate species: ***Toxorhynchites* (*Toxorhynchites*) *albitarsis* (Brug, 1939)**. It should be noted that *albitarsis* is only known from Sulawesi and has not been identified in other areas of the Australasian Region where only *Tx. inornatus* has been found; thus, the two species appear to be isolated from one another. *Toxorhynchites albitarsis* is currently listed as a species in the Encyclopedia of Life.

Toxorhynchites (*Toxorhynchites*) *manicatus* (Edwards)

subspecies ***manicatus*** (Edwards, 1921a)—original combination: *Megarhinus manicatus*. Distribution: Japan, Taiwan (Wilkerson *et al*. 2021).

subspecies ***yamadai*** (Ôuchi, 1939)—original combination: *Megarhinus yamadai* (subspecific status by Tanaka *et al*. 1979). Distribution: Japan (Amami Ôshima, Ryukyu Archipelago) (Ôuchi 1939).

subspecies ***yaeyamae*** Bohart, 1956—original combination: *Toxorhynchites yaeyamae* (subspecific status by Tanaka *et al*. 1979). Distribution: Japan (Ryukyu-Retto) (Bohart 1956).

These three nominal forms were originally described as separate species: *manicatus* from Taiwan and *yaeyamae* and *yamadai* from islands of the Ryukyu Archipelago (see below). Tanaka (1971a, b) and Tanaka *et al*. (1975) recognized *yaeyamae* as a subspecies of *yamadai* based on examination of all life stages of the former from Iriomote (provenance of the type locality) and Ishigaki Islands and the latter from Amami Ōshima (provenance of the type locality), stating that the adults and larvae are identical with the exception that the postpronotal lobes of the adults have a broad dark-scaled dorsal area in *yamadai* and a narrow dark-scaled dorsal margin in *yaeyamae*. The subspecific status of *yamadai* and *yaeyamae* was established by Tanaka *et al*. (1979), who provided the following explanation.

> The characteristics differentiating *yamadai*, *yaeyamae* and *manicatus* do not appear sufficient to consider them as 3 distinct species. However, they may be recognized as 3 subspecies, because of the existence of rather distinct and not clinal local variations and their definite allopatricity. The posterior pronotal lobe is covered with dark metallic purple

> or indigo-blue scales on upper 0.5–0.6 in *yamadai* and *manicatus*, and the upper 0.25 or less in *yaeyamae*. White scaling on the tarsi is most developed in *manicatus*, least in *yamadai* and intermediate in *yaeyamae*; this may be clinal. Transverse bands of white scales on female abdominal terga are most developed in *yamadai*, least in *yaeyamae* and intermediate in *manicatus*, but these are also highly variable within each subspecies. Lateral bristles [setae] of abdominal terga VI–VIII are most developed in *manicatus*, the bristles are stiffer and denser than in the other 2 subspecies, though not so conspicuous as in the *towadensis* group; these bristles are nearly equal to those on anterior terga in *yaeyamae*, while in *yamadai*, they are more developed than in *yaeyamae* and less so than in *manicatus*. Purple scaling on the median line of the abdominal sterna is most developed in *manicatus*, IV is usually golden only in narrow lateral margins or small lateroapical patches, VII has a broad median line of purple scales, II, V and VI usually have complete, narrow to moderately broad median lines, II often has an incomplete one. The purple scaling is least developed in *yaeyamae* and intermediate in *yamadai*. Male tergum IX is broad, parallel-sided, with the apical margin straight, having 21,22 bristles on each side in one specimen of *yamadai*. In *yaeyamae* and *manicatus*, it is fairly variable, but usually more or less apically narrowed, or having the more strongly rounded lateroapical angle, and the apical margin slightly to deeply concave; the setae are 12–16 (6) in *yaeyamae*, 10–14 (2) in *manicatus*. The claspette is 0.96–1.09 (1) as wide as long in *yamadai*, while it is 1.10–l.40 (7) in the other 2. The shape of tergum IX is usually quite variable in this genus. At present, we have only 1 male specimen of *yamadai*, and consider its 9th tergite [tergum IX] as a case of individual variation which is rather more remarkable than other variable characters of this species.

As mentioned above for *Culex hayashii* Yamada, 1917, the islands of the Ryukyu Archipelago are separated from Palaearctic Japan and Taiwan by two large gaps, and the flora and fauna of the Archipelago tend to be very different from the flora and fauna on the northern and southern sides of those gaps, respectively. We noted above that Toma *et al*. (2019) had elevated *Tripteroides bambusa yaeyamensis* Tanaka, Mizusawa & Saugstad, 1979, which is found in the central and southern regions of the archipelago, to specific status based on molecular and genetic distinctions from *Tp. bambusa* (Yamada, 1917) in the northern Palaearctic region of Japan. What we neglected to mention is that *Tp. bambusa*, which like *Tx. manicatus* develops in plant cavities, is actually three species: *Tp. bambusa* in the Palaearctic region of Japan north of the northern gap; *Tp. yaeyamensis* Tanaka, Mizusawa & Saugstad, 1979, originally described as a subspecies of *Tp. bambusa*, in the central and southern regions of the archipelago; and an undescribed *bambusa*-like species in Taiwan. Considering (1) the morphological comparisons of Tanaka *et al*. (1979), (2) the parallel distributions of *manicatus sensu stricto* (Taiwan) and *yaeyamae* with the *bambusa*-like species (Taiwan) and *Tp. yaeyamensis* (Yaeyama Islands), respectively, (3) the allopatric occurrence of *yaeyamae* and *yamadai* in the southern and central regions of the Ryukyu Archipelago, respectively, and (4) because island species are known to evolve independently from species on other islands, we believe that molecular data, once available, will show that *manicatus*, *yaeyamae* and *yamadai* are separate species (a *COI* sequence is currently available for *yaeyamae*, GenBank accession LC441028, Toma *et al*. 2019). For these reasons, we hereby restore *yaeyamae* and *yamadai* to their original specific status: ***Toxorhynchites* (*Toxorhynchites*) *yaeyamae* Bohart, 1956** and ***Toxorhynchites* (*Toxorhynchites*) *yamadai* (Ôuchi, 1939)**. *Toxorhynchites yaeyamae* and *Tx. yamadai* are both currently listed as species in the Encyclopedia of Life.

Trichoprosopon compressum Lutz

subspecies ***compressum*** Lutz, 1905—original combination: *Trichoprosopon compressum*. Distribution: Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Panama, Paraguay, Venezuela (Wilkerson *et al*. 2021).

subspecies ***mogilasium*** (Dyar & Knab, 1907)—original combination: *Joblotia mogilasia* (varietal status by Stone 1944; subspecific status by Harbach & Howard 2007). Distribution: Brazil, Ecuador, French Guiana, Panama, Venezuela (Wilkerson *et al*. 2021).

Trichoprosopon is a very poorly known genus. As currently defined, it only includes 14 formerly recognized species (Wilkerson *et al*. 2021; Rivera-García *et al*. 2023), but there are an unknown number of undescribed species (T. J. Zavortink and the late E. L. Peyton, pers. comm., circa 1992). Based on this and what little is known about the morphology of the immature stages of *compressum sensu stricto* and *mogilasium*, it is difficult to know for certain whether they are the same or separate species. The pupa of *compressum* was fully illustrated by Knight & Chamberlain (1948) and the pupa and larva were briefly described and partially illustrated by Lane (1953). The immature stages of *mogilasium* have not been described.

The nominate subspecies was described from an "unspecified number of ♂ and ♀ from unspecified localities in the states of São Paulo and Rio de Janeiro, Brazil" (Belkin 1968). Lane (1953) listed the type locality as "Brasil, State of S. Paulo, Pindamonhanga". The locality, however, has been misinterpreted to be equivalent to São Paulo (Stone *et al*. 1959; Belkin 1968; Knight & Stone 1977; Wilkerson *et al*. 2021). The type locality is Pindamonhangaba, a municipality in the state of São Paulo located in the Paraíba Valley approximately 100 km northeast of the city of Sao Paulo. Subspecies *mogilasium* and *Joblotia trichorryes* Dyar & Knab, 1907, a synonym of *compressum* (see below), were both described from specimens collected at Tabernilla in the Canal Zone of Panama.

The three nominal forms, *compressum*, *mogilasium* and *trichorryes*, have an interesting history. *Joblotia mogilasia* and *J. trichorryes* were described as separate species on the same page (Dyar & Knab 1907), with the latter preceding the former. We believe the descriptions support their recognition as separate species, especially the presence of setae and scales on the clypeus of *mogilasia* and the presence of only setae on the clypeus of *trichorryes*. The two forms were listed as separate species in Panama by Dyar (1923), but five years later Dyar (1928) treated them as synonyms of *J. compressa* without explanation. This was in turn followed by Edwards (1932a), who listed them as synonyms of *Tr. compressum*. Lane (1936a), based on a single female collected on human bait at Nhandeara, a municipality in São Paulo State of Brazil, revalidated *mogilasia* as a species of *Joblotia*, based on "the fact that in our specimen the clypeus is laterally covered with dark scales and some setae that are barely perceptible" (translated from the Portuguese). Lane further noted that "If there really are no scales in the *mogilasia* type then our specimen is atypical or a new species." Strangely, Lane & Cerqueira (1942) reasoned that because the presence of setae and scales on the clypeus "is the only character that separates the adults of *T. mogilasium* from those of *T. digitatum* and as the existing material is represented only by some females, we believe that it is preferable to consider *T. mogilasium* as a variety of *T. digitatum* until other phases of biology are known and the systematic position definitively established" (translated from the Portuguese). Stone (1944) noted that Lane & Cerqueira had discovered that scales may be present on the clypeus of both *Tr. digitatum* (Rondani, 1848) and *Tr. compressum*, and they had incorrectly treated *mogilasium* as a variety of *digitatum*. Stone therefore established *mogilasium* as a variety of *compressum*, stating that it "agrees with typical *compressum* in all diagnostic characters save that there are some scales intermingled with the hairs [setae] on the sides of the clypeus." The taxonomic status of *mogilasium* was confused until it was clarified by Harbach & Howard (2007) as follows: "Knight & Stone (1977) indicated that *Joblotia mogilasia* was formally recognized as a subspecies of *Tr. compressum* by Stone (1944) and later afforded varietal status by Stone *et al*. (1959). This is incorrect as Stone (1944) unambiguously treated this nominal species as a variety of *Tr. compressum*. Because *mogilasium* was adopted (originally) as the valid name of a species prior to 1985, it is deemed to be subspecific with availability from its original publication ([ICZN] Article 45.6.4.1)."

