

Controversies over the scientific name of the principal mosquito vector of yellow fever virus – expediency versus validity

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Received 17 January 2018; Accepted 15 February 2018

ABSTRACT: The history of the scientific name of the yellow fever mosquito, the vector of yellow fever virus, ranges from 1757 to the early twenty-first century. In his 1757 work *Iter Palaestinum*, Frederic Hasselquist gave the name *Culex aegypti* to a mosquito species responsible for fierce attacks on humans in Egypt. That name was never later ascribed to Hasselquist as author, but to Linnaeus, although the name never appeared in any of Linnaeus' publications. In Cuba, at the end of the nineteenth century, the vector of the unknown infectious agent of yellow fever was first identified as *Culex mosquito* and later more validly named *Stegomyia fasciata*. Mosquito taxonomists differed strongly about the name of the mosquito through much of the twentieth century. Interventions by the International Commission on Zoological Nomenclature imposed a biologically invalid specific name, and in the early twenty-first century a phylogenetic analysis of the culicid tribe Aedini restored the genus *Stegomyia* from a century earlier. That action was short-lived. A phylogenetic reassessment resulted in the return of *Stegomyia* to subgeneric rank in *Aedes*; thus, the name of the yellow fever mosquito survives in the traditional classification of convenience as the trinomial *Aedes (Stegomyia) aegypti* (Linnaeus). **Journal of Vector Ecology 43 (1): 1-14. 2018.**

Keyword Index: *Aedes aegypti*, classification, *Culex mosquito*, Hasselquist, Linnaeus, *Stegomyia fasciata*.

INTRODUCTION

1. At the start of modern zoological nomenclature

The hierarchical classification of animals adopted by Carl Linnaeus in his multi-edition work *Systema Naturae*, first published in 1735, was based on the ranks of class, order, family, genus, and species. The principles and development of Linnaeus' classification of animals are described in this section. Subsections reveal information that existed before Linnaeus and influenced the beginning of binomial nomenclature, including the source of the names *Culex* and *aegypti*, among others, which are attributed to Linnaeus.

The contents of *Systema Naturae* have made such a great contribution to animal classification that there is a tendency to credit Linnaeus with more than is historically appropriate. So here, summarized accounts are given to pertinent accomplishments of Aristotle and Ulisse Aldrovandi, who had worked well over one millennium and more than one century before Linnaeus, respectively.

1.1. Aristotle 384–322 BCE

Aristotle's works 'The History of the Animals' and 'On the Parts of Animals,' the latter written in 350 BCE (Before Common or Current Era), provided detailed descriptions of the biology, behavior, and inter-relationships of animals of many types. The group he named *ἐντομον* (in Latin 'entomon'), meaning notch or insect, included not only insects but also myriapods and arachnids. Particular insect groups included locusts, cicadas, bees, and flies.

1.2. Ulisse Aldrovandi (1522–1605)

Ulisse Aldrovandi was born on 11 September 1522 in Bologna, which at that time was a part of the Papal States. He obtained a degree in medicine and philosophy and in 1561 became the first

professor of natural sciences at the University of Bologna. In 1568, he brought about the creation of the University's botanical garden. He was a great collector of natural history specimens, arranging expeditions for that purpose. Linnaeus was said to have considered him the father of natural history studies.

In 1602, near the end of his life, Aldrovandi published a book entitled *De animalibus insectis libri septem, cum cinglorum iconibus ad viuum expressis*. This work influenced successive editions of Linnaeus' *Systema Naturae*. Today, Aldrovandi and his achievements appear to be little known to animal taxonomists outside Italy.

In *De animalibus insectis*, the term *Insecta* embraced what are now the three invertebrate phyla Arthropoda, Annelida, and Mollusca. Their relationships, as perceived by Aldrovandi, were illustrated in a dendrogram (reproduced in Figure 1), at the base of which the *Insecta* were defined as follows (translated from Latin): "Insects are animals separated by incisions into equal parts like rings, whence annular as said by Alberto." The forms named *Limax* and *Toredo* by Aldrovandi are molluscs and not segmented. The first division on the dendrogram was into two branches, *Terrestria* (terrestrial) and *Aquatica* (aquatic). Further divisions produced 11 principal terminal groups (numbered 1–11 in Figure 1), associated with a total of 65 Latin names that were broadly comparable to the genera of later authors. The terrestrial invertebrates were separated into *Pedes habēt* (having feet, i.e. legs), now recognized as arthropods, and *Pedibus carent* (without legs, mostly now recognized as annelids). The former (legged taxa) were separated into *Alata* (winged) and *Aptera* (wingless). The winged *Insecta* were separated into forms with and forms without elytra. One branch of the winged insects was divided into four-winged and two-winged forms, the latter including the current dipteran names *Culex* and *Tabanus*. The *Aptera* were separated into *Paucipeda* and *Multipeda*. The aquatic animals were separated

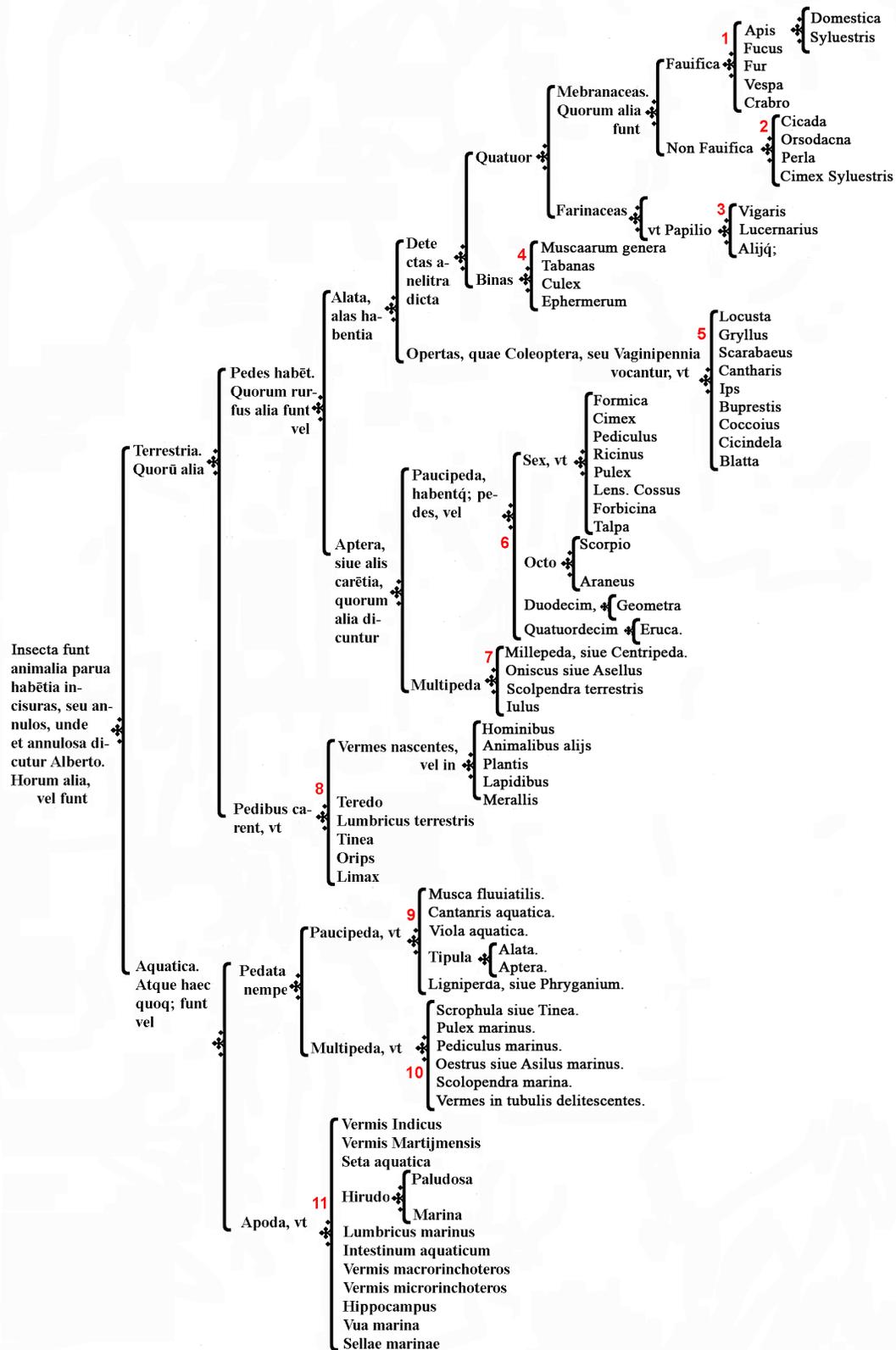


Figure 1. Reproduction (facsimile) of the dendrogram of Aldrovandi (1602) illustrating his view of the interrelationships of invertebrate animals. The basal separation is into terrestrial and aquatic groups. Aldrovandi did not italicize Latin names. The numbers in red indicate 11 principal terminal groups (not numbered in the original), many bearing names that are recognized as valid genera today.

into Pedata nempe (legged) and Apoda (legless), with the former divided into two branches, Paucipeda and Multipeda.

