

On the taxonomy of *Lasiurus*

Charles M. Francis¹, Nancy B. Simmons², Victor Van Cakenberghe³, Nathan S. Upham⁴, and Connor J. Burgin⁵ on behalf of the Global Bat Taxonomy Working Group of the IUCN SSC Bat Specialist Group⁶

¹ Carleton University, Department of Biology, Ottawa, Ontario, K1S 5B6 Canada; and Canadian Wildlife Service, Environment and Climate Change Canada, National Wildlife Research Centre, Ottawa, Ontario K1S 5B6 Canada

² American Museum of Natural History, Division of Vertebrate Zoology (Mammalogy), New York, New York, 10024 USA

³ University of Antwerp, Department of Biology (FunMorph lab), 2610 Antwerp, Belgium

⁴ Arizona State University, School of Life Sciences, Tempe, Arizona, 85284 USA

⁵ University of New Mexico, Department of Biology, Albuquerque, New Mexico, 87131 USA

⁶ Webpage: <https://www.iucnbsg.org/>

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Background:

In a recent series of papers, Baird et al. (2015, 2017, 2021) suggested that the widespread New World genus *Lasiurus* should be split into three separate genera, restricting *Lasiurus sensu stricto* to the “red bats” (*L. borealis* and relatives) and resurrecting *Dasypterus* for the “yellow bats” (*L. ega* and relatives) and *Aeorestes* for the “hoary bats” (*L. cinereus*, split into multiple species therein) plus the Big Red Bat (*L. egregius*). These authors based their argument on the fact that these three lineages are genetically distinct monophyletic clades with discrete morphotypes, and that their estimated divergence times are comparable to those of other vespertilionid genera.

The traditionally-recognized genus *Lasiurus* (containing red bats, yellow bats, and hoary bats) has expanded in content in recent years from 7 species (Koopman, 1993) to 17 species (Simmons, 2005) to 20 species (Simmons and Cirranello, 2022). Within this genus, hoary bats were traditionally considered to comprise a single species, *L. cinereus*, with three subspecies: *L. c. cinereus* (North America), *L. c. villosissimus* (South America including the Galapagos Islands), and *L. c. semotus* (Hawaiian Islands; Simmons, 2005), although several recent papers now recognize them as distinct species (Baird et al., 2015, 2017, 2021; Soto-Centeno and Simmons, 2022). However, nobody had questioned their inclusion in the genus *Lasiurus* until Baird et al. (2015, 2017, 2021) resurrected *Aeorestes* for these taxa as well as *L. egregius*. There has been more variation in treatment of a set of 4 species known as yellow bats (*L. ega*,

L. insularis, *L. intermedius*, and *L. xanthinus*), which have variously been included in the separate genus *Dasypterus* (Allen, 1894; Miller, 1907; Peracchi and Albuquerque, 1986; Barquez et al., 1999, Baird et al., 2015, 2017, 2021), as a subgenus within *Lasiurus* (Corbet and Hill, 1991, Koopman, 1993, 1994; Kurta and Lehr, 1995; Simmons, 2005; Simmons and Cirranello, 2022), or simply under *Lasiurus* without subgeneric recognition (Handley, 1960; Gardner and Handley, 2007). The remaining species (all various species of red bats) have remained in *Lasiurus* throughout their taxonomic history (the type species of *Lasiurus* being the Eastern Red Bat, *L. borealis*), with the recent exception of the Big Red Bat, *L. egregius*, which was placed under *Aeorestes* by Baird et al. (2015, 2017, 2021) based on genetic analyses indicating it is closely related to *L. cinereus* despite having a ‘red bat’ phenotype.

Contrary to the taxonomic recommendations of Baird et al. (2015, 2017, 2021), several sets of authors – Ziegler et al. (2016), Novaes et al. (2018), and Teta (2019) – independently argued that splitting *Lasiurus* into multiple genera is not warranted. While those authors did not dispute the genetic distinction of the three lineages, they noted the genus *Lasiurus sensu lato* is a monophyletic group, and hence it is not necessary to split the genus to ensure taxonomic integrity. They additionally noted that the generic epithet *Lasiurus* has been widely used for many decades for all of these taxa and that, in the interest of taxonomic stability, it is better to recognize *Dasypterus* and *Aeorestes* as subgenera within *Lasiurus*.