In summary, setae and scales are present on the clypeus of *mogilasium* whereas only setae are found on the clypeus of *compressum* and *trichorryes*. In comparison with the detailed morphological descriptions of adult mosquitoes published post-Belkin (1962), the available descriptions of *compressum*, *mogilasium* and *trichorryes* reveal that specimens were not studied in detail and were only superficially examined. Lane (1953) provided the most recent treatment of species currently included in the genus, and for the most part his descriptions are very superficial and unsatisfactory. The three nominal forms considered here are based entirely on adult characters, principally general coloration of scaling and the length of various appendages. The adults may actually show many good characters, but these need to be studied in much greater detail than has been done by the authors cited above. The larvae and pupae of sabethine mosquitoes are known to exhibit striking anatomical differences (Zavortink 1979), but these life stages, as indicated above, are either unknown or have not been studied in sufficient detail to evaluate their usefulness in recognizing and distinguishing similar species. In the case of the nominal forms of concern here, while it appears on superficial examination that only one variable species is involved, we suspect it is likely that several distinct sympatric forms may be present. This is supported by the recognition of a Compressum Complex by Zavortink (1981) that includes two "closely related [undescribed] allopatric taxa [which] occur in bamboo internodes and are apparently indistinguishable. However, in characteristics of the adults and male genitalia, these taxa differ to a much greater extent than do the sympatric species of the *Tr. digitatum* complex [see below], and so I consider these allopatric taxa to be distinct species." Zavortink did not mention subspecies *mogilasium*.

Based on the original descriptions, recorded distributions and the distinct possibility that morphological and genetic distinctions await discovery, and because it is important to determine with certainty whether or not the nominal species of our predecessors are distinct biological species, we believe it is befitting to return *mogilasium* and *trichorryes* to their original species status: ***Trichoprosopon mogilasium* (Dyar & Knab, 1907)** and ***Trichoprosopon***

***trichorryes* (Dyar & Knab, 1907)**, elevated from synonymy with *Tr. compressum* Lutz, 1905. *Trichoprosopon mogilasium* is currently listed as a species in the Encyclopedia of Life; *Tr. trichorryes* needs to be added to the list.

Trichoprosopon digitatum (Rondani)

subspecies ***digitatum*** (Rondani, 1848)—original combination: *Culex digitatus*. Distribution: Argentina, Belize, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, El Salvador, French Guiana, Guatemala, Guyana, Honduras, Lesser Antilles (includes Trinidad and Tobago), Mexico, Nicaragua, Panama, Paraguay, Peru, Suriname, Venezuela (Wilkerson *et al*. 2021).

subspecies ***townsendi*** Stone, 1944—original combination: *Trichoprosopon* (*Trichoprosopon*) *digitatus* var. *townsendi* (subspecific status by Harbach & Howard 2007). Distribution: Brazil, Lesser Antilles (includes Trinidad and Tobago), Panama (Wilkerson *et al*. 2021).

Rondani (1848) described and named *Tr. digitatum* (as *Culex digitatus*) based on one or more females (number not indicated) from an unspecified locality in Brazil (Belkin 1968). The location of the type(s) remains unknown, but the type locality was restricted to the vicinity of Rio de Janeiro (Guanabara) by Belkin *et al*. (1971). In the absence of type material, Stone (1944) aptly noted that "It cannot be determined whether the type of *digitatum* possessed scales on the clypeus, but lacking proof to the contrary, it is best to retain the name for the most frequently encountered, unscaled variety [*i.e.* species of *Trichoprosopon*]." Stone then confirmed the synonymy of *Tr. nivipes* Theobald, 1901c (synonymy originally by Howard *et al*. 1915), *Tr. splendens* Lutz, 1904 (in Bourroul, 1904) (synonymy by Lane & Cerqueira 1942) and *Joblotia splendens* var. *subsplendens* Martini, 1931b (synonymy by Lane & Cerqueira 1942) with *digitatum* based on the absence of scales (presence of setae only) on the clypeus of those nominal species. Stone also noted that four females of *Tr. wilsoni* Ludlow, 1918 in the "U. S. N. M." (National Museum of Natural History, Washington, D.C.) bear type labels but neither of those specimens nor others attributable to Ludlow bear the data provided in the original description of the species; thus, it was "not considered possible to select any one as a lectotype." In the absence of a definite type specimen, *Tr. wilsoni* has remained a synonym of *digitatum* ever since the synonymy was established by Dyar (1928). Of particular note, Stone observed that "One of the four females ['supposed cotype'] has scales intermingled with the hairs [setae] on the clypeus and therefore should be referred to the new variety [*Tr. digitatus* var. *townsendi*] described in this paper."

The presence of only setae on the clypeus of *digitatum sensu stricto* has been recognized by all investigators (Theobald 1901c, as *Tr. nivipes*; Howard *et al*. 2015, as *Joblotia digitatus*; Dyar 1928, as *Joblotia digitata*; Senevet & Abonnenc 1939; Stone, 1944; Lane & Cerqueira 1942; Lane 1953; Zavortink *et al*. 1983). The last authors (Zavortink *et al*.) defined *digitatum* as "the only species of *Trichoprosopon* with 3–5 (3–6) pairs of large preapical teeth on the aedeagus, with these teeth becoming progressively larger distad of the smallest basal tooth.... The pupa is the stage next most easily identified, by its normal countershading and the moderately strong to strong, more-or-less rigid seta 6-VI and usually also 6-V…. The adult of *digitatum* can be identified only by the combination of the densely setose clypeus… the presence of setae on the upper calypter of the wing… the presence of a small patch of light scales at the base of the first hindtarsal segment… and the light integument of the mesepimeron and meron. The larva of *digitatum* is the stage most difficult to identify. It can usually be told by the combination of a strong, long, single or double seta 0-P… a single or double seta 7-P… only a single ventral abdominal seta (12-II) arising from a sclerotized tubercle… and a long seta 6-VI".

Stone (1944) described "var. *townsendi*" from a type series comprised of the holotype and 17 paratypes (14 females and 3 males): "The holotype and 11 paratypes were collected at Boa Vista, Rio Tapajós, Pará, Brazil…. Four paratypes were reared by Dyar and Shannon at Porto Bello, Panama... along with a number of typical *digitatum*. One paratypes [*sic*] is the supposed cotype of *Trichoprosopon wilsoni* Ludlow, from Ancon, Panama. One paratype was reared at Montserrat, Trinidad… along with many of the typical variety." Stone did not indicate whether he examined the genitalia of the males or if the larval and pupal exuviae of the reared specimens were available or examined. He simply stated: "This [variety] agrees with typical *digitatum* in all diagnostic characters save that there are violaceous scales mingled with the hairs [setae] on the sides of the clypeus." Without mention of the male genitalia and immature stages of *townsendi*, Lane (1953) reiterated that "The only difference between this variety and the typical form is that there are scales as well as setae on [the] clypeus."

As noted above for *Tr. compressum*, Zavortink (1981) recognized *Tr. digitatum* as a species complex, consisting "of *Tr. digitatum* and at least two undescribed species." Zavortink elaborated: "By any measure, *Tr. digitatum* is the most successful species in the genus *Trichoprosopon*. It is widespread geographically, occupying the entire range of the genus from Mexico to Ecuador and Argentina. It is diverse ecologically, with the immatures being found in water in bamboo stumps and tree holes, in fallen fruits and nuts, in *Heliconia* flower bracts, and in fallen leaves and palm spathes. And it is abundant, with about 95% of the specimens of *Trichoprosopon* that I have examined being this one species. The undescribed species of the complex occur sympatrically with *Tr. digitatum*, one in the Pacific versant of eastern Panama and Colombia, the other farther south in the Pacific versant of Ecuador. The immatures of only one of the undescribed species are known, and they have been found most often in leaf axils, a habitat not utilized by *Tr. digitatum*. The differences between *Tr. digitatum* and the undescribed species whose immatures are known can be used to illustrate the size of the morphological gap separating related sympatric species in this genus." Zavortink then mentioned differences between *Tr. digitatum* and the undescribed species—differences in the coloration of the adults and pupae, the aedeagus and cercal setae of the male genitalia, and seta 7-P of the larvae—and emphatically stated: "The nature of the differences between *Tr. digitatum* and the new species are important to note, because these species are sympatric and their specific distinctness cannot be doubted." "Even after the separation of two undescribed species, *Tr. digitatum* remains a variable species and may indeed still be a complex." Zavortink did not mention *townsendi*, but the available evidence indicates that this form is also sympatric with the nominotypical form in Panama and Brazil. In view of the unknown immature stages of *townsendi* and the unique presence of scales on the clypeus in the absence of morphological information for the male genitalia, we suspect that further collections and integrated study will show that *townsendi* is a separate sympatric species of the Digitatum Complex; henceforth, it is afforded species status: ***Trichoprosopon townsendi* Stone, 1944**. *Trichoprosopon townsendi* is currently listed as a species in the Encyclopedia of Life.

***Tripteroides* (*Tripteroides*) *powelli* (Ludlow)**

subspecies ***escodae*** Baisas & Ubaldo-Pagayon, 1953—original combination: *Tripteroides* (*Tripteroides*) *powelli escodae*. Distribution: Philippines (Baisas & Ubaldo-Pagayon 1953).
subspecies ***laffooni*** Baisas & Ubaldo-Pagayon, 1953—original combination: *Tripteroides* (*Tripteroides*) *powelli laffooni*. Distribution: Philippines (Baisas & Ubaldo-Pagayon 1953).
subspecies ***mattinglyi*** Baisas & Ubaldo-Pagayon, 1953—original combination: *Tripteroides* (*Tripteroides*) *powelli mattinglyi*. Distribution: Philippines (Baisas & Ubaldo-Pagayon 1953).
subspecies ***powelli*** (Ludlow, 1909b)—original combination: *Uranotaenia powelli*. Distribution: Cambodia, Indonesia, Malaysia, People's Republic of China, Philippines, Thailand, Vietnam (Wilkerson *et al*. 2021).

