

SCIENTIFIC OPINION

THE GENUS AND SUBGENUS CATEGORIES WITHIN CULICIDAE AND PLACEMENT OF *OCHLEROTATUS* AS A SUBGENUS OF *AEDES*

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ABSTRACT. Many species of Culicidae are of major medical, veterinary, and economic importance. To facilitate discussion among taxonomists, medical entomologists, ecologists, and vector control specialists, it is essential that culicidologists be able to readily recognize individual genera. Adult female mosquitoes, the stage most often encountered in surveys, should be identifiable to genus without dissection with the aid of a good-quality dissecting microscope. Female adult specimens of *Ochlerotatus* and *Aedes* as defined by Reinert cannot be identified morphologically without dissection, and no distinct differences in biology, behavior, and ecology distinguish these 2 taxa as currently defined. Use of these names as genera complicates mosquito identification and interferes with information retrieval and communication among taxonomists, medical entomologists, and vector control specialists. Therefore, it is our opinion that *Ochlerotatus* Lynch Arribalzaga should be placed as a subgenus of *Aedes* Meigen, *Aedes* (*Ochlerotatus*). We believe that the usage of the genus *Aedes* and the subgenus *Ae.* (*Ochlerotatus*) should be restored to the traditional usage during the interval 1906–2000.

KEY WORDS *Aedes*, *Ochlerotatus*, Culicidae, genus and subgenus categories, mosquito control, oviposition behavior

Unlike the species category, the genus and subgenus categories are not based on a biological concept nor are they strictly defined. Usage and definition of generic and subgeneric taxa may vary among animal groups and even between authors working on the same group of animals. Traditionally, phylogenetic taxonomists defined genera as a group of related species sharing a common phylogenetic origin that differ from species of other related genera by a decided gap in morphological characters (Mayr 1969). Entomologists have tended to group species within genera such that the size of the morphological gap was in inverse ratio to the number of species within the genus (Michener 1957). Following these general concepts, genera with many species, such as *Culex* Linnaeus and *Anopheles* Meigen, should be well defined and recognizable, and separated by distinct morphological gaps from other related genera. Genera with few species, for example *Toxorhynchites* Theobald, would be separated from other genera by larger, more exclusive morphological gaps. In many animal groups, particularly vertebrates, morphological gaps were associated with adaptation to particular ecological zones or niches (Inger 1958), and genera differed in morphology and biology. The generic concept employed within a family often is a function of the professional groups who use the classification. For families such as the Culicidae that are

of interest to many professional groups such as epidemiologists, veterinarians, physicians, politicians, public health workers, urban planners, vector control specialists, and entomologists, the use of well-defined genera facilitates communication and information exchange. Such communication has seldom been more important in the United States and worldwide. Mosquito-borne diseases draw sincere attention from those charged with responsibility of public health at all levels. The professional and nonprofessional public relies heavily on simple distinctions between mosquito genera to make decisions about risk and remediation. Therefore, the distinctions between medically important mosquito genera should be as clear as possible morphologically and useful operationally.

Work on the taxonomy and classification of mosquitoes developed slowly. In the 10th edition of Linnaeus's (1758) *Systema naturae*, 2 mosquito species were placed in the single genus *Culex*. In 1818, Meigen (1818) established 2 new genera, *Anopheles* and *Aedes* Meigen, bringing the total number of genera to 3. During the remainder of the 19th century, 9 new generic names were published including 4 genera that remain in use today: *Haemagogus* Williston, *Psorophora* Robineau-Desvoidy, *Sabethes* Robineau-Desvoidy, and *Uranotaenia* Lynch Arribalzaga (Thompson and Gaimari 2000). In 1900, experimental transmission of human pathogens by mosquitoes was demonstrated. Patrick Manson experimentally infected 2 human volunteers with malaria by bites of mosquitoes in the genus *Anopheles* brought from Italy, where they had fed upon a malaria patient, and Walter Reed and colleagues working in Havana, Cuba, demonstrated the transmission of yellow fever virus to healthy volunteers by *Ae.* (*Stegomyia*) *aegypti* L.