Following this exchange of divergent opinions, the Mammal Diversity Database (starting with v1.5, 11 June 2021; MDD 2021) recognized *Dasypterus*, *Aeorestes*, and *Lasiurus* as distinct genera, while Batnames.org (Simmons and Cirranello, 2022) continued to recognize them only at the subgeneric level. Batnames is the taxonomic authority used by the IUCN Redlist, but MDD is widely cited by the scientific community, hence the differing taxonomies recognized in these databases have caused considerable confusion among researchers, managers, and government agencies. The MDD’s policy since starting in 2018 has been to accept the most recent peer-reviewed published opinion on a given taxon, but instances of controversy such as this one have prompted a move toward greater editorial oversight relative to the community of expert taxonomists. As a result, the MDD joined with the Global Bat Taxonomy Working Group, which was asked to make a recommendation for a consistent approach that would be recognized by both the MDD and Batnames.org.

Decision:

After careful review of both sets of papers, we recommend retaining the genus *Lasiurus* for all species within the tribe Lasiurini, but recognizing three subgenera within the genus: *Lasiurus (Lasiurus)* for the red bats (including *arequipae*, *atratus*, *blossevillii*, *borealis*, *castaneus*, *degelidus*, *ebenus*, *frantzii*, *minor*, *pfeifferi*, *seminolus*, and *varius*), *Lasiurus (Dasypterus)* for the “yellow bats” (including *ega*, *insularis*, *intermedius*, and *xanthinus*), and *Lasiurus (Aeorestes)* for the hoary bats and the Big Red Bat (*cinereus*, *egregius*, *semotus*, and *villosissimus*).

The basis for our decision is as follows:

The International Code of Zoological Nomenclature (ICZN 1999) does not specify any criteria for determining an objective level of differentiation of genera vs. subgenera (or any other taxonomic level) above species, provided that species within a genus are each other's closest relatives, i.e., that the genus is monophyletic. As such, recognition of *Lasiurus*, *Dasypterus*, and *Aeorestes* as either genera or subgenera is consistent with the ICZN code. Thus, the more applicable question is which arrangement best serves the goals of taxonomic stability and communication within the scientific community.

Baird et al. (2021) argued that treating the three lineages in *Lasiurus* as subgenera within the genus *Lasiurus* is inappropriate for various reasons. First, they indicated that the use of subgenera (keeping *Lasiurus* as the genus name for all) would be undesirable because it would render the content of the tribe Lasiurini identical to the genus *Lasiurus*, which they considered inappropriate. However, there are many instances in the higher-level taxonomy of bats where tribes, subfamilies, and even families contain only a single genus. Currently there are 10 monogeneric chiropteran families (Rhinopomatidae - *Rhinopoma*, Craseonycteridae - *Craseonycteris*, Nycteridae - *Nycteris*, Rhinolophidae - *Rhinolophus*, Noctilionidae - *Noctilio*, Thyropteridae - *Thyroptera*, Myzopodidae - *Myzopoda*, Cistugonidae - *Cistugo*, Miniopteridae - *Miniopterus*, Mystacinidae - *Mystacina*), as well as 8 monogeneric subfamilies (Eidolinae - *Eidolon*, Notopterisinae - *Notopterus*, Caroliinae - *Carollia*, Lonchorhininae - *Lonchorhina*, Macrotinae - *Macrotus*, Rhinophyllinae - *Rhinophylla*, Scotophilinae - *Scotophilus*, Tomopeatinae - *Tomopeas*) and 6 monogeneric tribes (Eonycterini - *Eonycteris*, Plerotini - *Plerotes*, Rousettini - *Rousettus*, Stenonycterini - *Stenonycteris*, Sturnirini - *Sturnira*, Lasiurini - *Lasiurus*). Second, Baird et al. (2021) suggested subgenera are not appropriate because they are not widely used and hence not useful. This is simply not the case, as was recently summarized by Teta (2019).

A tremendous amount of research has been done on hoary bats in the last several decades, including work on ecology, behavior, reproduction, migration, echolocation, population genetics, conservation, and systematics. As a measure of this activity, we note that the binomial *Lasiurus cinereus* appeared in over 2,600 publications in the last decade alone (based on citation records in Google Scholar using the keywords "*Lasiurus cinereus*" in the date range 2013-2023). In contrast the name *Aeorestes* has been rarely used thus far to refer to hoary bats. As of February 2023, only 79 instances of use of the combination "*Aeorestes cinereus*" are returned, all of them subsequent to Baird et al. (2015).