The genus *Tripteroides*, with species distributed throughout the Australasian and Oriental Regions, has never been the subject of a comprehensive taxonomic revision; consequently, the majority of its species are poorly known. This is particularly true of species of the subgenus *Tripteroides*, for which the immature stages of only a "small minority" of species have been described in detail and those that are known are currently indistinguishable (Mattingly 1981).

Tripteroides powelli sensu stricto and the subspecies *escodae*, *laffooni* and *mattinglyi* were all described from different islands of the Philippines, and only the nominotypical form has been recorded in other countries of the Oriental Region (see above). The four forms have been found on various Philippine islands: *escodae*—Balabac, Jolo, Mindanao and Palawan (type locality) Islands; *laffooni*—Leyte (type locality), Mindanao and Samar Islands; *mattinglyi*—Culion (type locality) and Palawan Islands; *powelli sensu stricto*—widely distributed from Luzon (type locality) to Mindanao (Baisas & Ubaldo-Pagayon 1953; Basio 1971). Thus, *escodae*, *laffooni* and *powelli sensu stricto* are found on Mindanao and *escodae* and *mattinglyi* both occur on Palawan.

The immature stages are known for the four nominal forms, but they have not been studied or described in comparative detail. In fact, there is some doubt concerning the identity of the larva of *powelli sensu stricto*, as revealed by Baisas & Ubaldo-Pagayon (1953).

> The type specimen described by Ludlow, being a female with unknown larva, is not distinguishable from four kinds of *powelli* now known in the Philippines. Even were its larva known, it could not be separated from the others unless it was the one which had two-branched ventral siphon tufts [seta 1-S]. The other three are alike in larval characters. Brug's description of *powelli* larva (1939), based on Dutch East Indian specimens, does not definitely prove that is the kind of larva Ludlow's type *powelli* has. By coincidence, however, the materials we have on hand from Luzon Island (type locality) represent only the kind of larvae which has two-branched ventral siphon tufts, the

> same as that descried by Brug, but at the same time it differs in certain details from the Dutch East Indian form. It is not at all unlikely other forms of *powelli* may also be found in Luzon Island if more extensive collections are made, in which case it is only by assumption that the type specimen could be regarded as that whose larva has two-branched ventral siphon tufts.

Assuming the specimens reared from larvae that were studied by Baisas & Ubaldo-Pagayon are conspecific with the type female of *powelli*, it seems the larvae, as well as the pupae, of the four forms recognized by the authors, based albeit on apparent cursory examination of specimens, are indistinguishable. As stated by Baisas & Ubaldo-Pagayon, "Definite differences between [the] subspecies [are] found only in [the] male terminalia [genitalia]."

The anatomical terminology used by Baisas & Ubaldo-Pagayon (1953) and most other authors for structures of the phallosome of the male genitalia of *Tripteroides* is confusing. References to the phallosome generally apply to features of the aedeagus, which consists of two lateral plates (aedeagal sclerites) that are normally connected in tergal aspect by a narrow submedian tergal bridge, each plate with a variously developed apical sternal process (ventral arm, VA, of Baisas & Ubaldo-Pagayon) and a less distinctively developed median tergal process (dorsal arm, DA, of Baisas & Ubaldo-Pagayon). Considering this clarification, Baisas & Ubaldo-Pagayon distinguished the subspecies of *powelli* as follows.

> Phallosome of *mattinglyi* is quite distinct from those of others, not only in *powelli* complex but also from all species in Group B, because its VA is represented only by teeth which arise directly from rim of tube at point where, in other species of Group B, VA arises. Moreover, *mattinglyi* has a few teeth, of which three or four arise from a small prominence at base (tergal wall) of DA. *Laffooni* has finer and more (over twelve) teeth at this point, but they arise not from a prominence but directly from wall of DA. *Mattinglyi* is strikingly similar in phallosome to *rozeboomi* of Group A. Beyond that, however, there is no other similarity between them. VA in *powelli powelli* much shorter than that of *escodae* or *mattinglyi*. Viewed in whole terminalia [genitalia] mounts VA in *powelli powelli* may be seen beneath and at about or below middle of DA. This is because VA is only about half length of DA. VA in either *escodae* or *laffooni* measures equal or nearly equal length of DA. Because of long VA, and partly because of usual slight upward tilting of organ, the teeth are well exposed beyond apex of DA (see text fig. 2d) in whole mounts; and teeth coarser. Presence of teeth toward base of DA distinguishes *laffooni* from *escodae*; latter does not have any trace of such teeth.

In many species-rich groups of animals, structures of the male genitalia provide better means for distinguishing species than any other morphological characters. Thus, evolution of genital form is thought to be involved in the origin of species. This would seem to be true of species of *Tripteroides*, which like many species of the genus *Culex*, and others, are difficult to distinguish except by features of the male genitalia. Based on the distinct differences in the structure of the aedeagal sclerites of the male genitalia and the apparent sympatry on different islands, as well as significant doubts about the identification of specimens of *powelli sensu stricto* in countries other than the Philippines, we are confident that the four nominal forms, *escodae*, *laffooni*, *mattinglyi* and *powelli*, are separate species, which further morphological study, coupled with molecular analyses, will corroborate. Based on this conviction, the three subspecies described by Baisas & Ubaldo-Pagayon are hereby formally raised to specific status: ***Tripteroides* (*Tripteroides*) *escodae* Baisas & Ubaldo-Pagayon, 1953**; ***Tp.* (*Trp.*) *laffooni* Baisas & Ubaldo-Pagayon, 1953**; and ***Tp.* (*Trp.*) *mattinglyi* Baisas & Ubaldo-Pagayon, 1953**. *Tripteroides escodae* and *Tp. mattinglyi* are currently listed as species in the Encyclopedia of Life; *Tp. laffooni* should be added to the list.

Uranotaenia (*Pseudoficalbia*) *anhydor* Dyar

subspecies ***anhydor*** Dyar, 1907—original combination: *Uranotaenia anhydor*. Distribution: Mexico (Baja California), United States (Arizona, southern California, Nevada) (Carpenter & LaCasse 1955; Belkin & McDonald 1956).

subspecies ***syntheta*** Dyar & Shannon, 1924—original combination: *Uranotaenia syntheta* (subspecific status by Belkin & McDonald 1956). Distribution: Mexico (eastern and central), United States (New Mexico, Oklahoma, Texas) (Dampf 1943; Carpenter & LaCasse 1955; Belkin & McDonald 1956).

Uranotaenia anhydor and *Ur. syntheta* were both originally described as distinct species, the former from a single larva taken from a swamp at Sweetwater Junction near San Diego, California and the latter from an adult female collected at Mission, Texas. The authors of the latter species (Dyar & Shannon 1924), prior to describing *syntheta*, noted that *anhydor* was "not yet known outside of southern California". The two nominal forms continued to be recognized as separate species by Dyar (1928), Edwards (1932a), Dampf (1943), Yamaguti & LaCasse (1951), Brookman & Reeves (1953), Galindo *et al*. (1954) and Carpenter & LaCasse (1955); however, the authors of the last three articles observed that the two forms are so similar morphologically that they may constitute two subspecies or a single species.

The two forms remained as separate species until Belkin & McDonald (1956) formally treated *syntheta* as a subspecies of *anhydor* based on comparisons of all life stages of specimens from a population sampled at Saratoga Springs in Death Valley (San Bernardino County, California) with populations of "*anhydor* from San Diego County, Baja California and Arizona, and *syntheta* from several localities in Texas." They noted "…that the Saratoga Springs population is distinct from both *anhydor* and *syntheta* and that it is in no way intermediate between the two." Despite these findings, they concluded "that all these populations are so close morphologically that they should be considered to form one species…. The populations in the United States east of the Continental Divide, and in all probability those in eastern and central Mexico, constitute the subspecies *syntheta*, easily recognizable only in the adult stage by the thoracic ornamentation. The Saratoga Springs population cannot be considered to be in any way intermediate between the typical *anhydor* from San Diego Co. and *syntheta* but rather an extreme development of the former. It is suggested that the Saratoga Springs population, which is quite distinct morphologically and ecologically from the other western populations, has been isolated in the Amargosa drainage of the Death Valley System since late Pleistocene times… and that it may represent a third subspecies in the *anhydor* complex." This concept subsequently has been accepted in all later works (Bohart & Washino 1978; Darsie & Ward 1981, 2005; Nava & Debboun 2016).

All published treatments of *anhydor* and *syntheta* agree that the adults of the two forms are reliably distinguished by the development of a line (single row) of iridescent blue scales along the lateral margins of the scutum. In *syntheta*, this line is distinct (conspicuous) from the scutal fossa to the base of the wing, with a narrow gap at mid-length, whereas in *anhydor* the line is faint or obsolete (indistinct) with a wide gap in the middle (Dyar & Shannon 1924; Dyar 1928; Galindo *et al*. 1954; Yamaguti & LaCasse 1951; Carpenter & LaCasse 1955; Belkin & McDonald 1956). In contrast, the Saratoga Springs form has an elongate patch of several rows of iridescent light blue scales on each side of the scutum (Belkin & McDonald 1956). Based on the morphological distinction and lack of evidence for gene flow across the Continental Divide, we believe molecular data will show that *anhydor* and *syntheta* are separate species, and for that reason we hereby restore *syntheta* to its original specific rank: ***Uranotaenia* (*Pseudoficalbia*) *syntheta* Dyar & Shannon, 1924**. *Uranotaenia syntheta* is currently listed as a species in the Encyclopedia of Life. Contrary to Belkin & McDonald (1956), we believe the morphological and ecological distinctions of the Saratoga Springs form are a clear indication that it is a genetically distinct species, *i.e.* it is an unnamed species pending formal taxonomic validation.

Uranotaenia (*Pseudoficalbia*) *novobscura* Barraud

subspecies ***novobscura*** Barraud, 1934—original combination: *Uranotaenia novobscura*. Distribution: Bangladesh, Cambodia, India, [Palaearctic] Japan, Laos, Malaysia, People's Republic of China, Taiwan, Thailand (Wilkerson *et al*. 2021).

subspecies ***ryukyuana*** Tanaka, Mizusawa & Saugstad, 1979—original combination: *Uranotaenia* (*Pseudoficalbia*) *novobscura ryukyuana*. Distribution: Japan, Ryukyu Archipelago (Amani, Okinawa, Yaeyama) (Tanaka *et al*. 1979).