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infected by feeding on hospitalized patients (Philip and Rozeboom 1973). These events of 1900 spurred work on the taxonomy and biology of mosquitoes. Just 10 years later, Theobald (1910) recognized 1,050 species in 149 genera (Edwards 1932). When Edwards (1932) began work on the *Genera Insectorum* he faced taxonomic chaos and the task of reviewing 327 generic and subgeneric names (Thompson and Gaimari 2000). Edwards (1932) placed 1,400 species in 30 genera and 89 subgenera and developed a classification of the Culicidae that forms the basis for the present classification. Edwards (1932) pointed out that the use of more inclusive generic concepts made the relationships among species clearer and the generic limits more easily defined. Edwards (1932) also pointed out that smaller groups of species can be usefully designated by subgeneric names. The broad definitions of genera developed by Edwards (1932) allowed adult females to be identified to genus in the laboratory with a good-quality dissecting microscope and allowed mosquito genera to be recognized in the field as morphological and ecological units (Service 1993).

We believe that recognition of genera by medical entomologists is essential in order to use taxa for the generalization of biological characteristics and to facilitate subsequent species identification. Adult female mosquitoes, the stage most often encountered in surveys, should be identifiable to genus without dissection with the aid of a good-quality dissecting microscope. Field personnel should be able to recognize the common genera (e.g., *Culex*, *Anopheles*, and *Aedes*) of Culicidae in the field by morphological characters, general appearance, and biological and behavioral characteristics.

With the advent of cladistics (Hennig 1966), taxonomists began to emphasize that genera should be monophyletic assemblages of species and that gap criteria were inappropriate (Wiley 1981). The establishment of monophyletic genera and subgenera is a laudable goal, and progress toward this goal will facilitate information retrieval and communication among culicidologists. However, for most groups of insects including the Culicidae, the rigorous phylogenetic studies required to demonstrate the monophyletic nature of genera are in their infancy or lacking. It is important to note that even though some mosquito genera including *Aedes* (sensu lato) appear heterogeneous, no author has presented any data or argument that *Aedes* (sensu lato) is polyphyletic. Although only the manuscript of Isoe (2000) provided data to suggest that *Aedes* is paraphyletic (that is that some or perhaps all of the nominal genera in the tribe Aedini may have evolved from within *Aedes*), many mosquito taxonomists believe that *Aedes* is paraphyletic (Zavortink, personal communication).

Zavortink (1990) suggested that the classification of genera within the Culicidae is unnatural based on observed species/genus ratios, and that more,

smaller genera will result from future taxonomic study and phylogenetic analysis. We agree that phylogenetic analysis is desperately needed within the family Culicidae, but suggest that the best way to advance toward a natural classification is to focus on the use of subgenera. Whenever possible, subgenera should be defined as monophyletic groups of species. We encourage all mosquito workers to report the subgeneric name upon 1st usage of a species name in tables or text, for example *Aedes* (*Stegomyia*) *albopictus* (Skuse) or *Culex* (*Neoculex*) *territans* Walker. If the monophyletic nature of subgenera becomes firmly established, then analysis of the evolutionary relationships among the subgenera will eventually lead to a natural classification of genera and other higher level taxa. As subgenera become well defined, taxonomists may choose to elevate selected subgenera to genera based on firm phylogenetic evidence.

In 1906, Dyar and Knab defined *Aedes* based primarily on larval morphology. This broad usage of the genus *Aedes* was accepted by Edwards (1917) and by Barraud (1928), and the name *Aedes* was universally employed in this inclusive sense during the interval 1906–2000. In 1918, Dyar pointed out that species of *Aedes* could be placed in 2 groups based on differences in the claspette of the male genitalia ("harpago" of Dyar [1918]). The claspette was developed into a columnar stem bearing a terminal bladelike filament in *Ae.* (*Ochlerotatus*) Lynch Arribalzaga and related subgenera, whereas in *Ae.* (*Aedes*) Meigen and *Ae.* (*Aedimorphus*) Theobald the claspette is rudimentary and represented by setae on a conical base. Edwards (1921) confirmed Dyar's finding and noted that the 2 groups also could be defined by distinct differences in the shape of the phallosome of the aedeagus ("mesosome" of Edwards [1921]). One group, represented by the subgenera *Ae.* (*Ochlerotatus*) and *Ae.* (*Finlaya*) Theobald, has a simple tubelike phallosome, whereas the phallosome in the 2nd group, represented by *Ae.* (*Aedes*), *Ae.* (*Aedimorphus*), and *Ae.* (*Stegomyia*) Theobald, is a paired structure with spiny, brushlike structures apically (Edwards 1921). This dichotomy was so distinctive that Edwards (1921) stated "Both these distinctions are so well marked that one would expect to find corresponding distinctions in the body characters or in the larvae." Edwards (1941) reiterated that the subgenera of *Aedes* could be divided into 2 groups based on the 2 characters of the male genitalia mentioned above, the phallosome and claspette. In subgeneric descriptions, Edwards (1941) pointed out that the shape of the insula of the female genitalia differed among subgenera, but we are unable to find a clear statement in Edwards's publications indicating that he realized that differences in the shape of the insula also corresponded to the dichotomy in male genitalia. Belkin (1962) added 2 additional characters to those supporting the dichotomy of subgenera within *Aedes*, the presence or absence of

