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Elevation of *Pseudoskusea*, *Rusticoidus* and *Protomacleaya* to valid subgenera in the mosquito genus *Aedes* based on taxon naming criteria recently applied to other members of the Tribe Aedini (Diptera: Culicidae)

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Abstract

Background: *Pseudoskusea, Rusticoidus* and *Protomacleaya* were well-recognized, morphologically distinct subgenera within the genus *Aedes* prior to a series of taxonomic changes over the past 15 years by Reinert, Harbach and Kitching, when they were recognized as subgenera of the genus *Ochlerotatus*. In our recent effort to stabilize the Tribe Aedini, we synonymized these subgenera and associated species back into the genus *Aedes*, but incorrectly assigned them as putative informal groups, instead of reinstating them to subgenera.

Conclusion: Here we formally elevate three traditionally recognized subgenera (*Pseudoskusea, Rusticoidus* and *Protomacleaya*) within the genus *Aedes*.

Keywords: Tribe Aedini, *Aedes*, Subgenera, Elevation

Findings

The tribe Aedini is comprised of about a third of all recognized mosquito species, and includes many vectors of debilitating viral diseases to humans, such as Dengue and Chikungunya. Within the tribe, the genus Aedes, in the traditional sense, is the largest genus in the tribe with 932 species. Other aedine genera are Armigeres, Eretmapodites, Haemagogus, Heizmannia, Opifex, Psorophora, Udaya and Verrallina. During the past 11 years, based on a series of morphological phylogenetic studies by Reinert, Harbach & Kitching (RH&K) [1–4], and the taxonomic actions resulting from those studies, the original genus Aedes was split into 74 genera, reducing the genus Aedes from over 900 species [5–8], to only 12. Chief among the reasons given by

RH&K to elevate so many genera was the author's claim of an unreferenced "principle of equivalent rank." This implied that if traditionally accepted genera were phylogenetically co-equal with other clusters of species in their analyses, the newly recognized groups should also be given similar taxonomic status. These taxonomic actions were highly controversial [9, 10] and resulted in wide-spread confusion about which names to apply to most vectors of disease organisms in genus *Aedes* (see Table one in [12]). For example, during this period, *Aedes japonicus* (Theobald), an invasive species and proven vector of West Nile virus and Cache Valley virus, was known variously as *Aedes* (*Finlaya*) *japonicus* [5], *Ochlerotatus* (*Finlaya*) *japonicus* [1] and *Hulecoeteomyia japonica* [2].

Close scrutiny of the RH&K phylogenetic results and a reanalysis of their dataset led Wilkerson et al. [12] to the conclusion that based on the evidence provided by RH&K the classification changes they promoted and that

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resulted in the split of the well-known genus Aedes into so many genera, were not warranted. Aedes was therefore reinstated [12], but to preserve their phylogenetic hypotheses the RH&K genera were reduced in rank to subgenera of Aedes. Any subgenera in the fragmented RH&K system were reduced to putative informal group status [12]. Rationalization for reinstatement of genus Aedes to include all "traditionally" accepted species was based on opinions promoting a conservative approach to classification change based on new phylogenetic analyses [13–15]. These opinions were comprehensively solidified by Vences et al. [16] who, in detail, discussed the relationship between nomenclatorial utility and phylogenetic accuracy. As a guide to determine the suitability for classification changes they proposed a number of Taxon Naming Criteria (TNCs). Appropriate TNCs were cited to reinstate the "traditional" species in genus Aedes [12]. Central to these arguments reinstating genus Aedes, while retaining other traditional aedine genera were: TNC 2, Clade Stability; TNC 3, Phenotypic Diagnosibility; TNC 8, Manageability; TNC 10, Nomenclatural Stability, and; TNC 11, Community Consensus. Since, to these authors [12], there was no compelling evidence warranting changing the classification of traditional diagnosable genera, the traditional genera in tribe Aedini should be retained until strong, multiple lines of evidence are produced showing the contrary.

Following our recent publication reinstating the genus Aedes [12], we revisited the above rationale and realized that three traditionally recognized Aedes subgenera (Pseudoskusea, Rusticoidus and Protomacleaya), recognized as subgenera by RH&K in their genus Ochlerotatus, were incorrectly synonymized as putative informal groups [12], when they should have been reinstated as bona fide subgenera of the genus Aedes. All are diagnosable, well-known traditional groupings and should be retained as such. Taxonomic information for each subgenus, including important references and component species are given in Appendix.

Conclusion and formal taxonomic action

Here, we formally retrieve Pseudoskusea, Rusticoidus and Protomacleaya from synonymy within the Aedes subgenus Ochlerotatus [12], and elevate all three as subgenera of the genus Aedes.

Appendix

Taxonomic Catalog Citation

Subgenus Pseudoskusea Theobald 1907 (as genus) [17].