The historical interest of this study of invertebrate animals, and also its pertinence here, lies in its preceding by 133 years Linnaeus' 1735 work *Systema Naturae*. Both Aldrovandi and Linnaeus distinguished invertebrates from vertebrates, but Linnaeus went further and separated invertebrates into the two Classes, Insecta and Vermes. Certain of the biological units distinguished by Aldrovandi, such as those named Vespa, Locusta, or Hirudo, were ranked as genera by later authors. Some of the Latin names which are recognized today, e.g., Tinea as *Tinea* Linnaeus, would not now be placed in their positions on the dendrogram. Paired names used by Aldrovandi, such as *Lumbricus terrestris* and *Musca fluviatilis* (Figure 1), as well as *Culex communis* and *Culex maximus* (p. 386), indicate the recognition of species as constituents of genera. The groupings of 'genera' indicate recognition of higher taxonomic ranks: crudely Hymenoptera, Diptera, Arachnida, and Myriapoda. Centuries later, the name *Culex* provided the generic name used on the first identification and naming of the yellow fever mosquito, i.e., *Culex mosquito* Robineau-Desvoidy¹ (Section 2.1).

A second edition of *De animalibus insectis* appeared in 1638, from a different publisher, 33 years after Aldrovandi's death. Pages 1–767 were almost identical in text and pagination with those in the first edition. A portrait of Aldrovandi was omitted, while a list of earlier authors (Catalogus Authorum) was added, as was a species index (Aldrovandi 1638).

1.3. Carl Nilsson Linnaeus (1707–1778)

Carl Linnaeus, or in his titled name, Caroli von Linné, is universally credited with developing hierarchical classifications of plants and animals, and with assigning binomina (genus and species names) to many species. His work on animals was published principally in the magisterial work *Systema Naturae*, which he edited through 12 editions between 1735 and 1772. The 10th edition, dated 1758, has particular significance because no scientific names of animals published before those in that edition are now accepted as valid (Section 4.1). On most of his publications, which were in Latin, his name as author was spelled in the Latin genitive form as Caroli Linnæi. In 1761, he was ennobled, and in 1762 he adopted the title Carl von Linné. On his later publications, his name as author was given as Caroli a Linné. Linnaeus collected many specimens during his travels within Sweden, and he received plant and animal specimens from across the world, from his students, colleagues, and correspondents.

In 1735, Linnaeus published a work entitled *Systema Naturae*, comprising just nine leaves (of 53.5 x 41.0 cm), with 16 of the 18 pages carrying printed material. It was the first edition of works under that name, in which he grouped objects of the natural world into three Kingdoms: Lepideum (minerals), Vegetabile, and Animale. The Kingdoms Vegetabile and Animale were each divided and subdivided into taxa of four subsidiary ranks: Classes, Orders, Genera, and Species – there were no ranks of Tribe or Family. The Kingdom Animale consisted of six numbered Classes: I, Quadrupedia; II, Aves; III, Amphibia; IV, Pisces; V, Insecta; and VI, Vermes. The Class Insecta, for example, consisted of four Orders: Coleoptera, Angioptera, Hemiptera, and Aptera. The order

Angioptera consisted of nine genera, one being *Musca*, which itself consisted of some seven species: *Oestrum Vet.*, *Oestrum Laponum*, *Tabanus*, *Culex*, *Teredo nav.*, *Tipula*, and *Formica-leo*.

In 1746, Linnaeus published a similar work to the *Systema Naturae*, but restricted to animals, entitled *Fauna Svecica*, in which a numbering system was introduced that persisted through the subsequent volumes of *Systema Naturae*. The Classes of animals were numbered I–VI, while Orders were numbered sequentially within each Class. Genera were numbered sequentially from the opening of the first Class, Quadrupedia, while Species were numbered sequentially within their genus. The numbers assigned to individual genera, and particularly to individual species, increased with time as the number of named taxa increased. This system followed the increase in numbers of genera and species with time. Species were numbered in ways that could respond to their increase in numbers while still making it possible to trace them within the increasingly large number of known fauna.

During almost six decades after the appearance of the 1735 edition, the *Systema Naturae* was published in 12 further editions of increasing size. By the 9th edition published in 1756, Class I of the Kingdom Animale, formerly named Quadrupedia, was named Mammalia. Plants were grouped according to Linnaeus' *Systema Sexuale*, for use in identification not classification; animals were accorded a somewhat different classification into Classes, Orders, Genera, and Species. The 12th edition (1766–1772), in three volumes, was the last under Linnaeus' authorship, and a 13th edition (1788–1793), also in three volumes, was published by J. G. Gmelin after Linnaeus' death.

Because of the importance of the assignment of a particular mosquito species to the genus *Culex* (Section 2.2), interest here focuses on the assignment of species to the genus *Culex* in Linnaeus' publications (see Note 1, p. 11).

After Linnaeus' death in 1778, his collections passed to his son and then into other hands. In 1829, they were purchased by the Linnean Society of London. Of the zoological collections, the insects consisted chiefly of Lepidoptera and Coleoptera (Gage and Stearn 1988).

Over many years, Linnaeus made great contributions to the classification of animals, but in terms of taxonomic descriptions he is often credited with more than is historically justified. Many genera and species were described by other taxonomists before and during the first 50 years of Linnaeus' life. One remarkable example is Ulisse Aldrovandi, who in 1602, as noted above, published a book entitled *De animalibus insectis* in which invertebrates, his 'Insecta', were grouped in taxa (Figure 1) that now are assembled in the three phyla Arthropoda, Annelida, and Mollusca. Among the insect taxa he grouped such familiar names as *Apis*, *Crabro*, and *Vespa*; *Culex* and *Tabanus*; *Cimex*, *Formica*, and *Pulex*. The molluscs included *Limax* and among the annelids were *Lumbricus* and *Hirudo*. As noted above, binomials such as *Culex communis* and *Lumbricus terrestris* indicate his recognition of species as constituents of genera.

As described in Section 4.1, one outcome of the international regulation of zoological nomenclature was the arbitrary fixing of 1 January 1758 as the starting date of zoological nomenclature. The 10th edition of Linnaeus' *Systema Naturae* was deemed to have been published on 1 January 1758, and no name published before that date or that work was from then on accepted into zoological

¹ Curiously, "Culex Mosquito" appears in *De animalibus insectis* (Aldrovandi 1602: p. 385).

nomenclature. The problem of validating the many scientific names published before 1 January 1758 was solved by adopting Linnaeus as their author in place of the original authors, an action seemingly not later rendered acceptable in the *International Code of Zoological Nomenclature* (International Commission on Zoological Nomenclature 1999).

1.4. Frederic Hasselquist (1722–1752)

Frederic Hasselquist was a student and later a protégé of Linnaeus. When in 1747 he heard Linnaeus, in one of his botanical lectures, mention Palestine as a country of which the natural history was scarcely known, he was inspired to go there, and from 1749 to 1752 he traveled through the Levant (the eastern region of the Mediterranean), collecting specimens and keeping records of his observations. He described the natural history of the animals and plants that he observed, and wrote descriptions of minerals and of anything else that caught his interest. Hasselquist prepared anatomical descriptions of many plant and animal species, and he sent collections of specimens to Linnaeus and other biologists. He was one of 18 protégés of Linnaeus who travelled abroad collecting specimens and who Linnaeus referred to as his ‘apostles.’