As summarized in Ziegler et al. (2016), the generic name *Aeorestes* Fitzinger, 1870, listed in Gardner and Handley's (2008) synonymy for *Lasiurus*, was never used to refer to hoary bats in other scientific literature until resurrected by Baird et al. (2015). Prior to 2015, a Google Scholar search returns only 14 citations for the name *Aeorestes* since 1900—and in every case *Aeorestes* was used as a subgenus in *Myotis* (e.g., see Hooper and Van Den Bussche, 2003; Hooper et al., 2006; and Lim, 2009), not in reference to hoary bats. However, Fitzinger (1870, p.428) unambiguously designated the type species of *Aeorestes* as *Vespertilio villosissimus* É. Geoffroy Saint-Hilaire, 1806, as previously noted by Gardner and Handley (2008): 'Diese Form, welche mir der Typus einer besonderen Gattung zu sein scheint, für die ich den Namen „*Aeorestes*" in Vorschlag bringe, wurde zuerst von Azara beschrieben und von Geoffroy mit dem

Namen „*Vespertilio villosissimus*“ bezeichnet.’ The past confusion likely arose because Fitzinger (1870) also included *Vespertilio albescens* E. Geoffroy Saint-Hilaire, 1806 [currently *Myotis albescens*], *Vespertilio nigricans* Schinz, 1821 [currently *Myotis nigricans*], and *Vespertilio levis* E. Geoffroy Saint-Hilaire, 1824 [currently *Myotis levis*] in the genus; However, as *villosissimus* is a hoary bat, it therefore seems clear that the name *Aeorestes* should not be used as a subgenus of *Myotis*. While we agree with Gardner and Handley (2008) and Baird et al. (2015, 2017, 2021) that *Aeorestes* Fitzinger, 1870, is an available and appropriate name for a grouping that includes hoary bats, we believe that additional confusion will be caused if the name is elevated to generic status, as proposed by Baird et al. (2015, 2017, 2021) due to the odd history of usage of *Aeorestes*.

Lastly, the argument in favor of time equivalence among vespertilionid genera advanced by Baird et al. (2021; Table 1) is not valid for two reasons. First, fossil-calibrated molecular divergence times vary widely across analyses as they are dependent on many factors, including the extent of taxon sampling, which exons or non-coding regions are compared, and the assumptions of the phylogenetic model, especially which fossil calibrations are used to constrain node ages (Ho & Phillips 2009, Scornavacca et al. 2020). As a result, it is critical to consider the temporal uncertainty that results from node age estimates, both within a given analysis and across analyses (Huelsenbeck et al. 2000), when presenting time equivalence arguments. The point-age estimates given in Baird et al. (2021) mislead the reader into thinking that these node ages are established with high precision, when in fact considerable uncertainty remains, in most cases plus or minus several million years (Ma). For example, the estimated crown age of 20 Ma given for *Lasiurus* sensu lato by Baird et al. (2021) is unlikely to be significantly different from that of several other genera with estimated crown ages of 19 Ma or even 17 Ma. By comparison, the VertLife mammal trees (Upham et al. 2019) gave the crown age of *Lasiurus* sensu lato as 13.8 Ma with a 95% highest posterior density of 10.8–17.5 Ma across the 10,000 trees in the credible set. Similarly, the ages of 17, 19, and 20 Ma given for *Murina*, *Myotis*, and *Kerivoula* by Baird et al. (2021) compare to mammal tree ages of 13.0 Ma (10.6, 15.5), 13.5 Ma (11.0, 16.3), and 15.8 Ma (12.4, 19.1; for full divergence-time summaries, see: Upham 2019). The substantial overlap among the credible intervals for crown ages of *Lasiurus* relative to *Murina*, *Myotis*, and *Kerivoula* argues against the idea that the former is an especially old genus. Second, if time-equivalency arguments are to be applied credibly, they would need to be applied uniformly, at least within a group like Vespertilionidae, but likely across all mammals or all vertebrates (Avice and Johns 1999). The comparisons noted above make it clear that we currently lack the precise knowledge of divergence times and data infrastructure to maintain taxonomic coherency in biodiversity databases, both of which would be needed if a time-standardization schema like that suggested by Baird et al. (2021) were to be adopted on a broad scale (or even just within vespertilionid bats).