Type species: Skusea multiplex Theobald. Subgenus Synonym Caenocephalus Taylor 1914 [18] (not Caenocephalus van der Wulp, 1898 [19]) bancroftianus Edwards, 1921

culiciformis (Theobald, 1905) multiplex (Theobald, 1903) postspiraculosus Dobrotworsky, 1961

Important References:

Dobrotworsky 1961 (tax., bion.; Australia) [20] Dobrotworsky 1965 (tax., key, bion.; Australia) [21] Lee et al. 1984 (tax., key, distr., bion.; Australia) [22] Reinert 2000 (to subg. of genus Ochlerotatus) [11] Reinert 2002 (F gen.*) [23] Reinert et al. 2006 (phyl., class.; to genus) [2] Reinert et al. 2008 (to subg. of genus Ochlerotatus) [3] Wilkerson et al. 2015 (phyl., class.; to syn. of subg. Ochlerotatus of genus Aedes) [12] Herein: to subg. of genus Aedes

Subgenus Protomacleaya Theobald 1907 (as genus) [17].

Type species: Culex trisereatus Say aitkeni Schick, 1970 alboapicus Schick, 1970 amabilis Schick, 1970 argyrothorax Bonne-Wepster and Bonne, 1920 berlini Schick, 1970 bertrami Schick, 1970 braziliensis Gordon and Evans, 1922 brelandi Zavortink, 1972 buenaventura Schick, 1970 burgeri Zavortink, 1972 campana Schick, 1970 casali Schick, 1970 chionotum Zavortink, 1972 daryi Schick, 1970 diazi Schick, 1970 gabriel Schick, 1970 galindoi Schick, 1970 hendersoni Cockerell, 1918 heteropus Dyar, 1921 homoeopus Dyar, 1922 idanus Schick, 1970 impostor Schick, 1970 insolitus (Coquillett, 1906) knabi (Coquillett, 1905) kompi Vargas and Downs, 1950 metoecopus Dyar, 1925 niveoscutum Zavortink, 1972 podographicus Dyar and Knab, 1906 sandrae Zavortink, 1972 schicki Zavortink, 1972 schroederi Schick, 1970 sumidero Schick, 1970 tehuantepec Schick, 1970 terrens (Walker, 1856) thorntoni Dyar and Knab, 1907 triseriatus (Say, 1823)

vargasi Schick, 1970 zavortinki Schick, 1970 zoosophus Dyar and Knab, 1917

Important References:

Sourcouf & Gonzalez Rincones 1912 (as *Promacleaya*: emend.) [24]

Schick 1970 (keys, Terrens Group) [25]

Schick 1970 (keys, Terrens Group) [26]

Zavortink 1972 (tax.: resurrected from syn. with Finlaya) [27]

Reinert 2000 (to subg. of genus Ochlerotatus) [11]

Reinert et al. 2009 (as 'Ochlerotatus' ('Protomacleaya') sensu auctorum) [4]

Wilkerson et al. 2015 (to syn. of subg. Ochlerotatus of genus Aedes) [12]

Herein: to subg. of genus Aedes

Subgenus *Rusticoidus* Shevchenko and Prudkina 1973 (as subg. of genus *Aedes*; M*, key) [28].

Type species: Aedes refiki Medschid albescens Edwards, 1921 bicristatus Thurman and Winkler, 1950 krymmontanus Alekseev, 1989 lepidonotus Edwards, 1920 provocans (Walker, 1848) quasirusticus Torres Canamares, 1951 refiki Medschid, 1928 rusticus (Rossi, 1790) ssp. subtrichurus Martini, 1927 subdiversus Martini, 1926

Important References:

Reinert 1999 (tax., review) [29]

Reinert 2000 (to subg. of genus Ochlerotatus) [11]

Reinert 2002 (F gen.*) [23]

Reinert et al. 2008 (phyl., class.) [3]

Reinert et al. 2009 (phyl., class.) [4]

Wilkerson et al. 2015 (to syn. of subg. Ochlerotatus of genus Aedes) [12]

Herein: to subg. of genus Aedes

Important taxonomic information and key references for the three *Aedes* subgenera treated herein (www.mosquitocatalog.org, 13 Sept. 2015); associated species are listed by subgenera. [Tax. = taxonomy, phyl. = phylogenetics, class. = classification, bion. = bionomics, distr. = distribution, subg. = subgenus, syn. = snynomy, * = all or part of life stage is illustrated, F = female, M = male, gen. = genitalia, emend. = emendation]

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

RCW and YML contributed equally to the final paper. Both authors read and approved the final version of the manuscript.