While in the Levant, Hasselquist visited Smyrna (now Izmir in Turkey), Egypt, Palestine, and Cyprus. He remained in Egypt for almost a year, traveling widely. From Cyprus he sailed via Rhodes to Smyrna to wait for an opportunity to return to Sweden, taking with him many specimens “collected in the three kingdoms of nature.” Hasselquist published extensively during his travels, contributing to the Transactions of the Royal Academies at Uppsala and Stockholm and to other journals, and he attained a sufficient reputation in Sweden to be appointed, while in Cairo, Professor Extraordinary of Physic. He had long suffered poor health, and he died in Smyrna on 9 February 1752, age 30. Hasselquist had contracted substantial debts on his travels, and upon his death his creditors took possession of “all his collections of natural curiosities, observations and manuscripts, which they would not part with until their demands were satisfied.” Queen Louisa Ulrica of Sweden, who took an active interest in science, paid the debt and redeemed the collections, and when Hasselquist’s original manuscripts were received she ordered Linnaeus to arrange and publish them. (This brief account of Hasselquist’s career was taken from the biographical notes by Linnaeus that appeared in *Iter Palæstinum*.)

In 1757, a volume with the title *Frederic Hasselquists Iter Palæstinum... År 1749 til 1752...* (i.e., Frederic Hasselquist’s *Journey to the Holy Land...* during the years 1749 to 1752)..., which had been assembled by Linnaeus from Hasselquist’s journals, manuscripts, and letters, was published with Linnaeus named as editor (Hasselquist 1757). The greater part of this work was written in Swedish and consisted of distinct sections: (1) A short biographical introduction written by Linnaeus. (2) Descriptions of Hasselquist’s voyage and his travels through the Levant, presumably taken from his journals, which included many observations of natural history. (3) Descriptions of the principal natural curiosities found by Frederic Hasselquist. (4) Detailed anatomical descriptions of many species of animals and plants which Hasselquist had collected, arranged by Linnaeus according to the Linnaean classification. Almost all descriptions were in Latin, a very few in Swedish. The Latin description of

the species *Culex aegypti* is replicated in Table 1, accompanied by its English translation. (5) Six items written by Hasselquist, and variably in Swedish or Latin, which were entitled *Historia Naturalis Palæstinae, Philologica Sacra, Materia Medica, Medica, Commercia, and Doct. Hasselquists Bref Til Arch. och Ridd. C. Linnaeus*. The last item contained copies of 13 letters sent to Linnaeus, which were packed with biological observations. (Other letters sent to Linnaeus are available online in ‘The Linnaean Correspondence – Letters.’ http://linnaeus.c18.net/Letters/letter_list.php/). *Iter Palæstinum* was translated into English by an unnamed Swedish visitor to England and published in London in 1766 under the title *Voyages and Travels In the Levant; In the Years 1749, 50, 51, 52...* (Hasselquist 1766). Considerably modified, notably by replacement of the taxonomic section with lists of species with occasional observations on their natural history, it was reprinted in Volume 4 of *The Linnaeus Apostles: Global Science and Adventure* (Hansen 2009).

For almost three decades before publication of the 10th edition of Linnaeus’ *Systema Naturae* in 1758, specimens had accrued to Linnaeus’ insect collection (Gardiner and Morris 2007). However, only 188 species of Diptera, assigned to ten genera, were named and described in that edition. Of the six species assigned to *Culex*, only two were culicids as currently defined, namely *pipiens* and *bifurcatus*, the latter now a junior synonym of *pipiens* (Harbach et al. 1985). One further valid species of *Culex* was named in the 13th edition (1788–1793), viz. *Culex argenteus* Poir.

Many specimens collected by Hasselquist were sent to Linnaeus. The Introduction to the 1758 edition of *Systema Naturae* lists 11 collectors who had contributed specimens, including “F. HASSELQUIST in *Ægyptum & Palæstinum*. 1749.” The ‘Linnaean collection,’ which is now at the Linnaean Society of London, contains two mosquito specimens, one of which is a male of the *Anopheles maculipennis* complex. The other is a female which bears Linnaean labels inscribed ‘Culex’ and ‘1. Pipiens’; it is a species of *Aedes* (*Ochlerotatus*) but is damaged and unidentifiable to species (Harbach et al. 1985).

Comparison of the formal descriptions of insect species in Hasselquist’s 1757 *Iter Palæstinum* with those in Linnaeus’ 1758 10th edition of *Systema Naturae* reveals that Hasselquist provided much greater anatomical detail than Linnaeus. Thus, for 33 species described by Linnaeus (1758), the length of the anatomical descriptions ranged from four to 26 words, with a mean of 10.4 words. For 16 species described in Hasselquist (1757), the length of the descriptions ranged from seven to 503 words, with a mean of 134.2 words. Excluding the longest and the shortest of Hasselquist’s descriptions, the range was 34 to 293 words, with a mean of 116.9 words. The much greater anatomical detail provided by Hasselquist is clear indication that in editing the taxonomic section of *Iter Palæstinum*, Linnaeus copied the descriptions available in Hasselquist’s manuscripts.

In the biographical introduction that Linnaeus wrote for *Iter Palæstinum* (Hasselquist 1757), he stated “I have accordingly digested the Work in the best manner I could, arranged every thing under its proper *Tribe*; added *Names* to plants and animals, altered the *Technical terms* and manner of writing, without changing at least the Author’s meaning” and further “I imagined it needless to add *Synonyms*, which would have swelled the book; especially as they may easily be found in the 10th edition of my *System of*

Table 1. A replication of the species number and description of *Culex aegypti* in Hasselquist's *Iter Palaestinum* (1757: pp. 430–431), with translations of the Latin description and published comments on the species with which the name should be associated.

121. CULEX (*aegypti*) *articulationibus candidis*.

MAGNITUDO Culicis vulgaris[*]. *Linn. Syst N. I.*

COLOR. Ex fusco canus. *Crura* cana cum annulis candidis, parvis, circa articulationes & in articulis.

Puncta candida ad marginem dorsi in corpore sub alis utrinque, plura, longitudinaliter sita.

Annulus candidus ad basin thoracis, inter illum & corpus.

Linea candida, perpendicularis juxta oculos, utrinque una, parva.

LOCUS *Aegyptus*, Culice communi rarior.

*Culicis vulgaris, the common gnat, is identifiable by reference to earlier works of Linnaeus. In *Fauna Svecica* (Linnaeus 1746), the species numbered 1116 was *Culex cinereus*. In the 9th edition of *Systema Naturae* (Linnaeus 1756), species *Fn.* 1116 was *Culex vulgaris*. In Tomus I of the 10th edition of *Systema Naturae* (Linnaeus 1758), species *Fn. Svec.* 1116 was *Culex pipiens*. The English equivalent of the Latin word *culex* is gnat, midge, mosquito. English derivatives of *culex* (stem *culic-*) include *Culex*, Culicidae, Culicinae, Culicini and culicine.

The following literal translation of Hasselquist's description into English by Professor James Mountford, a Latin scholar, was reproduced in Patton (1933). Patton italicized sentences which, in his opinion, were "the most important in arriving at a conclusion as to the identity of *aegypti*."

"*Culex aegypti* with white articulations. The size of the common gnat. Colour grey from dusky (tawny blending into grey). Legs grey with white rings, small ones about (around) the articulations and in the joints. White spots on the edge of the back on the body, beneath the wings on each side, several of them, placed longitudinally. One white ring at the base of the thorax between it and the body. A white perpendicular line near the eyes, on each side a single small one. Place: Egypt, rarer than the common gnat."

Using his knowledge of the structure and appearance of mosquitoes, Mattingly (1957) retranslated certain of the original Latin words and phrases to modify Mountford's description.

"*Culex aegypti* with white articulations. The size of the common gnat. Colour hoary (suggesting a sprinkling of pale scales on a dark ground). Legs grey with white rings, small ones about (around) the articulations and in the joints. White spots on the abdomen, situated beneath the wings on either side when laid back. The first abdominal tergite pale. A white perpendicular line near the eyes, on each side a single small one. Place: Egypt, rarer than the common gnat."