setae on the proctiger of the male genitalia, and the presence or absence of seta 12-I in the larvae. Mattingly (1958) and Belkin (1962) knew of the publications of Edwards and the obvious dichotomy within the genus *Aedes*, yet both cautioned against formalizing this dichotomy with taxonomic names. Mattingly (1958) stated "The genus *Aedes* is a very large one, comprising more than five hundred currently recognized species. To split it would involve using various familiar names in unfamiliar combinations and this is not to be undertaken lightly in a group of medical importance. It is not felt that it can be justified at the present time." A few years later Belkin (1962) concurred, stating "suggest caution in proposing a reclassification of the genus or its dismemberment."

Reinert (2000) recently elevated the subgenus *Ochlerotatus* to generic rank and divided the subgenera formerly placed in *Aedes* (sensu lato) among the elevated genus *Aedes* and the elevated genus *Ochlerotatus*. Reinert (2000) based his decision to elevate *Ochlerotatus* on characters of the insula of the female genitalia that are not visible without dissection and a refined statement of differences in the male genitalia and larval seta 12-I following Edwards (1921, 1941) and Belkin (1962). Reinert (2000) also noted exceptions to the characters he used to separate these 2 new putative genera. As a result of Reinert's action (2000), medical entomologists were forced to identify specimens 1st to species, and then to select a generic name associated with the subgenus in which the species currently is placed. We resisted initial pleas from medical entomologists and vector control specialists to correct this situation because the elevation of *Ochlerotatus* resulted in 2 groups of subgenera that corresponded to the division of subgenera based on male genitalia discussed by Edwards (1941), and because we hoped that the elevation of *Ochlerotatus* would lead to new characters that would allow for the identification of these genera. Unfortunately, no additional support for the elevation of *Ochlerotatus* has been published.

Although not mentioned by Reinert (2000), the most important aspect of his paper is that he defined characters that support the basal furcation (lineages 2a and 2b in Fig. 1) within *Aedes* (sensu lato). Based on his work and that of Dyar (1918), Edwards (1921, 1941), and Belkin (1962), there is strong support for a basal furcation within *Aedes* (sensu lato), with 1 branch leading to *Aedimorphus*, *Stegomyia*, and related subgenera and the other leading to *Ochlerotatus* and related subgenera (Fig. 1). However, not all furcations within phylogenetic trees need to be associated with formal zoological nomenclature. In fact, nearly all furcations are not associated with formal taxonomic names. The basal furcation within *Aedes* (Fig. 1) may actually represent the basal furcation within the tribe Aedini. The Aedini genera *Armigeres* Theobald, *Ayurakitia* Thurman, *Eretmapodites* Theobald, *Heizmannia*

Ludlow, *Udaya* Thurman, *Verrallina* Theobald, and *Zeugnomyia* Leicester appear to have evolved from within lineage 2b (Fig. 1), whereas the genera *Haemagogus*, *Opifex* Hutton, and *Psorophora* appear to have evolved from within lineage 2a (Zavortink, personal communication). We have little if any information on the phylogenetic relationships among the subgenera of *Aedes* (sensu lato) and the other Aedini genera, and it will likely be many years before rigorous phylogenetic studies are conducted. Interpretation of the phylogenetic relationships among genera and subgenera of the Aedini will likely vary considerably in the foreseeable future. We believe that it is unwise to modify the generic and subgeneric classification within the Aedini until phylogenetic relationships become stable and well documented.