Uranotaenia novobscura ryukyuana is endemic to the Ryukyu Archipelago of Japan. It has an interesting taxonomic history. Roth (1946) recognized two larval forms of this taxon on Okinawa Island, which he identified as Forms A and B of *Ur*. *bimaculata* Leicester, 1908. Since its original description, *Ur. novobscura* was mistakenly identified as *Ur. bimaculata* until its identity was resolved by Peyton (1977). Although not explicitly stated, it is obvious that Roth considered the two larval forms to belong to a single variable species. Peyton, in his revision of the subgenus *Pseudoficalbia* in Southeast Asia, likewise concluded that the various populations of *Ur. novobscura* that he studied "represent a single plastic species and that the adult population from Okinawa is a recognizable variant."

Tanaka *et al*. (1979) disagreed that specimens from Okinawa were merely a variant of *novobscura sensu stricto* and distinguished and described the form as a distinct subspecies, *ryukyuana*, as follows: "The population of the Ryukyu Archipelago is characterized by the entirely pale pleura; the scutum is also rather paler, and the supraalar dark patches are smaller than in the populations of Palaearctic Japan. The latter is identical with specimens from Taiwan and Malaya*. [The asterisk refers to specimens from the two countries that were examined.] The female antenna appears slightly shorter, 1.30–1.40 (8) length of proboscis and male antennal flagellomere 12 is shorter relative to Flm 13, *viz*., Flm 12 1.11–1.25 (7) length of Flm 13. Remigium scales are all dark in the Amami and Okinawa populations, but pale ochreous in the basal half in the Yaeyama population. Bristles [setae] on each side of tergum IX of the male genitalia are fewer, 1–4 (x = 2.7, mode = 2) in Amami and Okinawa, 1–3 (x = 1.6, mode = 1) in Yaeyama, while they are 2–6 (x = 3.4, mode = 3) in Palaearctic Japan. Differences in the larvae are rather obscure…. Six larvae from Yaeyama do not appear distinctly different from specimens from Okinawa Is."

Despite the morphological similarity of other subgeneric forms described from the Ryukyu Archipelago, molecular studies have revealed that these forms are genetically distinct, reproductively isolated allopatric populations which required recognition as independent species (Toma *et al*. 2019; Somboon *et al*. 2020a; Wilkerson *et al*. 2022). In view of those studies, and in accordance with the above treatments of the former subspecies of *Culex hayashii* Yamada, 1917 and *Toxorhynchites manicatus* (Edwards, 1921a), we believe it is likely that molecular and genetic studies will show that *ryukyuana* is a separate species. Accordingly, *ryukyuana* is hereby formally accorded species status: ***Uranotaenia* (*Pseudoficalbia*) *ryukyuana* Tanaka, Mizusawa & Saugstad, 1979**. *Uranotaenia ryukyuana* is currently listed as a species in the Encyclopedia of Life; however, the date of authorship of the species is incorrectly listed as 1975, and should be corrected to 1979.

Uranotaenia (*Pseudoficalbia*) *unguiculata* Edwards

subspecies ***pefflyi*** Stone, 1961a—original combination: *Uranotaenia unguiculata pefflyi*. Distribution: Saudi Arabia (Stone 1961a).

subspecies ***unguiculata*** Edwards, 1913c—original combination: *Uranotaenia unguiculata*. Distribution: Afghanistan, Albania, Algeria, Armenia, Austria, Azerbaijan, Bulgaria, Crimea, Croatia, Czech Republic, Egypt, France, FYRO Macedonia, Georgia, Germany, Greece, Hungary, India, Iran, Iraq, Israel, Italy, Jordan, Kazakhstan, Kosovo, Kyrgyzstan, Lebanon, Malta, Moldova, Montenegro, Morocco, Pakistan, Portugal, Romania, Russia, Saudi Arabia, Serbia, Slovakia, Spain, Syria, Tajikistan, Tunisia, Turkey, Turkmenistan, Ukraine, Uzbekistan (Wilkerson *et al*. 2021, see below regarding Saudi Arabia).

Edwards (1913c) described *Ur. unguiculata* from a single adult male collected at Tiberias, a city in Israel located on the western shore of the Sea of Galilee. The species is widely distributed in the Mediterranean region, extending northward to Germany, eastward to southern Ukraine and the Volga delta, to middle and southwestern Asia [subspecies *pefflyi*], Iran and Pakistan (Becker *et al*. 2020; Bromley-Schnur 2021).

Stone (1961a) described subspecies *pefflyi* from eight females and 10 males collected at "Qatif Oasis, Al Hasa Province, Saudi Arabia". Today, Qatif Oasis is an urban area known as Qatif or Al-Qatif Governorate on the Persian Gulf coast of Saudi Arabia's Eastern Province (the former Al Hasa Province is now the largest governorate of the Eastern Province). Wilkerson *et al*. (2021) listed Saudi Arabia for the distribution of *unguiculata*, but this obviously came from outdated reports or records published by various researchers, *e.g.* Alahmed (2012) and Khater *et al*. (2013), who apparently were unaware of the description of subspecies *pefflyi*, as noted by Alahmed *et al*. (2019). In addition to Qatif, specimens identified merely as *Ur. unguiculata* have been collected at other locations on the Persian Gulf coast of the Eastern Province (Al Dammam and Al Khobar); Al Hasa (or Al Ahsa), the largest city of Al Hasa Governorate located about 65 km west of the Persian Gulf, named after Al Hasa Oasis; and Jezan (Jazan, also spelled Jizan, Gizan or Gazan), a port city and capital of Jazan Province, located on the Red Sea coast directly north of Yemen in southwestern Saudi Arabia (Wills *et al*. 1985; Alahmed 2012; Khater *et al*. 2013). Based on these records, Alahmed *et al*. (2019) stated that "it is unlikely that the typical form, *Ur. unguiculata unguiculata*, is present in the country".

The typical form is recorded as far south as Baghdad and Karbala, located about 100 km southwest of Baghdad, in central Iraq (Khattat 1955). Subspecies *pefflyi* has not been recorded north of Qatif in Saudi Arabia, located approximately 320 km southeast of Karbala, Iraq. Alahmed (2012) made collections of adult and larval mosquitoes at "Hafar Al Batin" (also spelled Hafr Al Batin), located about 74 km from the Iraq border in the north of Saudi Arabia's Eastern Province, but no specimens of *Ur. unguiculata* were collected.

Filatov (2017) mapped the available distribution records for *Ur. unguiculata unquiculata* in the western Palaearctic, from Portugal eastward to northern India and Kyrgyzstan, but no records were included for Saudi

Arabia. Filatov then applied a species distribution modelling approach, using maximum entropy (Maxent) software, to predict the potential distribution of the subspecies in the region based on habitat suitability determined by comparing environmental data at sites where the subspecies had been recorded with sites across the region. Most areas of the region where the typical form has been recorded were ranked as highly suitable, with some intervening and flanking areas ranked as very highly suitable, including the type locality in Israel, and moderately suitable. Except for a few small areas in northern Saudi Arabia that were rated as moderate or low suitability, all areas of the country where subspecies *pefflyi* has been recorded were found to be unsuitable. Oddly, sites in Egypt along the Nile River some distance south of the Mediterranean coast and at Siwa Oasis near the Libyan border where *Ur. unguiculata* has been recorded were also classified as environmentally unsuitable.

For his description of subspecies *pefflyi*, Stone (1961a) compared specimens from Qatif Oasis with the original description of *unguiculata* and 10 specimens (adults) from Algeria, France, Iran, Iraq, Israel and Macedonia. He noted that *pefflyi* agreed "with the typical subspecies in all particulars except as shown in the following comparative statements.

> ssp. *pefflyi*: Smaller, the wing length 1.78–2.38 mm (mean of 10 ♀♀, 10 ♂♂ 1.9 mm). Integument of thorax nearly black, paler only below the pleural scale stripe; dark scales of thorax and abdomen nearly black; usually some dark scales on venter of abdomen; lateral patches of white scales usually confined to terga 5–7.
>
> ssp. *unguiculata*: Larger, the wing length 2.21–3.4 mm (mean of 5 ♀♀, 5 ♂♂ 2.81 mm). Integument of thorax orange brown, slightly darker just mediad of marginal pale scale stripe of scutum; pleura mostly yellowish brown; dark scales of thorax and abdomen rich orange brown, but distinctly not black brown; scales of venter all pale; pale lateral scale patches of abdomen usually start on tergum 2.

The adults of the typical subspecies have been described by a number of authors (Edwards 1913c; Barraud 1934; Harant *et al*. 1952; Senevet & Andarelli 1959; Gutsevich *et al*. 1971, 1974; Becker *et al*. 2020), but most of the information in the descriptions is not comparable with the information provided by Stone (1961a). None of the authors measured the length of the wings and, not surprisingly, they do not agree on the color of the thoracic and abdominal scaling. Barraud (1934) is the only author who mentioned the color of the thoracic integument: Mesonotum dark brown or black, not orange brown (Stone); pleura brownish-black, not mostly yellowish brown (Stone).

It is obvious that *Ur. unguiculata* in Saudi Arabia is only found in isolated locations. A question which cannot be answered at this time is whether subspecies *pefflyi*, as described by Stone, can be identified as such in areas other than Qatif Oasis—after all, isolated populations more recently found in other parts of the country (Wills *et al*. 1985; Alahmed 2012; Khater *et al*. 2013) have been identified as merely "*unguiculata*".

Our impression is that the isolated populations in Saudi Arabia are relicts of a species that was more widespread in the past, with populations throughout the Arabian Peninsula until it began to dry up and become desert about 5,000 years ago (Brand 2018). In as much as the populations in Saudi Arabia are readily identifiable as *Ur. unguiculata*, and the available data indicate that it is a morphologically variable species, we believe it is in the best interests of science to regard *pefflyi* as nothing more than a morphological variant of a single species. Consequently, we hereby formally classify subspecies *pefflyi* as a synonymous name: ***pefflyi* Stone, 1961a, junior subjective synonym of *Uranotaenia* (*Pseudoficalbia*) *unguiculata* Edwards, 1913c**. Synonym *pefflyi*, which is currently listed as a species in the Encyclopedia of Life, should be removed from the list of recognized species of the genus *Uranotaenia*.