Both Patton (1933) and Mattingly *et al.* (1962) considered that the description of *Culex aegypti* in Linnaeus (1758) bore a poor resemblance to *Stegomyia fasciata* (Fabricius) but a closer resemblance to *Aedes (Ochlerotatus) caspius* (Pallas) from Egypt (Section 2.4). However, the International Commission on Zoological Nomenclature (1964) validated the specific name *aegypti* Linnaeus with reference to a neotype, with the result that the name *Ae. caspius* (Pallas) remained valid (Section 4.2).

Nature, in which I have introduced these names” (cited from the 1766 English translation of Hasselquist 1757). It is apparent from those excerpts that Linnaeus introduced some specific names into *Iter Palæstinum*, which later were included in the 1758 edition of *Systema Naturae*, but how many and which are not known. The assertion by Mattingly et al. (1962), quoted by Knight (1972) and others, that “In the *Iter Palæstinum* Hasselquist employed in a number of cases Latin binominal names supplied to him by Linnaeus” is misleading.

Two species of *Culex*, numbered 120 (see Note 2, p. 12) and 121, were described in the taxonomic section of the *Iter Palæstinum*, but only the latter was named. The unnamed mosquito was described as endemic to Cyprus, and giving painful bites at night which leave inflamed pustules of longer duration than those of the common gnat. In his journal, Hasselquist described being bitten fiercely by mosquitoes (Swedish, ‘myggorne’) when near rice fields along the Nile, their density making them “intolerable and invincible.” This species was the one numbered 121 and named *Culex aegypti*. Table 1 provides the Latin description of *Culex aegypti* with English translations.

Two lines of evidence indicate that almost certainly Hasselquist, not Linnaeus, was author of the name *Culex aegypti*. (1) The description of *Culex aegypti* in the taxonomic section of *Iter Palæstinum* was of a length and detail characteristic of Hasselquist’s descriptions of insect species generally, and distinct from Linnaeus’ much briefer descriptions. (2) In his Introduction to *Iter Palæstinum* (Hasselquist 1757), Linnaeus stated that the names of animals and plants that he had introduced to that work would be found in the 10th (1758) edition of *Systema Naturae*. However, *Culex aegypti* was not among the insect species mentioned in the preceding 9th edition (1756), nor was it mentioned in either part of the 10th edition (1758, 1759a), or in any parts of the 11th (1760), 12th (1776–1772) or 13th (1788–1793) editions of *Systema Naturae*, or in his work *Animalium Specierum* (Linnaeus 1759b).

In 1762, the *Iter Palæstinum* was republished under the title *Reise nach Palästina*, with the parts that had been in Swedish translated into German by T. H. Gadesbusch. It appears that subsequently the name *Culex aegypti* was lost from the literature until it was listed as ‘aegypti Culex, Linnaeus in Hasselquist, Palast. 1762, 470’ in the volume of Sherborn’s *Index Animalium* (Sherborn 1902) for the period 1758–1800. The year 1762 suggests that Sherborn knew that a code of zoological nomenclature published after 1878 had arbitrarily fixed 1 January 1758 as the date of the starting point of zoological nomenclature (Section 4.1) (Melville 1995), but why Sherborn listed Linnaeus as author of the species named *Culex aegypti* is not known.

It is revealing to know that Linnaeus acted freely with specimens that came into his hands from other collectors overseas, as in the case of the Swedish biologist Daniel Rolander, one of his ‘apostles.’ During a visit from June, 1755 to January, 1756, Rolander collected many plants and insects in Suriname, a country on the northwestern coast of South America and under Dutch rule. After his return to Stockholm, and following a dispute over promised specimens, Linnaeus forced his entry into Rolander’s apartment where he seized a specimen of the plant *Sauvagesia* which he had been promised. In consequence, Rolander never allowed Linnaeus to examine his collections again. Yet in the 10th edition of *Systema Naturae*, published two years after Rolander’s return

from Suriname, Linnaeus used his own specific names for over 80 insects from Suriname collected by Rolander, having seen them, probably as duplicates, in the collection of the Swedish entomologist Charles de Geer. Later, in preparing the manuscript of his work *Diarium Surinamicum*, Rolander was obliged to adopt Linnaeus’ names (Dobreff 2010). The *Diarium Surinamicum* was published many years later (Rolander 2008), in English translation, as a part of Volume 3 of *The Linnaeus Apostles: Global Science and Adventure* (Hansen 2008).

2. Naming of the mosquito vector

2.1. Nineteenth century concepts

During the nineteenth century, almost all mosquito species postulated to be the vector of the infectious agent of yellow fever had initially been assigned to the genus *Culex* Linnaeus. The first five of those species to have been described and named were, in historical sequence and with their type localities, *Culex aegypti* in Hasselquist (1757) (Egypt), *Culex argenteus* Poiret, 1787 (Barbary²), *Culex fasciatus* Fabricius, 1805 (Antilles), *Culex calopus* Meigen, 1818 (Portugal), and *Culex mosquito* Robineau-Desvoidy, 1827 (Cuba). The last four of the five nominal species are now treated as junior synonyms of the first, *Culex aegypti*.

Use of certain of these names for the yellow fever mosquito, or recommendations for their use, continued into the twentieth century, e.g., *Culex argenteus* as *Aedes argenteus* by Knab (1916), Edwards (1921), and Mattingly (1957), and *Culex calopus* as *Aedes calopus* by Howard et al. (1917). In the world catalog of mosquitoes (Knight and Stone 1977), only two mosquito species were recognized as having Linnaeus as the author in their original names: *Culex pipiens* and *Culex aegypti*.

2.2. Frederick V. Theobald (1868–1930)

A committee set up by the Royal Society in 1899 to inquire into the causes and control of malaria appointed F. V. Theobald to work at the British Museum (Natural History) to prepare a monograph of the mosquitoes of the world. Theobald’s classification took shape in the first volume, published in 1901, of his five-volume series *A Monograph of the Culicidae or Mosquitoes* (Theobald 1901b, 1901c, 1903, 1907, 1910). From the outset, Theobald’s classification was criticized for the morphological characters used in the definition of genera, particularly for too much importance being given to the shape and arrangement of scales that adorn the bodies of mosquitoes. Later, other mosquito taxonomists reclassified many of the genera recognized by Theobald, reducing them to subgeneric rank or treating them as junior synonyms of other genera. However, of 28 aedine genera designated by Theobald that were subsumed by Dyar (1928) into the genus *Aedes* as subgenera, or that were reduced to junior synonyms of other genera, 14 were restored to generic rank in the series of publications by Reinert et al. (2004, 2006, 2008, 2009).

Theobald (1901a, 1901b) was concerned that the search for mosquito vectors of the malarial parasite was restricted by the belief that only species of *Anopheles* were their hosts, so that species of the large and varied genus *Culex* Linnaeus were not considered.

²The collective land of the Berber people – the region of North Africa encompassing Egypt, Libya, Tunisia, Algeria, Morocco, Niger, Mali, and the Canary Islands.