The decision made here to maintain the single-genus arrangement of Lasiurini mirrors a broader question within systematics as a whole: when is the splitting of an already monophyletic genus justified? In this case, we argue that the splitting of *Lasiurus* is unjustified and that it is better to retain this genus as traditionally recognized in order to preserve taxonomic stability in the clade. However, we note there are a number of other mammal-specific examples of the splitting of

monophyletic genera that have received varying levels of support from systematists and the broader biological community. These include examples both within bats and among other mammal orders, such as splitting *Dermanura* and *Koopmania* from *Artibeus* (Hooper et al., 2008), *Neotamias* and *Eutamias* from *Tamias* (Patterson & Norris, 2016), *Sapajus* from *Cebus* (Lynch Alfaro et al., 2012), *Leontocebus*, *Oedipomidas*, and *Tamarinus* from *Saguinus* (Rylands et al., 2016, Brcko et al., 2022), and *Cheracebus* and *Plecturocebus* from *Callicebus* (Byrne et al., 2016). Justifications for these splits have generally relied on several arguments: the philosophy that mammal genera should be considered distinct at specific divergence time estimates (often cited as 4-7 million years, as suggested by Groves, 2001); the fact that there are corresponding morphotypes with each clade; and the belief that genera are more taxonomically useful than subgenera. Others have also suggested using levels of sympatry between species and between different clades and their biogeography as evidence for generic status (e.g., Lynch Alfaro et al., 2012, Byrne et al., 2016, Rylands et al., 2016). Although there needs to be discussion of each of these examples explicitly, Teta (2019) advocated for the use of subgenera rather than full genera when considering how to demonstrate the cladistic and biogeographic diversity within an already monophyletic genus, especially when that genus has been maintained as a single genus historically. This philosophy has been echoed in discussions regarding the splitting of some of the aforementioned mammal genera (particularly in Neotropical primates; Garbino, 2015, Gutiérrez & Marinho-Filho, 2017), and is implemented here as justification for the retention of *Lasiurus* as a single genus with three subgenera (*Lasiurus*, *Dasypterus*, and *Aeorestes*).

In summary, we recommend recognition of *Lasiurus*, *Dasypterus*, and *Aeorestes* as subgenera within the genus *Lasiurus* for the following reasons: the genus *Lasiurus* thus defined is monophyletic; the use of subgenera is appropriate to recognize groupings within the genus; there are no objective criteria for suggesting that a particular timing or degree of divergence merits elevating these subgenera to genera, and in any case there is considerable uncertainty in estimated divergence times of these groups and other genera in the family Vespertilionidae; and finally that retention of the genus *Lasiurus* for all members of the tribe Lasiurini meets the ICZN (1999) goal of promoting maximum stability in nomenclature.

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Appendix: Nomenclature details for the genus, subgenera and species currently recognized within *Lasiurus* as recommended in this decision paper.

GENUS:

Lasiurus Gray, 1831. *Zool. Misc.*, 1: 38. Type species: *Lasiurus borealis* (Müller, 1776), by subsequent designation (Miller and Rehn 1901).

SUBGENUS:

Aeorestes Fitzinger, 1870. *Sber. k. Akad. Wiss. Wien, math. naturw. Kl.*, 62 (1): 427. Type species: *Vespertilio villosissimus* E. Geoffroy Saint-Hilaire, 1806, by original designation.

Species:

Lasiurus (Aeorestes) cinereus (Palisot de Beauvois, 1796). *Cat. Raisonne Mus. Peale Philadelphia*: 18. Type locality: USA, Pennsylvania, Philadelphia.

Lasiurus (Aeorestes) egregius (Peters, 1871). *Monatsb. k. preuss. Akad. Wiss. Berlin*, 1870: 912. Type locality: Brazil, Santa Catarina State.

Lasiurus (Aeorestes) semotus (H. Allen, 1890). *Proc. U.S. Natl. Mus.*, 13 (807): 173. Type locality: USA, Hawaii.