Uranotaenia (*Uranotaenia*) *novaguinensis* Peters

subspecies ***alticola*** Peters, 1963—original combination: *Uranotaenia novaguinensis alticola*. Distribution: Papua New Guinea (Peters 1963).

subspecies ***novaguinensis*** Peters, 1963—original combination: *Uranotaenia novaguinensis*. Distribution: Australia, Papua New Guinea (Wilkerson *et al*. 2021).

Peters (1963) described both the nominate form of this species and subspecies *alticola*, the former reared from larvae collected at the "edge of a slow running stream" near Maprik town in the present-day Maprik District of East Sepik Province in Papua New Guinea, and the latter from a male (holotype) and female collected at Goroka, the capital of the Eastern Highlands Province and Minj in Western Highlands District of Papua New Guinea, respectively. Peters stated that the larva of the nominate form was indistinguishable from the larva of *Ur. paranovaguinensis* but the pupa differed slightly from the pupa of that species, which he described as a new species in the same paper. He distinguished subspecies *alticola* from *novaguinensis sensu stricto* based principally on "less extensive pale hind tarsal scaling in both sexes" and noted that the larval and pupal stages, although "not definitely associated" with the adults, were "apparently indistinguishable, except for slightly greater size, from the type form." The descriptions of both forms were very superficial, especially for the immature stages, and Peters only crudely illustrated the aedeagus of the nominate form. The following extract from Peters (1963) is insightful.

> In the absence of distinguishing features in the females of *U. paranovaguinensis* and *novaguinensis*, it is difficult to be dogmatic about their respective distributions.… Males of *novaguinensis* have been found in association with the former species at Maprik and Koitaki but so far not in the Milne Bay area. Females, so far unidentified, have been found in all three areas as well as at Iamalele (Fergusson Island, D'Entrecastaux Islands, Milne Bay District). No differences could be observed between any of these females.
>
> A series of eight females of this **complex** [emphasis ours] was taken in a light trap at Yambi (about 15 miles south of Maprik). These were slightly different from "typical" females….
>
> The highland subspecies *alticola* has been taken in all three highland districts at altitudes of 5000 feet [1,524 m] and above, but so far nowhere below this altitude. Much more extensive collecting, particularly of associated larvae, pupae and adults is required to define the distribution of **this species complex** [emphasis ours]. It is most likely that such collecting will reveal not only that the complex is widely distributed throughout the New Guinea mainland, including that of Netherlands New Guinea, but that several other species or subspecies exist that have so far evaded identification.

Peters (1964) diagrammatically compared the lengths of the proboscis and legs of seven *Uranotaenia* species and the two subspecies of *novaguinensis* that were known at the time to occur on New Guinea Island. Those comparisons clearly indicate, as observed by Peters (1963), that the male of subspecies *alticola* is larger than the male of the nominate form, approximately 1.3 times larger, which is a significant difference.

In a summary of what is known about subspecies *alticola*, Lee *et al*. (1989b) noted that "Peters (1963d) examined unassociated larvae from Minj which showed no apparent differences from the larva of the type form, *n. novaguinensis*. At a later date he collected larvae associated with adults of *n. alticola* which differed at least superficially from the original batch. He concluded that it is possible that more than one species or subspecies of *Uranotaenia* is present at Minj, although he originally considered that only the form described as *n. alticola* existed there." We were unable to find a reference to a "later date" when Peters "collected larvae associated with adults of *n. alticola*."

Species of *Uranotaenia*, especially those of the subgenus *Uranotaenia*, are markedly "homogeneous" (Galindo *et al*. 1954; Peyton 1972). That said, the immature stages of most species are not fully known and have not been adequately studied. In his study of the subgenus *Pseudoficalbia* in Southeast Asia, Peyton (1977) flatly stated that "The immature stages are extremely diverse and offer many good characters for subgeneric, group and specific determinations. These are often of paramount importance in the diagnosis of species with extremely similar adults and male terminalia [genitalia]." Consequently, in view of differences in body size, pale scaling of the hindtarsi and altitudinal distribution, we believe that features of the immature stages, when definitely known for *alticola* and fully compared with those of *novaguinensis*, will show that the two forms are separate species. Accordingly, we hereby formally recognize *alticola* as a distinct species: ***Uranotaenia* (*Uranotaenia*) *alticola* Peters, 1963**. *Uranotaenia alticola* is currently listed as a species in the Encyclopedia of Life.

Uranotaenia (*Uranotaenia*) *palmeirimi* de Meillon & Rebêlo

subspecies ***dundo*** da Cunha Ramos, 1993—original combination: *Uranotaenia* (*Uranotaenia*) *palmeirimi dundo*. Distribution: Angola (Dundo) (da Cunha Ramos 1993).

subspecies ***palmeirimi*** de Meillon & Rebêlo, 1941—original combination: *Uranotaenia palmeirimi*. Distribution: Mozambique, South Africa (Jupp 1996).

Uranotaenia palmeirimi was supposedly described from a male (holotype) and a female from the Portuguese East African "Colony of Moçambique", a northern coastal area of present-day Mozambique, but "Through an error the type locality was omitted from the text originally describing this species. It was taken at Pebane in Quelimane District" (Worth & de Meillon 1960). Today, Pebane is a town and district in Zambezia Province and Quelimane is the administrative capital of the province.

All accounts of *palmeirimi* contain confusing contradictions. De Meillon & Rebêlo (1941) described the adult of the species without reference to either sex but indicated that two specimens were examined: "Type ♂ in the collection of the South African Institute for Medical Research [SAIMR], Johannesburg" and "One other female from the same locality." This was taken by catalogers to denote that the species was described from a male and a female (Stone *et al*. 1959; Knight & Stone 1977; Wilkerson *et al*. 2021). As revealed by da Cunha Ramos (1993), the listing of a type male by de Meillon & Rebêlo was in error, because the holotype is actually a female, which explains the reference to "One other female…". Despite this, da Cunha Ramos distinguished the male of the typical form from the male and female of subspecies *dundo* in a key (see below).

Subspecies *dundo* was named and described based on a series of females from Dundo, Angola, including the holotype female, nine paratype females and 14 topotypic females (da Cunha Ramos 1993). In view of this, it is disturbing that the author contrasted the female and the unknown male with the unknown male of the typical form, as follows (translated from the Portuguese).

> 2 — ♂: With a short but well-defined line of pale scales on the sides of the scutum, above the wing root; *ppn* [postpronotum] with darker, black lower half . . . . **palmeirimi palmeirimi**
>
> — ♂♀: Scutum with only a few light scales above the wing root; *ppn* uniformly light brown. . . . . **palmeirimi dundo** ssp. n.

Prior to the introduction of subspecies *dundo*, Service (1990) provided a revamped version of the original description of the female of *palmeirimi* and indicated that the male was unknown. The irony is that Service pre-empted da Cunha Ramos (1993) in noting that the type specimen of *palmeirimi* is a female: "Holotype female in the collection of South African Institute of Medical Research, Johannesburg, is badly rubbed and has all legs missing except for one hind leg. In addition there is another female in the collection, not marked as a paratype, but with the same date and collection site as holotype; this specimen has only one fore leg, with tarsomere 5 missing, no wings and is badly rubbed."

Nothing is known about the biology of either subspecies (Service 1990; da Cunha Ramos 1993). According to published records, *palmeirimi sensu stricto* has been collected at the type locality on the coast of Mozambique and Richards Bay, a town on the coast of KwaZulu-Natal Province, South Africa (Worth & de Meillon 1960; Eckard *et al*. 1988; Jupp 1996, see note below), whereas subspecies *dundo* is only known from the type locality of Dundo, Angola, where it was collected in gallery forest amid savannah (da Cunha Ramos 1993) located approximately 24 km south of the border with the Democratic Republic of the Congo. The type locality of *dundo* lies approximately 2,000 km northwest of the type locality of *palmeirimi sensu stricto*. Although the adult males, larvae and pupae of the two nominal forms are unknown, considering the distance between the type localities, the coastal versus savannah environment and the morphological features which clearly distinguish the adult females, we believe that discovery and integrated study of the unknown life stages will reveal that the two forms are distinct species. Consequently, we agree with the Encyclopedia of Life that *dundo* should be recognized as a separate species, at least until proven otherwise, and we hereby recognize it as such: ***Uranotaenia* (*Uranotaenia*) *dundo* da Cunha Ramos, 1993**.

Note. Wilkerson *et al*. (2021), in error, indicated that Jupp (1996) provided illustrations of the male and female of *Ur. palmeirimi*. Jupp distinguished *palmeirimi* from *Ur. hopkinsi* Edwards, 1932b in a key to the adults of the subgenus *Uranotaenia* in southern Africa, but he did not include illustrations for either of the two species.

Uranotaenia (*Uranotaenia*) *pulcherrima* Lynch Arribálzaga

subspecies ***elnora*** Paterson & Shannon, 1927—original combination: *Uranotaenia pulcherrima elnora*. Distribution: Argentina (Paterson & Shannon 1927).

subspecies ***pulcherrima*** Lynch Arribálzaga, 1891b—original combination: *Uranotaenia pulcherrima*. Distribution: Argentina, Belize, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, El Salvador, French Guiana, Guatemala, Guyana, Honduras, Lesser

Antilles (includes Trinidad and Tobago), Mexico, Nicaragua, Panama, Paraguay, Peru, Suriname, Uruguay, Venezuela (Wilkerson *et al*. 2021).

The recognition of *elnora* as a subspecies requires explanation, which was provided by Harbach & Howard (2007): "Paterson & Shannon (1927) published the name *elnora* as an addition to a binomen denoting subspecific rank, but labelled it as a new variety: '*Uranotaenia pulcherrima Elnora* nueva variedad'. In as much as the authors did not unambiguously indicate that the name was proposed for an infrasubspecific entity, it has subspecific rank from the date of its original publication." However, until Harbach & Howard ruled that the third part of the trinomial must be considered an indication of subspecific rank, *elnora* was regarded as a variety of *pulcherrima*, as originally specified (Edwards 1932a; Lane 1953; Stone *et al*. 1959; Knight & Stone 1977). That aside, we were surprised to discover that Belkin *et al*. (1968), in their treatment of the mosquitoes originally described from Argentina, had considered *elnora* to be a subspecies of *pulcherrima*: "*Uranotaenia elnora* Paterson & Shannon, 1927 [ssp. of *pulcherrima*]."