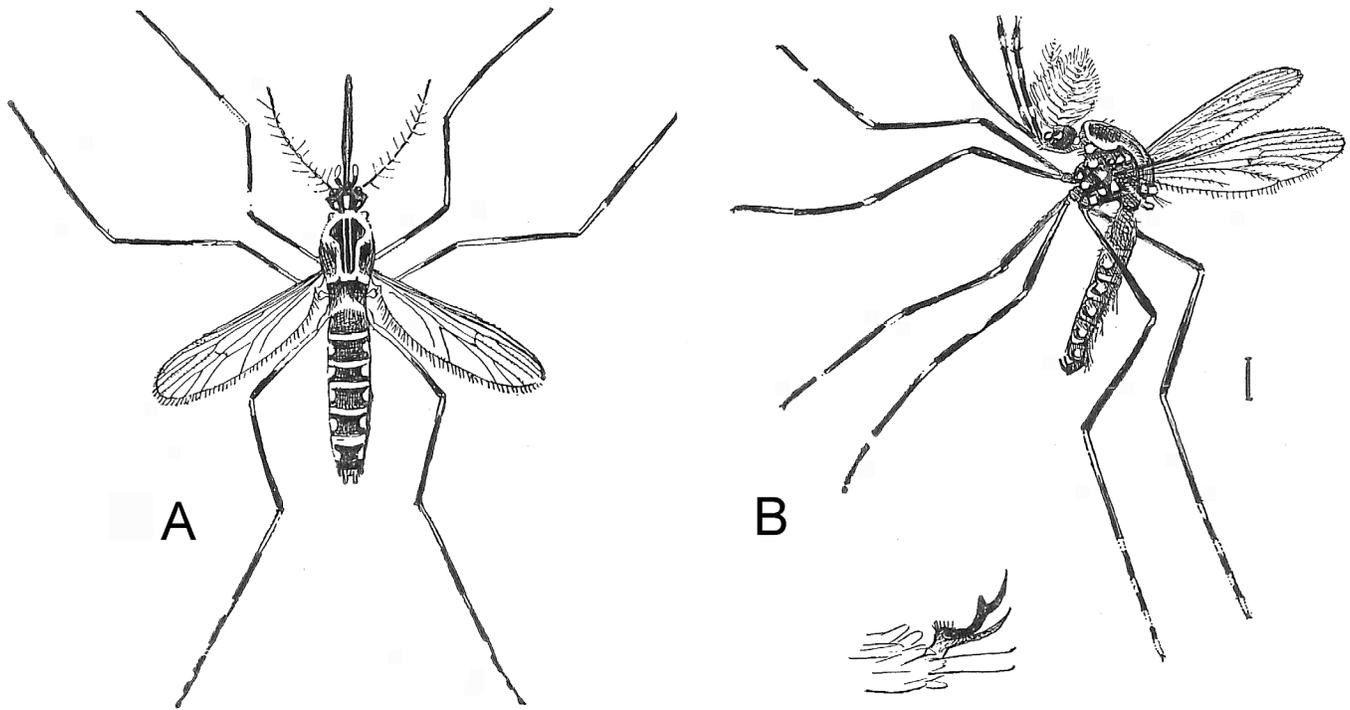


Figure 2. The yellow fever mosquito, which should be *Stegomyia aegypti* (Hasselquist), originally named *Culex fasciatus* Fabricius, 1805 = *Stegomyia fasciata* of Theobald (1901b). The drawings and the following captions, cited verbatim, are from Howard (1901). A) “FIG. 30.—*Stegomyia fasciata*, adult female; enlarged. (Author’s illustration.)” B) “FIG. 32.—Adult Male of *Stegomyia fasciata* from side: enlarged. (Author’s illustration.)” Inset shows the unguis (claws) from the tip of a leg, probably a foreleg. Characteristics that distinguish the yellow fever mosquito from *Culex aegypti* Linnaeus, as it was described by Hasselquist (1757), are the distinct white scale patterns over a black background on the scutum, notably the two lyre-shaped marks, and the distribution of white rings on the hindlegs.

He examined “some thousands of specimens, embracing three hundred odd species from different parts of the world,” finding that the structure and distribution of scales was the only character on which he could “form a satisfactory division of these insects.” He designated 12 new genus-groups from among species of the genus *Culex*, of which ten are recognized today (*Aedeomyia*, *Armigeres*, *Deinocerites*, *Eretmapodites*, *Janthinosoma*, *Mucidus*, *Stegomyia*, *Toxorhynchites*, *Trichoprosopon*, *Wyeomyia*).

Theobald (1901a) introduced the genus *Stegomyia*³, with a brief description of *Stegomyia fasciata* (Fabricius). A few months later he described 16 species of *Stegomyia*, describing *Stegomyia fasciata* in particular detail, based on specimens from the Caribbean and coastal regions of North, Central, and South America, West and East Africa, India, Southeast Asia, and eastern Australia (Theobald 1901b). From earlier correspondence with Theobald, the American taxonomist L. O. Howard was aware that Theobald had considered *Culex fasciatus* Fabricius not to be a species of *Culex*, and that he planned to “separate this mosquito from the old genus *Culex* [sic], and that he has proposed the name *Stegomyia* [sic] for the genus” (Howard 1901) (see footnote 3). Howard had earlier identified specimens of the yellow fever mosquito sent to him from Cuba as *Culex fasciatus*, so he used the name *Stegomyia fasciata* for illustrations of the yellow fever mosquito (reproduced here in Figure 2). Howard’s book was

published on 1 June 1901, preceding Theobald’s (1901a) first mention of that name in a journal article (published 15 July 1901) and the first volume of his monograph (1901b, published 23 November 1901), thus creating a problem of nomenclatural precedence. Neveu-Lemaire’s (1902) response to that problem was to replicate Theobald’s (1901b) definition of the genus *Stegomyia* and to designate *Stegomyia fasciata* (Fabricius, 1805) as the type species. More than 60 years later, this was formally recognized by the International Commission on Zoological Nomenclature (1964): “The generic name *Stegomyia** Theobald, 1901 (gender: feminine), type-species, by designation by Neveu-Lemaire, 1902, *Culex fasciatus* Fabricius, 1805, is hereby placed on the Official List of Generic Names in Zoology.” The species *Stegomyia fasciata* (Fabricius) was a logotype, i.e., determined from a written description in the absence of both a specimen and an illustration. For clarification, the asterisk in the quote above refers to a footnote which states “It has been suggested that those unfamiliar with nomenclatural procedure may form the impression that the above declaration prejudices the use of the name *aegypti* in such combinations as *Aedes aegypti* (Linnaeus) or *Aedes (Stegomyia) aegypti* (Linnaeus). This is not the case. It remains perfectly proper to employ the name in these combinations or any others that further taxonomic study may render desirable. P. F. Mattingly.”

2.3. Frederick W. Edwards (1888–1940)

Succeeding Theobald at the British Museum in 1910, F. W.

³*Stegomyia* was first validated and credited to Theobald in Howard (1901).

Edwards published extensively on mosquito taxonomy from 1911 until his death in 1940. In an article entitled “The African species of *Culex* [sic] and allied genera,” Edwards (1911) keyed and described species of *Culex*, *Mucidus*, and *Ochlerotatus* but for lack of time excluded species of the ‘*Stegomyia* group.’ Among the 12 species described in a section headed “African species not included in the preceding tables” was an entry “*C. aegypti*, Linn., Hasselquist’s *Reise nach Palestina*, p. 470 (1762)” followed by the original Latin description of the species. Presumably on the grounds that *Culex aegypti* had not been included in the three genera analyzed, Mattingly (1957) concluded that Edwards had regarded it as a *nomen incertae sedis*, i.e., a name of uncertain taxonomic position.

By re-publishing Hasselquist’s 1762 description of *Culex aegypti*, Edwards made it widely available. Unfortunately, his own later inaccurate use of it led to, and supported, serious taxonomic misconceptions. In a brief note, Dyar (1920b) wrote that Edwards had informed him that *Culex aegypti* Linnaeus “can not be other than” the yellow fever mosquito. Later, by including the trinomen *Aedes* (*Stegomyia*) *aegypti* (Linnaeus), as “*A. (S.) aegypti* Linnaeus,” in the first world catalog of mosquitoes, Edwards (1932)⁴ incorrectly established it in the traditional classification as the specific name of the yellow fever mosquito.

2.4. L. H. Gough

When working as entomologist at the Ministry of Agriculture in Egypt, Gough (1914) identified 17 local mosquito species. One was *Stegomyia fasciata* (Fabricius), which he described as “Not rare.” He identified another species as *Ochlerotatus aegypti* (Linné), with *Culex dorsalis* Meigen and *Ochlerotatus dorsalis* of Edwards (1911) listed as synonyms. Gough wrote “This is one of the commonest Culicine mosquitos [sic] in our collection, and as Linné’s description of *Culex aegypti* [actually Hasselquist’s 1762 description] fits it very well, there can remain very little doubt that it is really the same species, especially as there appears to be no other common Egyptian species fitting the description.” As noted by G. H. E. Hopkins (in Patton 1933), Gough had identified *Culex aegypti* Linnaeus as *Aedes caspius* (Pallas) (viz. *dorsalis* Gough non Meigen).