At least 3 aspects of the inclusive genus *Aedes* are unifying (lineage 1 in Fig. 1). First, all members of the genus deposit an egg with a characteristic structure (Horsfall and Craig 1956; Horsfall et al. 1970, 1973; Linley 1989; Linley and Clark 1989). One common element is the nature of the exochorion (consisting of the maternal follicular epithelium). In *Aedes*, the exochorion forms a temporary pellicle that lasts for only a few weeks after the egg is deposited. Another consistent feature of the eggs is that a sagittal cross section is not symmetrical; the dorsal side is more arched than the ventral with respect to the final orientation of the larva. Finally, on hatching, the larva cuts the chorion about one quarter of the way from the anterior end, forming a neatly separated cap. Although this line of dehiscence has no external sign, the internal structure of the serosal cuticle (secreted by the developing larva) appears to include a line of separation corresponding to the eventual hatching line (Clements 1992). The presence of a preformed hatching line also is supported by the common observation that an embryonated egg of *Aedes* will pop open at the hatching line when exposed to gentle pressure from a small probe.

The eggs of *Psorophora*, *Haemagogus*, *Opifex*, and *Eretmapodites* are probably the most similar to those of *Aedes*. The spinose pattern of the exochorion of *Psorophora* is distinctive and typical of the entire genus (Horsfall et al. 1952, Bosworth et al. 1983). Horsfall et al. (1970) further distinguished eggs of *Psorophora* from those of *Aedes* based on the carinate shape of the chorionic pattern and on the more strongly arched shape of the eggs. *Haemagogus* have fibers projecting from the dorsal side of the chorion forming attachments to the substrate on which the female oviposits. Although this character is different from the vast majority of *Aedes*, several Asian species of *Aedes* are reported to have eggs that are very similar to those of *Haemagogus* (Linley and Chadee 1991, Linley et al. 1991). The eggs of *Eretmapodites* are elongated relative to most *Aedes* and possess a more complicated chorionic structure (Linley and Service 1994). Mat-