We find it extraordinary that there has been no taxonomic treatment or recognition of *elnora* as a distinct taxon since it was described by Paterson & Shannon (1927). Lane (1953) listed *elnora* as a variety but only described the nominate form, with no mention of *elnora*. Mitchell & Darsie (1985), in keys to the mosquitoes of Argentina, noted: "The type locality of the typical species is Las Conchas, Buenos Aires Province (Knight & Stone 1977). A valid subspecies, *elnora* Paterson & Shannon, was described in 1927 from an adult female collected in Tres Posos, Embarcacion, Salta Province. The distribution records given above for *pulcherrima* (var. *pulcherrima*) include those for var. *elnora*." Subspecies *elnora* is not listed in the recent checklists of the mosquitoes known to occur in Argentina (Rossi 2015). There is a single *COI* sequence (658 bp) in GenBank (accession MW363468) obtained from a female of *Ur. pulcherrima* collected at Formosa, Lahisi Province, Argentina. The sequence was generated in the study of Laurito *et al*. (2022), who indicated that the "current distribution" of *pulcherrima* in Argentina includes the provinces of Chaco, Corrientes, Lahisi, Salta and Tucumán. It is noteworthy that Salta Province includes the type locality of *elnora*.

Paterson & Shannon (1927) provided the following brief description of the holotype female of *elnora*: "In addition to having the median line and golden scales reduced to a spot, which is normal in typical specimens of *pulcherrima*, the white rings of the anterior and middle tarsi are missing and the fifth article [tarsomere 5] of the posterior tarsus [hindtarsus] is very dark white" (translated from the Spanish). The significance of the tarsal banding is questionable, as Galindo *et al*. (1954) pointed out in a taxonomic discussion of *Ur. apicalis* Theobald, 1903a: "As usual in the *pulcherrima*-series, the extent of white on the hind tarsal segments [tarsomeres] shows much variation but with no apparent significance as to geographical distribution."

Since there is no evidence to suggest that *elnora* is anything more than a variant of *pulcherrima*, as originally perceived, we believe it is prudent to formally recognize it as a synonymous name: ***elnora* Paterson & Shannon, 1927, junior subjective synonym of *Uranotaenia* (*Uranotaenia*) *pulcherrima* Lynch Arribálzaga, 1891b**. The nominal variety *elnora*, which is listed as a species in the Encyclopedia of Life, must be removed from the list of valid species of *Uranotaenia*.

In addition to *elnora*, *Ur. pulcherrima* has two other synonyms: *Ur. urania* Shannon & del Ponte, 1928 (synonymy by Lane 1951) and *Ur. pulcherrima* var. *modesta* Martini, 1935 (synonymy by Lane 1953). The former was described from a male and a female captured at Resistencia, Chaco Province, Argentina and the latter was described from a female collected in virgin forest, 5 km south of Rio Cacao (New River?, Orange Walk District), British Honduras (present-day Belize). It is possible that comparative morphological and molecular study of topotypic material may show that *Ur. pulcherrima* is a complex of species.

Wyeomyia (*Miamyia*) *hosautos* Dyar & Knab

subspecies ***hosautos*** Dyar & Knab, 1907—original combination: *Wyeomyia hosautus* [*sic*]. Distribution: Brazil, Colombia, Panama (Wilkerson *et al*. 2021).

subspecies ***leucotarsis*** Lane, 1936b—original combination: *Wyeomyia hosautos* var. *leucotarsis* (subspecific status by Harbach & Howard 2007). Distribution: Brazil (Lane 1936b).

Wyeomyia hosautos has two synonyms: *Wy. euethes* and *Wy. symmachus*, both described by Dyar & Knab (1909b). The three nominal forms were all described from females and have the same type locality, *i.e.* Tabernilla, Canal

Zone, Panama. Howard *et al*. (1915) synonymized *euethes* with *symmachus*, which they treated as a species separate from *hosautos*. That synonymy was recognized by Dyar (1919a), but he later (Dyar 1922) recognized both *euethes* and *symmachus* as synonyms of *hosautos* (without explanation but apparently for the reason given below). In summary, Dyar (1922) is credited with the synonymy of *euethes* and *symmachus* with *hosautos*, which continued to be recognized until the present (Dyar 1923; Bonne & Bonne-Wepster 1925; Dyar 1928; Edwards 1932a; Lane 1953; Stone *et al*. 1959; Knight & Stone 1977; Harbach 2018; Wilkerson *et al*. 2021).

The nominotypical form was described from a single adult. Dyar & Knab (1909b) did not mention the sex of the specimen; consequently, it was indicated merely as an adult (A) in the catalogs of Stone *et al*. (1959), Knight & Stone (1977) and Wilkerson *et al*. (2021). However, the specimen is obviously a female based on Dyar (1928), who described the female and explicitly stated that the male and larva were unknown. The specimen (holotype) is in the collection of the National Museum of Natural History, Washington, D.C. (Stone & Knight 1957b). *Wyeomyia euethes* was described from one female and *Wy*. *symmachus* was described from two females bred from larvae (Dyar & Knab 1909b).

Subspecies *leucotarsis* was described from eight specimens captured on human bait in forest in Bôa Esperança and Pocinho, state of Mato Grosso, Brazil (Lane 1936b). The location of the eight syntypes is unknown (Belkin *et al*. 1971).

The recognition of *leucotarsis*, originally described as a variety (Lane 1936b) and raised to subspecific rank by Harbach & Howard (2007), "Because Lane clearly did not propose the name for an infrasubspecific entity" (Article 45.6.4, *International Code of Zoological Nomenclature*), is based solely on the presence of more extensive pale scaling on the hindtarsus than is present in *hosautos sensu stricto*. Lane (1936b) stated: "…in this species [*hosautos*] only the two distal tarsi [tarsomeres] of the hind tarsi are marked in white. In our specimens this marking is much more extensive and goes from the distal portion of the second to fifth tarsus [hindtarsomeres 2–5]. For this reason, we believe that this species is new, which could only be proven with a more complete biology, or a variety. Since this is the only difference, we prefer to take this last option [translated from the Portuguese]."

It is interesting that Dyar & Knab (1907) only mentioned the pale scaling of the midleg, not the hindleg, in the original description of *hosautos*: "the middle legs with the tip of the second and the succeeding joints [tarsomeres] silvery white on the inner side". In contrast, Dyar & Knab (1909b) described *euethes* as having "…the mid tarsi with the tip of the second, the third to fifth joints white below, hind tarsi with the fourth and fifth joints white below except at the tip" and described *symmachus* as having the "hind tarsi with the last two joints white-scaled beneath nearly to their apices; mid tarsi with the apical three-fourths of the second, and all of the succeeding joints silvery white-scaled beneath". Obviously, the synonymy of *euethes* and *symmachus* with *hosautos* by Dyar (1922) signifies that hindtarsomeres 4 and 5 of *hosautos* are also white-scaled beneath (ventrally). We note that midtarsomere 2 is more extensively pale-scaled in *symmachus*, which may be a specific difference, but choose to retain it as a synonym of *hosautos* pending further study.

Based on what is presently known about pale scaling on the legs of other New World sabethines, there seems to be little doubt that the position and degree of pale markings, particularly on the mid- and hindlegs, is a distinctive feature of individual species. For this reason, we feel that Lane (1936b) should have acted on his intuitive belief and should have described *leucotarsis* as a new species. Accordingly, we hereby upgrade *leucotarsis* to the rank of species: ***Wyeomyia* (*Miamyia*) *leucotarsis* Lane, 1936b**. We firmly believe that further collection and comparative study of link-reared adults with associated larval and pupal stages and dissected male genitalia will confirm that *Wy*. *leucotarsis* and *Wy*. *hosautos* are separate species, which appear to have separate geographic distributions. *Wyeomyia leucotarsis* is currently listed as a species in the Encyclopedia of Life.

Discussion

The genesis of this detailed review came from the realization that the subspecies category in mosquitoes does not fulfill theoretical, operational or practical functions. We unequivocally conclude that it should not be used as a taxonomic rank.

We found this opinion about subspecies to be widespread among animal taxonomists, as articulated by de Queiroz (1998, 1999, 2005a, 2005b, 2007, 2020, 2021), Padial & De la Riva (2021) and Burbrink *et al.* (2022). Crucially, there is no phylogenetic definition of a subspecies. Without a definition, researchers have been left to imagine what a subspecies might be and usually applied the rank to describe variation. We presume it was a common belief among mosquito taxonomists in the early to mid-20th century that if a form is similar to a given species, but somewhat different, it could be interpreted as a subspecies. This variation could be local or temporal, or represent a valid species. Because of a lack of a definition, attributes and distributions of subspecies are often combined with the nominotypical form (really just the oldest name), thus possibly obscuring significant genetic differences. Or, subspecies are simply ignored, for example, Irish *et al.* (2020) published a list of *Anopheles* species in the Afrotropical Region and stated that "Subspecies names are not included in the current list, only the nominal species is given." Consequently, the following *Anopheles* species, elevated by us, were not acknowledged to exist: *Anopheles* (*Cellia*) *hispaniola*, *basilewskyi*, *nigeriensis*, *rupicolus*, *rufipes*, *macmahoni*, *ugandae* and *ungujae*. There are many other such examples throughout this monograph.

In accordance with the above first-mentioned authors, we sought indications that a subspecies either met the definition of a phylogenetic species, and therefore was a species, or, conversely, did not meet the criteria for specific status and was a synonym (see the Material and Methods for the four criteria that guided our methodology). We scrutinized original descriptions, re-descriptions, taxonomic notes, biological research papers, and regional and taxonomic monographs for indications of internal phylogenetic unity, or lack thereof. There were many instances where we were unsure of or even mystified by author's decisions to name subspecies. We often had to fill in or guess at missing information since standard parallel sets of characters for species descriptions are not common, especially in earlier works. Typically, molecular evidence was not available to inform our decisions about phylogenetic relatedness. We therefore mostly based our assessments on morphological, biological and distributional data. Our primary species indicators were consistent correlated characters and expert opinions, mostly our own.