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References

- Reinert JF, Harbach RE, Kitching IJ. Phylogeny and classification of Aedini (Diptera: Culicidae), based on morphological characters of all life stages. Zool J Linn Soc. 2004;142:289–368. doi:10.1111/j.1096-3642.2004.00144x.
- Reinert JF, Harbach RE, Kitching IJ. Phylogeny and classification of Finlaya and allied taxa (Diptera: Culicidae: Aedini) based on morphological data from all life stages. Zool J Linn Soc. 2006;148:1–101. doi:10.1111/j.1096-3642. 2006.00254 x.
- Reinert JF, Harbach RE, Kitching IJ. Phylogeny and classification of Ochlerotatus and allied taxa (Diptera: Culicidae: Aedini) based on morphological data from all life stages. Zool J Linn Soc. 2008;153:29–114. doi:10.1111/j.1096-3642.2008.00382x.
- Reinert JF, Harbach RE, Kitching IJ. Phylogeny and classification of tribe Aedini (Diptera: Culicidae). Zool J Linn Soc. 2009;157:700–94. doi:10.1111/j. 1096-3642.2009.00570.x.
- Knight KL, Stone A. A catalog of the mosquitoes of the world (Diptera: Culicidae). 2nd ed. College Park, Maryland: Entomological Society of America; 1977. 611 p.
- Knight KL. Supplement to a catalog of the mosquitoes of the world (Diptera: Culicidae). College Park, Maryland: Entomological Society of America; 1978. 107 p.
- Ward RA. Second supplement to "A catalog of the mosquitoes of the world" (Diptera: Culicidae). Mosq Syst. 1984;16:227–70.
- Ward RA. Third supplement to "A catalog of the mosquitoes of the world" (Diptera: Culicidae). Mosq Syst. 1992;24:177–230.
- Savage HM, Strickman D. The genus and subgenus categories within Culicidae and placement of Ochlerotatus as a subgenus of Aedes. J Am Mosq Control Assoc. 2004:20:208–14.
- Savage HM. Classification of mosquitoes in tribe Aedini (Diptera: Culicidae): Paraphylyphobia, and classification versus cladistic analysis. J Med Entomol. 2005;42:923–7. doi:10.1093/jmedent/42.6.923. PMID: 16465729.
- Reinert JF. New classification for the composite genus Aedes (Diptera: Culicidae: Aedini), elevation of subgenus Ochlerotatus to generic rank, reclassification of the other subgenera, and notes on certain subgenera and species. J Am Mosq Control Assoc. 2000;16:175–88.
- Wilkerson R, Linton Y-M, Fonseca D, Schultz T, Price D, Strickman D. Making mosquito taxonomy useful: A stable classification of tribe Aedini that balances utility with current knowledge of evolutionary relationships. PLoS One. 2015;10, e0133602. doi:10.1371/journal.pone.0133602.
- Wiley EO. An annotated Linnaean hierarchy, with comments on natural taxa and competing systems. Syst Zool. 1979;28:308–37. doi:10.1093/sysbio/28.3.308.
- Wiley EO. Phylogenetics. The Theory of Phylogenetic Systematics. New York: Wiley-Interscience; 1981. 439 p.

- Wiley EO, Liebermann BS. Phylogenetic Systematics. Theory and Practice of Phylogenetic Systematics. Hoboken, New Jersey: Wiley-Blackwell; 2011.
- Vences M, Guayasamin JM, Miralles A, de la Riva I. To name or not to name: Criteria to promote economy of change in Linnaean classification schemes. Zootaxa. 2013;3636:201–44. doi:10.11646/zootaxa.3636.2.1.
- 17. Theobald FV. A monograph of the Culicidae or mosquitoes. London: British Museum (Natural History); 1907. 639 p.
- Taylor FH. The Culicidae of Australia. -I. Trans Entomol Soc London. 1914;61:683–708.
- van der Wulp FM. Dipteren aus Neu-Guinea in der Ungarischen National-Museums. Termeszetrajzi Fuzetek, kiadja a Magyar nemzeti Muzeum, Budapest. 1898;21:409–26.
- Dobrotworsky NV. Notes on Australian mosquitoes (Diptera, Culicidae). V. Subgenus *Pseudoskusea* in Victoria. Proc Linn Soc New South Wales; 1961. 257–267.
- 21. Dobrotworsky NV. The mosquitoes of Victoria (Diptera, Culicidae). London and New York: Melbourne University Press; 1965. 237 p.
- Lee DJ, Dyce AL, O'Gower AK. The Culicidae of the Australasian region, vol.
 Canberra, Australia: Australian Government Publishing Service; 1984.
- Reinert JF. Comparative anatomy of the female genitalia of genera and subgenera in tribe Aedini (Diptera: Culicidae). Part XIII. Ochlerotatus Lynch Arribalzaga. Cont Amer Entomol Inst. 2002;33:1–117.
- Surcouf J, Gonzalez-Rincones R. Dipteres piqueurs et suceurs de sang actuellement connus de la Republique de Venezuela. Archives de Parasitologie Paris. 1912;15:248–314.
- Schick RX. Mosquito studies (Diptera, Culicidae) XX. The terrens group of Aedes (Finlaya). Cont Amer Entomol Inst. 1970;5:1–158.
- Schick RX. Mosquito studies (Diptera, Culicidae) XXIII. Additions and corrections to the revision of the *Aedes terrens* group. Cont Amer Entomol Inst. 1970:7:13–40.
- Zavortink TJ. Mosquito Studies (Diptera, Culicidae) XXVIII. The new world species formerly placed in *Aedes (Finlaya)*. Cont Amer Entomol Inst. 1972:8:1–206.
- 28. Shevchenko AK, Prudkina NS. On morphology of genitals in mosquito males from the *Aedes* genus. Vestnik Zoologii. 1973;6:40–7.
- Reinert JF. The subgenus Rusticoidus of genus Aedes (Diptera: Culicidae) in Europe and Asia. Europ Mosq Bull. 1999;4:1–7.

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