As just noted, the mosquito *Culex aegypti* was first described and named by Hasselquist (1757). When in the region of the Nile, Hasselquist had been attacked intolerably by dense numbers of *Culex aegypti*, which he also called the Gnat of Egypt and described as ash-colored, with white spots on the joints of the legs (cf. Table 1). Two centuries later, Gad and Salit (1972) found *Aedes caspius* in “high densities” in the Red Sea area of Egypt, attacking humans “viciously” during the day.

The species *Aedes* (*Ochlerotatus*) *dorsalis* (Meigen) and *Aedes* (*Ochlerotatus*) *caspius* (Pallas) are similar. After examining fresh specimens of *Aedes caspius* from Egypt, Patton (1933) concluded that the description in Hasselquist (1757) of the body color of *Culex aegypti* as (in English) “tawny shading into grey” fit *Aedes caspius* exactly but most definitely did not fit *Stegomyia fasciata*. Further, his description of the color pattern of the legs fit *Aedes*

caspius rather than *Stegomyia fasciata*. Mattingly (1957), who also examined fresh specimens of *Aedes caspius* from Egypt, agreed with Patton. He wrote, “There can, in my view, be no reasonable doubt that the present attachment of Linnaeus’ name to a species of *Stegomyia* is wrong. Read in the abstract, Linnaeus’ description may seem equivocal, but I do not believe that any trained taxonomist with a working knowledge of Latin could hold in his hand a specimen of the pale Egyptian form of ‘*A. caspius*’ and doubt for a moment that it is a naked-eye or low-magnification description of this species.” It was then clear that *Culex aegypti* Linnaeus was a species of *Aedes* (*Ochlerotatus*) and that the specific name of the yellow fever mosquito could not be *aegypti* Linnaeus [viz. *aegypti* Hasselquist].

3. An alternative name for the yellow fever mosquito

3.1. Harrison G. Dyar (1866–1929)

In 1897, Harrison Dyar moved to Washington, D.C. to take up his life’s work at the United States National Museum (now the National Museum of Natural History administered by the Smithsonian Institution), where he was appointed Custodian of Lepidoptera. He was first noted, however, as an expert on mosquitoes, and eventually published 207 papers on Culicidae. Two aspects of his work on mosquitoes are relevant to this review. One was his action, with other mosquito taxonomists, in subsuming many existing genera into a small number of genera, on the grounds that characters were not known that could separate them with certainty. The other was the decision that he reached and promulgated on the binomial name of the yellow fever mosquito.

Dyar and Knab (1906) criticized Theobald’s reliance on the structure and distribution of scales to group mosquitoes into genera and higher taxa and proposed an alternative classification of the Culicidae based on larval characters, essentially the setae of the terminal abdominal segments. Thirteen genera, including *Stegomyia*, *Ochlerotatus*, and *Haemagogus*, were subsumed into *Aedes* as junior synonyms. After studying the larvae and adults of many species of the “*Aedes* group,” Edwards (1917) wrote that he was “inclined to accept” that decision. Dyar (1923) published a review of the mosquitoes of the United States in which tribes and genera were distinguished based on rather few characters. Many former genera were listed as junior synonyms of *Aedes*, which Dyar “divided into a number of subgenera on the characters of the male genitalia.” He recognized six subgenera, including *Stegomyia*, for species occurring in the United States. Other mosquito taxonomists also merged mosquito genera, notably into *Anopheles* or *Culex*, with taxonomic consequences that have lasted to the present time.

Dyar’s influence on the accepted binomial name of the yellow fever mosquito started with his examination of a collection of 640 mosquito specimens from the Philippines, which had been sent to the U. S. National Museum (Dyar 1920a). He listed 32 species, including six species of *Aedes*. One of the *Aedes* species was identified as “*Aedes* (*Stegomyia*) *aegypti* Linnaeus,” with “*Culex aegypti* Linnaeus, Hasselquist, *Palestina Reise*, 470, 1762” listed as the senior synonym. The long list of junior synonyms included *Culex argenteus* Poirlet, 1787 and *Culex fasciatus* Fabricius, 1805, indicating that this was the yellow fever mosquito. Dyar (1920b) showed that he was aware of Hasselquist’s description of *Culex*

⁴The catalog of Edwards (1932) was preceded by the catalog of Theobald (1905) but the former is regarded as the first because it gave birth to the accepted conservative classification based on broad genus-group concepts.

aegypti, referring to its replication in Edwards (1911). That description is inconsistent with the appearance (habitus) of the yellow fever mosquito (Table 1, Figure 2).

Dyar (1923) published a description of *Aedes aegypti* that resembled Theobald's (1901b) description of *Stegomyia fasciata*, while still citing the species *Culex aegypti* Linnaeus as the senior synonym. In neither of Dyar's 1920a or 1923 publications was mention made of the earlier findings by Gough (1914) in Egypt (the type locality of *aegypti*) that *Culex aegypti* was distinct from *Stegomyia fasciata* and should be classed as a species of *Ochlerotatus* (the genus recognized by Gough).

During 2012, while visiting the Smithsonian Institution in Washington, D.C., a colleague kindly located and examined the mosquitoes from the Philippines studied by Dyar. They included a single pinned specimen of *Aedes aegypti*, a male bearing two labels: (1) "Los Banos. P.I., 1-i-1915, Tuason D.R." and (2) "1311," the second label referring to the dissected genitalia mounted on a microscope slide labeled "Aedes (*Stegomyia*) *aegypti* L. Los Banos, P.I. Jan.1, 1915 1311" in Dyar's handwriting. Close examination of the pinned specimen and the dissected genitalia revealed that they matched Huang's (1979) description of *Aedes* (*Stegomyia*) *aegypti* (Linnaeus) in the Oriental Region. This was consistent with Gough's (1914) conclusion that the yellow fever mosquito does not have the characteristics of the mosquito originally given the specific name of *Culex aegypti*.

3.2. Catalogs of world mosquitoes

Discounting the catalog of Theobald (1905), the first fundamental catalog of world mosquitoes appeared in 1932 when Edwards published a classification of the family Culicidae which was based on both adult and larval characters, accompanied by diagnostic keys to taxa from subfamilies to subgenera. The family Culicidae comprised three subfamilies, Dixinae, Chaoborinae, and Culicinae. The subfamily Culicinae, which embraced all "true" mosquitoes, i.e., culicids bearing an elongate proboscis, comprised three tribes: Anophelini, Megarhini, and Culicini. In the same work, Edwards described what he considered to be five advantages of a classification recognizing few genera and many subgenera and reduced the 149 genera of true mosquitoes recognized by Theobald (1910) to 30 genera and 59 subgenera.

Edwards' (1932) acceptance of the trinomen *Aedes* (*Stegomyia*) *aegypti* (Linnaeus) established it in the traditional classification as the scientific name of the yellow fever mosquito. Patton (1933) attacked that decision, stating that due attention had not been given to Gough's (1914) evidence that *Culex aegypti* was a species of *Ochlerotatus*, a finding which Patton himself had confirmed. Patton argued "that the name *aegypti* should be dropped, and that the yellow fever mosquito be known in future as *Aedes* (*Stegomyia*) *fasciata*."

For some 25 years, Edwards' (1932) classification of the Culicidae was accepted in its original form, with the Culicinae (true mosquitoes) as one of three subfamilies within the family. The catalog of Stone et al. (1959), *A Synoptic Catalog of the Mosquitoes of the World (Diptera, Culicidae)*, differed by exclusion of the subfamilies Dixinae and Chaoborinae and elevation of the Culicinae to family rank. The subsequent catalog of Knight and Stone (1977), *A Catalog of the Mosquitoes of the World (Diptera: Culicidae)*, differed further by acceptance of the tribal structure

proposed by Belkin (1962). Where Edwards' (1932) classification of the Culicidae (his subfamily Culicinae) comprised 1,400 species in 30 genera and 59 subgenera, the catalog of Stone et al. (1959) listed 2,426 species in 31 genera with 95 subgenera and the catalog of Knight and Stone (1977) recognized 2,960 species in 34 genera and 130 subgenera. The classifications were phenetic in all three catalogs, i.e., they pertained to overall similarity based on many morphological characters selected without regard to evolutionary history.