We concluded that among 120 nominal subspecies (see Introduction) recognized prior to now that there are 94 distinct species, two incompletely separated species, 22 synonyms, one *nomen dubium* and a *species inquirenda*. We also revalidated four species previously considered to be synonyms.

A significant inference that can be made from this in-depth study of only about 3% of all currently recognized species is that there is a serious deficiency in what is known about mosquito taxonomy. This is the "tip of an iceberg". There are many species described herein that lack one or more life stages, lack detailed descriptions, reliable distributional records and molecular data. From our experience, information available for all the other mosquito species is equally deficient. Also, we note in the small number of species treated herein that 19 are probably associated with unrecognized species complexes. Closer examination of these and re-evaluation of the many culicid synonyms (2,000+) is critically needed. The magnitude of our ignorance of true species diversity in mosquitoes is suggested in Harbach's (2007) estimate that probably 3–5 times the number of currently known species are yet to be discovered and named. It is our hope that the analyses contained in this monograph will inspire researchers to resolve species boundaries—to determine whether the names of nominal species represent the same or different species, or species new to science.

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Authors' names and the wording of articles are written exactly as they were originally published, including compound names, diacritical marks, special symbols, improper italicization and the misspelling of mosquitoes (as 'mosquitos'). The word "*sic*" is only used to indicate obvious spelling mistakes. Also, titles published in capital letters are reproduced here in lower case letters, except for the first letter of proper names that must begin with a capital letter, and genus and species names are italicized in cases where they were not italicized in published titles.

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Conspectus of taxonomic changes

***Aedes* (*Aedimorphus*)**
- *adenensis* Edwards, 1941, to specific rank
- *angolae* Ribeiro & Ramos, 1974, to specific rank
- *arabiensis* (Patton, 1905), to specific rank
- *bwamba* van Someren, 1950, to specific rank
- *kabwachensis* Edwards, 1941, to specific rank
- *mesostictus* Harbach, 2018, to specific rank
- *nipponii* (Theobald, 1907), to specific rank
- *nocturnus* (Theobald, 1903a), to specific rank

***Aedes* (*Bifidistylus*)**
- *kumbae* Chwatt, 1948, synonymy with *boneti* Gil Collado, 1936

***Aedes* (*Collessius*)**
- *vicarius* Lien, 1968, to specific rank

***Aedes* (*Mucidus*)**
- *chrysogaster* (Taylor, 1927), to specific rank

***Aedes* (*Neomelaniconion*)**
- *aureus* Gutsevich, 1955, to specific rank

***Aedes* (*Ochlerotatus*)**
- *asiaticus* Edwards, 1926b, to specific rank
- *daisetsuzanus* Tanaka, Mizusawa & Saugstad, 1979, to specific rank
- *gyirongensis* Ma, 1982, to specific rank
- *hargreavesi* (Edwards, 1920), to specific rank
- *idahoensis* (Theobald, 1903a), to specific rank
- *ludlowae* (Blanchard, 1905), to specific rank
- *mathesoni* Middlekauff, 1944, synonymy with *canadensis* (Theobald, 1901c)
- *meirai* Ribeiro, da Cunha Ramos, Capela & Pires, 1980, synonymy with *caspius* (Pallas, 1771)
- *pallens* Ross, 1943, to specific rank
- *vansomerenae* Mattingly, 1955, to specific rank

***Aedes* (*Phagomyia*)**
- *kotiensis* Barraud, 1934, synonymy with *gubernatoris* (Giles, 1901a)

***Aedes* (*Pseudarmigeres*)**
- *dunni* Evans, 1928, synonymy with *argenteoventralis* (Theobald, 1909)
- *gurneri* (van Someren, 1946), to specific rank

***Aedes* (*Rampamyia*)**
- *montanus* Brug, 1939, to specific rank

***Aedes* (*Rusticoidus*)**
- *subtrichurus* Martini, 1927, synonymy with *rusticus* (Rossi, 1790)

***Aedes* (*Stegomyia*)**
- *downsi* Bohart & Ingram, 1946a, to specific rank
- *formosus* (Walker, 1848), to specific rank
- *imitator* (Leicester, 1908), to specific rank
- *miyarai* Tanaka, Mizusawa & Saugstad, 1979, to specific rank
- *quadricinctus* (Barraud, 1923b), synonymy with *annandalei* (Theobald, 1910a)

***Anopheles* (*Anopheles*)**
- *argentinus* (Brèthes, 1912), from synonymy to specific rank
- *barbiventris* Brug, 1938, to specific rank
- *crockeri* Colless, 1955, to specific rank
- *danaubento* Mochtar & Walandouw, 1934, to specific rank
- *formosus* Ludlow, 1909a, to specific rank

geometricus Corrêa, 1944, to specific rank
guatemalensis de León, 1938, synonymy with *parapunctipennis* Martini, 1932
levicastilloi Levi Castillo, 1944, to specific rank
neghmei Mann, 1950, to specific rank
noei Mann, 1950, to specific rank
oedjalikalah Nainggolan, 1939, synonymy with *danaubento* Mochtar & Walandouw, 1934
pantjarbatu Waktoedi Koesoemawinangoen, 1954, synonymy with *danaubento* Mochtar & Walandouw, 1934
patersoni Alvarado & Heredia, 1947, synonymy with *argentinus* (Brèthes, 1912)
peruvianus Tamayo, 1907, *nomen dubium*
refutans Alcock, 1913, to specific rank
rivadeneirai Levi-Castillo, 1945, to specific rank
tucumanus Lahille, 1912, synonymy with *argentinus* (Brèthes, 1912)

***Anopheles* (*Cellia*)**
basilewskyi Leleup, 1957, to specific rank
broussesi Edwards, 1929a, to specific rank
hispaniola Theobald, 1903, to specific rank
kalawara Stoker & Waktoedi Koesoemawinangoen, 1949, *nomen dubium*
macmahoni Evans, 1936, to specific rank
nigeriensis Evans, 1931, to specific rank
orientalis Swellengrebel & Swellengrebel de Graaf, 1920, *species inquirenda*
rupicolus Lewis, 1937, to specific rank
telamali Saliternik & Theodor, 1942, synonymy with *turkhudi* Liston, 1901
torakala Stoker & Waktoedi Koesoemawinangoen, 1949, to specific rank
ugandae Evans, 1934, to specific rank
ungujae White, 1975, to specific rank

***Culex* (*Culex*)**
abyssinicus Edwards, 1941, to specific rank
aenescens Edwards, 1941, to specific rank
bwambanus Edwards, 1941, to specific rank
draconis Ingram & de Meillon, 1927, to specific rank
elgonicus Edwards, 1941, to specific rank
eschirasi Galliard, 1931, to specific rank
farakoensis Hamon, 1955, to specific rank
gediensis Edwards, 1941, to specific status
joanae Muspratt, 1955, synonymy with *striatipes* Edwards, 1941
kartalae Brunhes, 1977, to specific rank
kingii (Theobald, 1913), to specific rank
macrophyllus Edwards & Gibbins, 1939, to specific rank
marianae Bohart & Ingram, 1946, to specific rank
pallens Coquillett, 1898, to specific rank
sudanicus Edwards, 1941, synonymy with *guiarti* Blanchard, 1905
ugandae van Someren, 1967, to specific rank
vexillatus Edwards, 1941, to specific rank
vicinalis de Meillon & Lavoipierre, 1944, to specific rank

***Culex* (*Culiciomyia*)**
pseudocinereus Theobald, 1901c, to specific rank

***Culex* (*Eumelanomyia*)**
rageaui (Hamon & Rickenbach, 1955), to specific rank
ryukyuanus Tanaka, Mizusawa & Saugstad, 1979, to specific rank

***Culex* (*Lophoceraomyia*)**
sumatranus Brug, 1931, to specific rank

***Culex* (*Maillotia*)**
capensis de Meillon, 1935, to specific rank
coursi Doucet, 1949, to specific rank
maderensis Mattingly, 1955, synonymy with *hortensis* Ficalbi, 1889
***Culex* (*Microculex*)**
retrosus Lane & Whitman, 1951, to specific rank
fuscatus Lane & Whitman, 1951, to specific rank
***Culex* (*Oculeomyia*)**
consimilis Newstead, 1907, to specific rank
ellinorae Ovazza, Hamon & Neri, 1956, to specific rank
jinjaensis Edwards, 1941, to specific rank
major Edwards, 1935, from synonymy to specific rank

***Culiseta* (*Culicella*)**
amurensis Maslov, 1964, synonymy with *ochroptera* (Peus, 1935)
minnesotae Barr, 1957, to specific rank
nipponica La Casse & Yamaguti, 1950, to specific rank

***Culiseta* (*Culiseta*)**
indica (Edwards, 1920), to specific rank
atritarsalis (Dobrotworsky, 1954), to specific rank

Eretmopodites
conchobius Edwards, 1941, to specific rank
douceti Adam & Hamon, 1959, to specific rank

***Mansonia* (*Mansonioides*)**
nigerrima Theobald, 1910, synonymy with *africana* (Theobald, 1901c)

***Mimomyia* (*Mimomyia*)**
clavipalpus (Theobald, 1908), to specific rank
metallica (Leicester, 1908), synonymy with *chamberlaini* Ludlow, 1904

***Toxorhynchites* (*Afrorhynchus*)**
voltaicus Ribeiro, 2005, synonymy with *viridibasis* (Edwards, 1935)
***Toxorhynchites* (*Lynchiella*)**
separatus (Lynch Arribálzaga, 1891), to specific rank
septentrionalis (Dyar & Knab, 1906c), to specific rank
superbus (Dyar & Knab, 1906a), to specific rank
***Toxorhynchites* (*Toxorhynchites*)**
abyssinicus Ribeiro, 1991, to specific rank
albitarsis (Brug, 1939), to specific rank
aurifluus (Edwards, 1921a), to specific rank
conradti Grünberg, 1907, to specific rank
yaeyamae Bohart, 1956, to specific rank
yamadai (Ôuchi, 1939), to specific rank