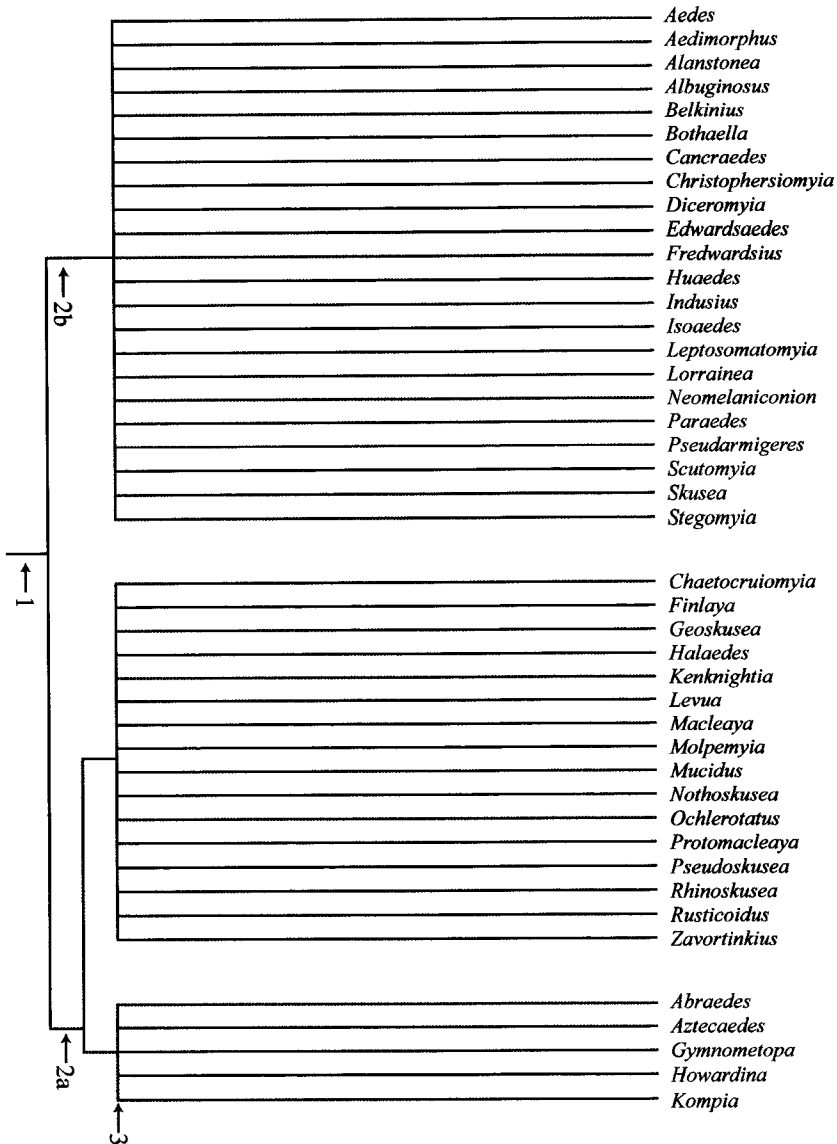


Fig. 1. Cladogram of subgenera of genus *Aedes* (sensu lato) as inferred from data presented by Reinert (2000). 1, lineage 1, *Aedes* (sensu lato); 2a, lineage 2a, *Ochlerotatus* sensu Reinert 2000; 2b, lineage 2b, *Aedes* sensu Reinert 2000; 3, lineages leading to subgenera of *Aedes* (sensu lato).

tingly (1970b) drew parallels between the eggs of *Opifex* and *Aedes*, but the basic difference that *Opifex* deposits eggs below the water surface (a characteristic shared only with *Mansonia* Blanchard) is significant.

Second, and of great biological significance, the eggs of *Aedes* are not deposited on the surface of the water. Specific morphological and physiological adaptations of the eggs allow hatching to delay for weeks, months, or, in some cases, years. This characteristic of the eggs probably is the cause of the adaptation of the genus to either container or flood-water habitats with latent periods spent as eggs

rather than as adults or larvae. Horsfall et al. (1973) reviewed all Culicidae in establishing a categorization of hatching stimuli for mosquito eggs. The eggs of many mosquito species do not require the stimulus of decreasing oxygen tension for hatching. These eggs (e.g., those of *Culex* and *Anopheles*) hatch as soon as the embryo completes development and are called type I. Hatching of type II eggs occurs after oxygen levels are depressed, the situation for eggs of *Aedes vexans* (Meigen) lying in the soil during a favorable season. Type III eggs require conditioning by light or temperature or both before hatching in water with decreasing oxygen

tension, corresponding to an egg in diapause. So far as is known, the development of biological strategies dependent on type II and type III eggs are unique to the genera *Aedes* and *Psorophora*. Although it seems likely that eggs of *Haemagogus* and, possibly, *Armigeres* would fit into the type II category, no information is available in the literature suggesting that the eggs of these genera undergo a latency period characteristic of type III eggs. The almost exclusively tropical distribution of *Haemagogus* and *Armigeres* may be associated with the lack of capability to withstand cold temperatures in the egg stage.

Horsfall's (1972) review of the bionomics of Culicidae remains the most thorough treatment of the entire family. This book is arranged by genera and provides a convenient overview of the basic ecological strategies for egg deposition and survival. Horsfall (1972) summarized the information on eggs available at the time, with the following results. Genera that deposit their eggs singly on the surface of the water include *Anopheles*, *Toxorhynchites*, *Trichoprosopon* Theobald (in part, *Tr. digitatum* [Rondani] eggs are deposited as a maternally protected raft [Lounibos 1983]), *Wyeomyia* Theobald (eggs sometimes stranded on sides of plants and subsequently hatch when flooded), *Orthopodomyia* Theobald, *Opifex* (eggs deposited below the water surface [Mattingly 1970b]), and *Mimomyia* Theobald (Clements 1999). Genera that deposit their eggs in structured assemblages on the surface of the water (rafts) include *Coquillettidia* Dyar, *Culex* (vast majority of species [Clements 1999]), *Culiseta* Felt, and *Uranotaenia*. Genera that cement their eggs to the leaves of aquatic plants include *Mansonia* and *Ficalbia* Theobald, and some species of *Cx.* (*Melanoconion*) Theobald, *Cx.* (*Neoculex*) Dyar, and *Cx.* (*Lophoceraomyia*) Theobald (Clements 1999). Genera that deposit their eggs singly above the waterline or in soil, waiting for inundation to hatch, include *Aedes*, *Armigeres* (in part, 6 species in the subgenus *Leicesteria* Theobald glue eggs to their own legs, with the female allowing larvae to hatch into water after embryonation [Lounibos 1983]), *Haemagogus*, and *Psorophora*.