Lasiurus (Aeorestes) villosissimus (E. Geoffroy Saint-Hilaire, 1806). *Ann. Mus. Hist. Nat. Paris*, 8: 204. Type locality: Paraguay, Asuncion.

SUBGENUS:

Dasypterus Peters, 1871. Monatsb. k. preuss. Akad. Wiss. Berlin, 1870: 912. Type species: *Atalapha intermedia* (Allen, 1862), by subsequent designation (Miller, 1897).

Species:

Lasiurus (Dasypterus) ega (Gervais, 1855). Exped. Partes Cen. Am. Sud., Zool. (Sec. 7), Vol. 1, pt. 2 (Mammifères): 73, pl. 14, figs 1, 1a - c. Type locality: Brazil, Amazonas, Éga.

Lasiurus (Dasypterus) insularis Hall and J.K. Jones Jr., 1961. Univ. Kansas Publ. Mus. Nat. Hist., 14 (5): 85. Type locality: Cuba, Las Villas Province, Cienfuegos.

Lasiurus (Dasypterus) intermedius H. Allen, 1863. Proc. Acad. Nat. Sci. Philadelphia, 14 (5) 16: 246 (for 1862). Type locality: Mexico, Tamaulipas, Matamoros.

Lasiurus (Dasypterus) xanthinus (Thomas, 1897). Ann. Mag. nat. Hist., ser. 6, 20 (120): 544. Type locality: Mexico, Baja California Sur, Sierra [de la] Laguna.

SUBGENUS:

Lasiurus Gray, 1831. Zool. Misc., 1: 38. Type species: *Lasiurus borealis* (Müller, 1776), by subsequent designation (Miller and Rehn 1901).

Species:

Lasiurus (Lasiurus) arequipae Málaga, Díaz, Arias and Medina, 2020. Rev. Mex. Biodiv., 91 (e913096): 4, figs 1, 2, 7. Type locality: Peru, Arequiba department, Castilla province, 11.5 km N Aplao, Huatiapa.

Lasiurus (Lasiurus) atratus Handley, 1996. Proc. Biol. Soc. Washington, 109 (1): 1, 5, fig. 2. Type locality: Suriname, Zuid River, Kaiserberg Airport.

Lasiurus (Lasiurus) blossevillii (Lesson and Garnot, 1826). Ferussac's Bull. Sci. Nat. Geol., 8: 95. Type locality: Uruguay, Montevideo.

Lasiurus (Lasiurus) borealis (P.L.S. Müller, 1776). Natursyst. Suppl., Register-Band (Suppl.): 20. Type locality: USA, New York, New York.

Lasiurus (Lasiurus) castaneus Handley, 1960. Proc. U.S. Natl. Mus., 112 (3442): 468. Type locality: Panama, Darién, Río Pucro, Tacarcuna Village [Specimen label: "Camp"].

Lasiurus (Lasiurus) degelidus Miller, 1931. J. Mamm., 12 (4): 410. Type locality: Jamaica, [Clarendon,] District of Vere, Sutton's [=Suttons].

Lasiurus (Lasiurus) ebenus Fazzolari-Corrêa, 1994. Mammalia, 58 (1): 119, fig. 1. Type locality: Brazil, São Paulo, Parque Estadual da Ilha do Cardoso.

Lasiurus (Lasiurus) frantzii (Peters, 1871). Monatsb. k. preuss. Akad. Wiss. Berlin, 1870: 908. Type locality: Costa Rica.

Lasiurus (Lasiurus) minor Miller, 1931. J. Mamm., 12 (4): 410. Type locality: Haiti, [Ouest,] Voûte l'Église, a cave near Jacmel road a few km N Trouin.

Lasiurus (Lasiurus) pfeifferi (Gundlach, 1862). Monatsb. k. preuss. Akad. Wiss. Berlin, 1861: 152. Type locality: Cuba, Trinidad.

Lasiurus (Lasiurus) seminolus (Rhoads, 1895). Proc. Acad. Nat. Sci. Philadelphia, 47: 32. Type locality: USA, Florida, Pinellas County, Tarpon Springs.

Lasiurus (Lasiurus) varius (Pöppig, 1835). Reise Chile Peru Amaz., 1: 451, footnote. Type locality: Chili, Bío-Bío province, Antuco.