Trichoprosopon
mogilasium (Dyar & Knab, 1907), to specific rank
townsendi Stone, 1944, to specific rank
trichorryes Dyar and Knab, 1907, from synonymy to specific rank
***Tripteroides* (*Tripteroides*)**

escodae Baisas & Ubaldo-Pagayon, 1953, to specific rank
laffooni Baisas & Ubaldo-Pagayon, 1953, to specific rank
mattinglyi Baisas & Ubaldo-Pagayon, 1953, to specific rank

***Uranotaenia* (*Pseudoficalbia*)**
pefflyi Stone, 1961a, synonymy with *unguiculata* Edwards, 1913c
syntheta Dyar & Shannon, 1924, to specific rank
ryukyuana Tanaka, Mizusawa & Saugstad, 1979, to specific rank
***Uranotaenia* (*Uranotaenia*)**
elnora Paterson & Shannon, 1927, synonymy with *pulcherrima* Lynch Arribálzaga, 1891b
alticola Peters, 1963, to specific rank
dundo da Cunha Ramos, 1993, to specific rank

***Wyeomyia* (*Miamyia*)**
leucotarsis Lane, 1936b, to specific rank

Species and the Encyclopedia of Life

With few exceptions, all taxa recognized as subspecies by mosquito workers (Harbach 2018; Wilkerson *et al.* 2021) were listed as species in the Encyclopedia of Life (EoL) without consulting mosquito taxonomists. The specific status of 91 of those taxa is formally established herein and they should continue to be listed in the EoL; 18 are synonymized with nominotypical forms and should not be listed as species therein. Furthermore, eight nominal taxa previously recognized as subspecies that are now recognized as species (not listed in the EoL) and two nominal taxa removed from synonymy need to be listed in the EoL. Two nominal species, one a *nomen dubium* and the other a *species inquirenda*, should be removed from the EoL until their status is formally resolved. Species to be retained, added or removed from the EoL, including the 13 nominal taxa (indicated with an asterisk*) for which their status was changed before or after they were listed as subspecies in the works of Harbach (2018) and Wilkerson *et al.* (2021) (see page 8), are detailed below, with corrections to the date of authorship of two species currently listed in the EoL.

Nominal taxa (previous subspecies) to be retained as species in the Encyclopedia of Life

***Aedes* Meigen, 1818**
adenensis Edwards, 1941
amamiensis Tanaka, Mizusawa & Saugstad, 1979*
angolae Ribeiro & Ramos, 1974—correct authorship to both authors
arabiensis (Patton, 1905)
asiaticus Edwards, 1926b
aureus Gutsevich, 1955
bwamba van Someren, 1950
chrysogaster (Taylor, 1927)
daisetsuzanus Tanaka, Mizusawa & Saugstad, 1979
downsi Bohart & Ingram, 1946a
formosus (Walker, 1848)
gurneri (van Someren, 1946a)
gyirongensis Ma, 1982
hargreavesi (Edwards, 1920)
idahoensis (Theobald, 1903a)
imitator (Leicester, 1908)
kabwachensis Edwards, 1941
ludlowae (Blanchard, 1905)
mesostictus Harbach, 2018—replacement name for *mediopunctatus* (Theobald, 1909)
miyarai Tanaka, Mizusawa & Saugstad, 1979
montanus Brug, 1939
nocturnus (Theobald, 1903a)
pallens Ross, 1943
shintienensis Tsai & Lien, 1950*
vansomerenae Mattingly, 1955
vicarius Lien, 1968
yaeyamensis Tanaka, Mizusawa & Saugstad, 1979*
***Anopheles* Meigen, 1818**
barbiventris Brug, 1938
basilewskyi Leleup, 1957
benguetensis King, 1931*
broussesi Edwards, 1929a
cameronensis Edwards, 1929b*

crockeri Colless, 1955
danaubento Mochtar & Walandouw, 1934
formosus Ludlow, 1909a
geometricus Corrêa, 1944
hispaniola Theobald, 1903
japonicus Yamada, 1918*
levicastilloi Levi-Castillo, 1944
macmahoni Evans, 1936
neghmei Mann, 1950
noei Mann, 1950
pleccau Koidzumi, 1924*
refutans Alcock, 1913
rivadeneirai Levi-Castillo, 1945
rupicolus Lewis, 1937
simlensis (James, 1911)*
torakala Stoker & Waktoedi Koesoemawinangoen, 1949
ugandae Evans, 1934
ungujae White, 1975

***Culex* Linnaeus, 1758**
aenescens Edwards, 1941
bwambanus Edwards, 1941
coursi Doucet (1949)
draconis Ingram & de Meillon, 1927
elgonicus Edwards, 1926a
ellinorae Ovazza, Hamon & Neri, 1956
eschirasi Galliard, 1931
farakoensis Hamon, 1955—change date of authorship, publication delayed to 1955
fuscatus Lane & Whitman, 1951
gediensis Edwards, 1941
jinjaensis Edwards, 1941
kartalae Brunhes, 1977
kingii (Theobald, 1913c)
macrophyllus Edwards & Gibbins, 1939
marianae Bohart & Ingram, 1946b
pseudocinereus Theobald, 1901b
rageaui Hamon & Rickenbach, 1955
retrosus Lane & Whitman, 1961
ryukyuanus Tanaka, Mizusawa & Saugstad, 1979
sumatranus Brug, 1931
ugandae van Someren, 1967
vexillatus Edwards, 1941
vicinalis de Meillon & Lavoipierre, 1944

***Culiseta* Felt, 1904**
atritarsalis (Dobrotworsky, 1954)
indica (Edwards, 1920)
minnesotae Barr, 1957
nipponica La Casse & Yamaguti, 1950

***Eretmapodites* Theobald, 1901c**
brevis Edwards, 1941*
conchobius Edwards, 1941
douceti Adam & Hamon, 1959—change date of authorship, publication delayed to 1959

***Mimomyia* Theobald, 1903a**
clavipalpus (Theobald, 1908b)

***Toxorhynchites* Theobald, 1901b**
abyssinicus Ribeiro, 1991
albitarsis (Brug, 1939)
aurifluus (Edwards, 1921a)
conradti Grünberg, 1907
separatus (Lynch Arribálzaga, 1891b)
septentrionalis (Dyar & Knab, 1906a)
superbus (Dyar & Knab, 1906a)
yaeyamae Bohart, 1956
yamadai (Ôuchi, 1939)

***Trichoprosopon* Theobald, 1901a**
escodae Baisas & Ubaldo-Pagayon, 1953
mattinglyi Baisas & Ubaldo-Pagayon, 1953
townsendi Stone, 1944

***Tripteroides* Giles, 1904**
mogilasium (Dyar & Knab, 1907)
yaeyamensis Tanaka, Mizusawa & Saugstad, 1979*

***Uranotaenia* Lynch Arribálzaga, 1891a**
alticola Peters, 1963
dundo da Cunha Ramos, 1993
ryukyuana Tanaka, Mizusawa & Saugstad, 1979
syntheta Dyar & Shannon, 1924

***Wyeomyia* Theobald, 1901a**
leucotarsis Lane, 1936b

Nominal taxa (previous subspecies) to be included as species in the Encyclopedia of Life

***Aedes* Meigen, 1818**
nipponii (Theobald, 1907)

***Anopheles* Meigen, 1818**
argentinus (Brèthes, 1912)
nigeriensis Evans, 1931

***Culex* Linnaeus, 1758**
abyssinicus Edwards, 1941
capensis de Meillon, 1935
consimilis Newstead, 1907
pallens Coquillett, 1898

***Tripteroides* Giles, 1904**
laffooni Baisas & Ubaldo-Pagayon, 1953

Nominal taxa (synonyms) to be removed from the Encyclopedia of Life

***Aedes* Meigen, 1818**
kumbae Chwatt, 1948
mathesoni Middlekauff, 1944
meirai Ribeiro, da Cunha Ramos, Capela & Pires, 1980
quadricinctus (Barraud, 1923b)

subtrichurus Martini, 1927
sureilensis Barraud, 1934*

***Anopheles* Meigen, 1818**
guatemalensis de León, 1938
kalawara Stoker & Waktoedi Koesoemawinangoen, 1949—*nomen dubium*
oedjalikalah Nainggolan, 1939
ohamai Ohama, 1947
orientalis Swellengrebel & Swellengrebel de Graaf, 1920—*species inquirenda*
pantjarbatu Waktoedi Koesoemawinangoen, 1954
patersoni Alvarado & Heredia, 1947
telamali Saliternik & Theodor, 1942

***Armigeres* Theobald, 1901b**
chrysocorporis Hsieh & Liao, 1956*

***Culex* Linnaeus, 1758**
joanae Muspratt, 1955
maderensis Mattingly, 1955
sudanicus Edwards, 1941

***Culiseta* Felt, 1904**
amurensis Maslov, 1964

***Mansonia* Blanchard, 1901**
nigerrima Theobald, 1910

***Toxorhynchites* Theobald, 1901b**
voltaicus Ribeiro, 2005

***Uranotaenia* Lynch Arribálzaga, 1891a**
elnora Paterson & Shannon, 1927
pefflyi Stone, 1961a

Previous synonymous taxa to be listed as species in the Encyclopedia of Life

***Culex* Linnaeus, 1758**
major Edwards, 1935

***Trichoprosopon* Theobald, 1901a**
trichorryes (Dyar & Knab, 1907)

The following subspecies, now recognized as synonyms of nominotypical forms, are not, and should not, be listed in the Encyclopedia of Life.

dunni Evans, 1928, synonym of *Aedes argenteoventralis* (Theobald, 1909)
kotiensis Barraud, 1934, synonym of *Aedes gubernatoris* (Giles, 1901a)
metallica (Leicester, 1908), synonym of *Mimomyia chamberlaini* Ludlow, 1904b

Index to taxonomic names

Family-group names and the names of genera, subgenera and species treated as valid in the works of Harbach (2018) and Wilkerson *et al*. (2021) are in **boldface type**; however, genus and subgenus names following specific names are in *italic type*. The names of subspecies treated as valid species in this work are also in boldface type. The names of subspecies newly considered to be synonyms or invalid herein, and species group taxa recognized as synonyms in the works cited above, are in *italic type*. Informal species groups are in Roman type.