4. Interventions by the International Commission on Zoological Nomenclature

4.1. First intervention

Written rules of zoological nomenclature were published as early as the 1840s by taxonomists in different countries, leading at around the turn of the century to the establishment of an International Commission on Zoological Nomenclature (founded in 1895). The Code was reprinted in 1926 in an (unauthored) article entitled "International rules of zoological nomenclature: rules and recommendations" with a footnote stating that "The International Code of Zoological Nomenclature has for some time been out of print" (Biological Society of Washington 1926). From 1939, authoritative *Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature* were published periodically, and in 1961 the first edition of what was later described as "the present International Code" appeared (International Commission on Zoological Nomenclature 1961), largely comprising regulations that had been formulated and accepted much earlier.

Article 26 in the 1926 Rules had broad importance for binomial names used in zoological nomenclature during Linnaeus' time and earlier. Essentially, 1 January 1758 was arbitrarily fixed as the starting point of zoological nomenclature. This appeared, elaborated, as Article 3 in later editions of the Code. The 4th edition (International Commission on Zoological Nomenclature 1999) states:

Article 3. Starting point. The date 1 January 1758 is arbitrarily fixed in this Code as the date of the starting point of zoological nomenclature.

3.1. Works and names published in 1758. Two works are deemed to have been published on 1 January 1758:

- Linnaeus' *Systema Naturae*, 10th Edition;
- Clerck's *Aranei Svecici*.

Names in the latter have precedence over names in the former, but names in any other work published in 1758 are deemed to have been published after the 10th Edition of *Systema Naturae*.

3.2. Names, acts and information published before 1758. No name or nomenclatural act published before 1 January 1758 enters zoological nomenclature, but information (such as descriptions or illustrations) published before that date may be used.

Clerck's *Aranei Svecici* was published in 1757; the 10th edition of *Systema Naturae* in 1758.

Despite the wording of Article 3.2, many of the names published before 1758 entered zoological nomenclature, but with Linnaeus as author. As one example, at least 25 generic names of invertebrates cited in Aldrovandi (1602), almost all still familiar

names, were assigned to Linnaeus (1758) as author. And with reference to Article 3.2 above, the larva illustrated by de Reaumur (1738: pl. 43, Figure 3) was designated the lectotype of *Culex pipiens* Linnaeus by Harbach et al. (1985) under provisions of Article 74b in the 3rd edition of the *Code* (International Commission on Zoological Nomenclature 1985).

The titles of works placed on the *Official Index of Rejected and Invalid Works in Zoological Nomenclature* were listed in *Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature*, Direction 32 (International Commission on Zoological Nomenclature 1956: p. 311). They included the following two items: “Hasselquist (F.), 1757, *Iter Palaestinum* (a work published before the starting point of zoological nomenclature)” and “Hasselquist (F.), 1762, *D. F. Hasselquists, Reise nach Palästina* (a German translation by T. H. Gadebusch of the *Iter Palestinum* of 1757), the entry to bear the endorsement that the pre-1758 names reproduced in this edition are not available for nomenclatorial purposes, those names not having been reinforced by adoption or acceptance.”

From that ruling, it followed that the specific name of the yellow fever mosquito could no longer be *aegypti* Linnaeus but should be *Culex argenteus* Poiret, 1787 or *Culex fasciatus* Fabricius, 1805, whichever was both valid and having nomenclatorial priority. *Culex argenteus*, “Habitat in Barbaria,” was among the 13 species assigned to *Culex* in the 13th edition of *Systema Naturae* (Linnaeus 1788–1793, Volume 1, Part 5). Poiret stated that *Culex argenteus* was the most common mosquito in Barbary (the western part of North Africa), frequently attacking humans. Part of Poiret’s description, “Tout son corps, particulièrement le dos, est couvert d’écaillés argentées,” is inconsistent with the appearance of most populations of the yellow fever mosquito; however, in the view of Knight (1972) it is a clear indication that Poiret was dealing with an extreme form of *Aedes aegypti* variety *queenslandensis* Theobald, which Christophers (1960) described as commonly found along the Mediterranean coast of North Africa. Unfortunately, Poiret reported that his specimens had not survived – “*Quoique cet insecte ait été détruit dans ma collection...*”. *Culex fasciatus* remained a valid candidate for the name of the yellow fever mosquito.

4.2. Second and solicited intervention

In an application to the International Commission on Zoological Nomenclature, Mattingly et al. (1962) argued that substitution of the specific name *aegypti* Linnaeus by another name would cause serious and widespread confusion. They suggested that the Commission use its plenary powers (1) to validate the specific name *aegypti* Linnaeus, 1762, as used in the combination *Culex aegypti* and (2) to direct that the validated name be interpreted by reference to a selected neotype specimen (a newly designated name-bearing type specimen selected in the absence of extant type material), which would be a specimen of the yellow fever mosquito from “Kuala Lumpur, Selangor, Malaya.” Their justification for naming Linnaeus as author of the binominal *Culex aegypti* was derived from their misreading of his biographical introduction to Hasselquist’s *Reise nach Palästina* (Hasselquist 1762) (Section 1.4 above).

Two years later, under their plenary powers and by a ruling of 28 to 1, the Commissioners agreed to the requests in the following terms. (1) The specific name *aegypti* Linnaeus, 1762, was validated,

interpreted by reference to the neotype specimen described by Mattingly et al. (1962). (2) The following names were placed on the Official List of Specific Names in Zoology: (a) *aegypti* Linnaeus, 1762, as published in the binomen *Culex aegypti* and (b) *caspius* Pallas, 1771, as published in the binomen *Culex caspius*. (3) The generic name *Stegomyia* Theobald, 1901 (see section 2.2 above) was placed on the Official List of Generic Names in Zoology (International Commission on Zoological Nomenclature 1964).

Some 40 years after that ruling, the Commissioners responded differently to a comparable request relating to the genus *Drosophila* Fallén. They were asked to set aside the type-species designation of *funnebris* Fabricius for the genus *Drosophila* and to replace it with *melanogaster* Meigen. The genus *Drosophila* is paraphyletic and splitting it could result in the subgenus *Sophophora* Sturtevant, of which *melanogaster* Meigen is the type species, being ranked as a genus (van der Linde et al. 2007). The Commissioners rejected the request by a margin of 23 to 4 (International Commission on Zoological Nomenclature 2010). Consequently, if at a future date the genus *Drosophila* were to be divided and the subgenus *Sophophora* afforded genetic rank, the specific name *melanogaster* would remain combined with the genus name *Sophophora*, giving the binomial *Sophophora melanogaster* (Meigen) (Vane-Wright 2011).

5. Phenetic and phylogenetic classifications of aedine mosquitoes

An updated equivalent of Knight and Stone’s (1977) catalog and supplements was provided much later in the online ‘Systematic Catalog of Culicidae’ of the Walter Reed Biosystematics Unit (<http://www.mosquitocatalog.org/>). This retained the phenetic classification of mosquitoes, with some very large genera. For example, the genus *Aedes* consisted of 928 species in 45 subgenera. The subgenus *Aedes* consisted of 12 species, the subgenus *Stegomyia* of 126 species, and the subgenus *Ochlerotatus* of 199 species. Another large genus, *Culex*, comprised 794 species, and the subgenus *Culex* 200 species.

Over a five-year period, a phylogenetic classification of mosquitoes of the tribe Aedini was produced from a series of cladistic analyses by Reinert et al. (2004, 2006, 2008, 2009) based on morphological data from all life stages. The classification was made available online in the Mosquito Taxonomic Inventory (<http://mosquito-taxonomic-inventory.info/>). Over one-half of the aedine taxa that were initially designated as genera but later reduced to subgenus rank (including *Ochlerotatus* and *Stegomyia*), or that were subsumed into the genus *Aedes* as junior synonyms (Dyar 1928), were restored to genus rank. In the phylogenetic classification at that time, the genus *Aedes* comprised 12 species and the genus *Stegomyia* comprised 127 species.

Responding to a recommendation of the *Journal of Medical Entomology* (Editor-in-Chief and Subject Editors of JME 2005), many entomological journals rejected the phylogenetic classification of aedine mosquitoes. The online ‘Systematic Catalog of Culicidae’ (above) displayed the phenetic classification of aedines until 2012 when it adopted the phylogenetic classification proposed by Reinert et al. (2009). Three years later, it hosted a highly modified ‘traditional classification’ of the genus *Aedes* based on a different method of analyzing the dataset of Reinert et al. (2009), in which most of the genera recognized by those

authors were reduced to subgenera and species groups (Wilkerson et al. 2015). Thus, *Stegomyia aegypti* of Reinert et al. reverted to the traditionally long-accepted *Aedes aegypti*.