The ability to deposit eggs that resist drying above the waterline is most completely developed in the genera *Aedes*, *Haemagogus*, and *Psorophora*. The great number of species in the genus *Aedes* suggests that the strategy of a resistant egg deposited above the water is highly adaptive under geologically recent ecological conditions. However, a few other species and genera of Culicidae display these attributes. Although details were not given, eggs of *Opifex* apparently are resistant to drying (Clements 1999), presumably when eggs deposited below the waterline are later stranded. *Orthopodomyia signifera* (Coquillett) apparently glues its morphologically distinctive egg ("shaped like an elm seed") above the water (Pratt and Kidwell 1969). Other species of *Orthopodomyia* (*Or. kummi*

Edwards, and *Or. alba* Baker) have been observed to deposit eggs above the waterline, but because eggs of *Or. signifera* hatch as soon as embryonation is complete (Zavortink 1968), it seems likely that larvae make their way to the water rather than wait for inundation. Mattingly (1970c) reviewed the bionomics of eggs of *Orthopodomyia* and found references to overwintering as an egg. Members of the genus *Eretmapodites* also deposit eggs above the waterline (in plant axils) or in dry snail shells, although these eggs apparently are not very resistant to drying (Mattingly 1970a). The eggs of *Anopheles dirus* Peyton and Harrison (Rosenberg 1982), *An. gambiae* Giles, and *An. arabiensis* Patton (Beier et al. 1990) are capable of survival under dry conditions for 1 or 2 wk. Barr and Barr (1969) reviewed the basic structure and function of sabethine genera, and briefly mentioned that several species of *Wyeomyia* and *Malaya* Leicester apparently deposit eggs on dry substrates. Although *Tripteroides bambusa* (Yamada) deposits eggs directly on the surface of the water, it reportedly overwinters as an egg in the northern part of its range (Hong and Kim 1995). Under colony conditions, females of *Tp. bambusa* were observed to deposit most of their eggs above the waterline on a piece of balsa wood (Zavortink, personal communication).

The final unifying characteristic of *Aedes* is that the larvae swim with sinusoidal motion (Strickman 1989) wherein the curvature of the anterior flexion is similar in extent to the posterior flexion. Although this behavior is not unique to the genus, its consistency within the genus is striking given the wide range of larval habitats occupied by the genus. The suite of morphological (egg structure), physiological (resistant egg), and behavioral (oviposition habits and swimming motions) characters may have arisen independently, but it seems more likely that these characters support the monophyletic origin of *Aedes* (sensu lato) or lineage 1 (Fig. 1).

The only formal names available to name lineages are subgenera and genera. Systematists often use additional names, species groups, lineages, and others, but these names are not recognized formally by the International Code of Zoological Nomenclature (ICZN 2000). Taxonomists must be very selective in assigning names to only the most important and well-defined lineages. It seems prudent not to formalize these 2 lineages associated with the basal furcation within *Aedes* (sensu lato) (lineages 2a and 2b in Fig. 1) with formal taxonomic names because they are not supported by morphological characters in the female adult that are visible without dissection and by biological differences. Indeed, Reinert (2000) noted several exceptions to his new classification, and examination of recent molecular data indicates that *Aedes* as defined by Reinert (2000) is paraphyletic (Isoe 2000). We believe that the wisest route at this juncture is to treat *Aedes* (sensu lato) (lineage 1 in Fig. 1) as a genus and to

focus on establishing the subgenera of *Aedes* (sensu lato) as monophyletic units (lineages at the level of arrow 3 in Fig. 1).

Female adult specimens of *Ochlerotatus* and *Aedes* as defined by Reinert (2000) cannot be identified morphologically without dissection, and no distinct differences in biology, behavior, and ecology distinguish these 2 taxa as currently defined. Use of these names as genera complicates mosquito identification and interferes with information retrieval and communication among taxonomists, medical entomologists, and vector control specialists. Therefore, it is our opinion that *Ochlerotatus* Lynch Arribalzaga should be placed as a subgenus of *Aedes* Meigen, *Aedes* (*Ochlerotatus*). We believe that the usage of the genus *Aedes* and the subgenus *Ae.* (*Ochlerotatus*) should be restored to the traditional usage during the interval 1906–2000.

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