6. Summary of nomenclatural decisions

The mosquito that transmits yellow fever virus was collected and investigated during the late nineteenth century and correctly named at the turn of that century as *Stegomyia fasciata* (Fabricius). Two decades later, due to an error of identification coupled with ignorance of earlier findings, an invalid, alternative name was proposed. Attempts to perpetuate this name were successful but required acts of expediency. The specific name *aegypti* featured repeatedly in this saga.

(1) Hasselquist's (1757) work *Iter Palæstinum*, edited after his death by Linnaeus, included a detailed description of the new species *Culex aegypti*; this description was replicated in his (1762) work *Reise nach Palästina*. Linnaeus assigned species to the genus *Culex* in successive editions of *Systema Naturae*, but *Culex aegypti* was not mentioned in any of the editions published after Hasselquist (1757) from the 10th (1758) to the 13th (1788–1793) editions.

(2) Research carried out in Cuba between 1870 and 1900 led to the discovery of the vector of the infectious agent of yellow fever. It was identified first as *Culex mosquito* Robineau-Desvoidy, next as *Culex fasciatus* Fabricius, and then as *Stegomyia fasciata* (Fabricius), the last which, as noted above, was accepted as a valid name for the next two decades.

(3) After the publication of Hasselquist's works in 1757 and 1762, the next known mention of *Culex aegypti* was in *Index Animalium* (Sherborn 1902), which included the entry "aegypti Culex, Linnaeus in Hasselquist, Palast. 1762." This appeared to identify Linnaeus as author of the name *Culex aegypti*. Indeed, use of the specific name *aegypti* Linnaeus for the yellow fever mosquito in many later publications carried the implication that (in ICZN terminology) Linnaeus was "alone responsible for the name." The evidence cited in (1) above suggests that Hasselquist, not Linnaeus, should have been identified as the author of *Culex aegypti*.

(4) Gough (1914) reported the presence in Egypt of populations of *Stegomyia fasciata* (Fabricius) and of another species which showed a close similarity to *Culex dorsalis* Meigen (misidentification of *Culex caspius* Pallas). He named the latter *Ochlerotatus aegypti* (Linnaeus) on the grounds of its very close similarity to "Linné's description of *Culex aegypti*" and of the precedence of that specific name. Patton (1933) and Mattingly (1957) supported his finding but considered that mosquito to more closely resemble *Aedes caspius* (Pallas).

(5) Dyar (1920a) named a specimen from the Philippines "*Aedes (Stegomyia) aegypti* Linnaeus," adding a list of synonyms that associated it with the yellow fever mosquito. However, his first description of *Aedes aegypti* Linnaeus (Dyar 1923) differed from the description of *Culex aegypti* in Hasselquist (1757, 1762) but closely resembled Theobald's (1901b) description of *Stegomyia fasciata* (Fabricius). This misidentification had serious consequences for mosquito nomenclature and mosquito taxonomy.

(6) Edwards' (1932) use of the name *Aedes (Stegomyia) aegypti* (Linnaeus) as "*A. (S.) aegypti* Linnaeus," in his catalog

of world mosquitoes repeated Dyar's error and was perpetuated in later catalogs by other compilers. Mosquito taxonomists who were aware of this faulty nomenclature appear to have accepted it because of the widespread use of that trinomen – a case of expediency prevailing over taxonomic and nomenclatural validity.

(7) In 1956, the International Commission on Zoological Nomenclature ruled that the name *Culex aegypti* was invalid, and therefore so was the name *Aedes aegypti*. For several years, no action was taken by mosquito taxonomists to replace it with one or other of the two earlier alternatives, *Culex argenteus* Poiret, 1787 and *Culex fasciatus* Fabricius, 1805.

(8) In an application to the International Commission, Mattingly et al. (1962) stated that the specific name *aegypti* Linnaeus had been in general use for the yellow fever mosquito for many years, having superseded the name *fasciata* (Fabricius), and that its substitution with another name would cause the greatest confusion. They requested that the International Commission use its plenary powers to approve a specimen of the yellow fever mosquito, a species of the subgenus *Stegomyia*, to serve as the neotype of *Culex aegypti*, a species of the subgenus *Ochlerotatus*.

(9) In 1964, the International Commission acceded to that request, ruling that "the name *aegypti* Linnaeus, 1762, as published in the binomen *Culex aegypti* is hereby validated," and directing that "the nominal species *Culex aegypti* Linnaeus, 1762, be interpreted by reference to the neotype specimen described by Mattingly et al. (1962)."

The specific name *aegypti* Linnaeus, interpreted by reference to a neotype specimen from Malaysia, has been assigned in perpetuity to the yellow fever mosquito. By the phylogenetic classification of aedine mosquitoes proposed by Reinert et al. (2009), its full scientific name is *Stegomyia (Stegomyia) aegypti* (Linnaeus), whereas in the widely accepted traditional classification of convenience the full scientific name is *Aedes (Stegomyia) aegypti* (Linnaeus), the names of which merely involve the transposition of two genus-group names. The species name and authorship are immutable; the genus name with which they are, or may be combined with in the future, is a subjective determination.

NOTES

(1) In Linnaeus' *Fauna Svecica* of 1746, genera were not numbered, but species were numbered from the start of Class I, Quadrupedia, through the Animal Kingdom. In the first genus, *Homo*, the first species was listed as "1. HOMINES inhabitantes Succiam sunt vel ...". The first insect listed, a species of *Scarabæus*, was numbered 337, while the six species of *Culex* were numbered from 1115 to 1120. Among those, species 1116 was *Cx. cinereus*. By the 9th edition of *Systema Naturae* (Linnaeus 1756), when both genera and species had long been numbered, *Culex* was genus 208 and consisted of four species, numbered 1 to 4, but given the supplementary numbers of *Fn.* 1116, *Fn.* 1117, *Fn.* 1119 or *Fn.* 1120 to show their correspondence with the *Culex* species listed in *Fauna Svecica*. The specific names associated with the different species numbers had been changed; for example, 1116 formerly *Cx. cinereus* was now *Cx. vulgaris*. In the 10th edition (Linnaeus 1758), *Culex* was genus number 224. Six species were assigned to it and numbered 1 to 6, of which the species 1 to 5 were linked to

the supplementary numbers 1115 to 1118 or 1120, each preceded by either *Fn. Svec.* or *Faun. Svecica*. Again all specific names had been changed, and the species numbered *Fn. Svec.* 1116 was now identified as *Culex pipiens*. By their current family affiliations only two were culicids, namely *bifurcatus*, *Fn. Svec.* 1115 and *pipiens*, *Fn. Svec.* 1116 (today the former is a junior synonym of *pipiens*), while the others were species of Ceratopogonidae, Simuliidae or Empididae. In the 12th edition (Linnaeus 1766–1772), *Culex* was genus number 255, while its six species were numbered 1 to 6. Additional information indicated that species 1, named *pipiens*, corresponded to the species named *cinereus* or *vulgaris* and numbered 1116 in earlier editions. In the 13th edition of *Systema Naturae* (Linnaeus 1788–1793, Volume 1, Part 5), 13 species were assigned to *Culex*, and numbered 1–13. Of the species not previously listed, only *Culex argenteus* Poirlet, 1787, was a true culicid.

(2) 120. CULEX. Cypri minimus subfuscus, antennis brevissimus fasciculis, alis ovatis. Insectum Cypro endemium est, summam creans molestiam, morsu sensibiliter doloroso quem noctu infligit, quique pustulas relinquit diuturniores & magis inflammatas illis; quæ ex culice ordinario.

Acknowledgments

We gratefully acknowledge Christine Dahl for providing information on the publications of Linnaeus and Hasselquist, Yvonne Linton for finding and examining the specimen from the Philippines described and named *Aedes aegypti* by Dyar (1923), Librarians of the Natural History Museum and the British Library for generous assistance with literature sources, and Philippa Colvin, former professional book editor, for carefully reviewing the manuscript.

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