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On the utility of taxonomy to reflect biodiversity: the example of Lasiurini (Chiroptera: Vespertilionidae)

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The taxonomic history of bats of the tribe Lasiurini (Chiroptera: Vespertilionidae) has undergone significant changes over time. Authors at different times have recognized various numbers of genera and subgenera within the tribe. The most recent proposed change to generic level taxonomy (that there should be three genera recognized instead of a single genus) has been debated in the literature. We reviewed papers that commented on the recent changes to lasiurine generic taxonomy, as well as those that have adopted the new taxonomy and the ones that have not. We also reviewed the relevant taxonomic literature from 1942 to the present that shows the fluid taxonomic history of these bats. The literature review shows that the recently proposed taxonomic change recognizing the three groups of lasiurine bats as distinct genera is the only taxonomy that differentiates the tribe from the genera. Examination of times to most recent common ancestor (TMRCA) of 24 vespertilionid genera shows *Lasiurus*, if it comprises all Lasiurini, to be an outlier. Here, we support the recognition of three genera and explain how this arrangement best reflects the evolutionary history and biodiversity of the tribe by bringing the three distinct lineages in line with other vespertilionid genera with respect to divergence times and genetic distances. Considering the Lasiurini to comprise a single genus, *Lasiurus*, that genus has the greatest TMRCA of all vespertilionid genera analyzed, comparable only to the genus *Kerivoula* of the monotypic subfamily Kerivoulinae. However, recognizing the three deeply diverged lasiurine lineages (red bats, yellow bats, and hoary bats) as genera brings their TMRCAs in line with other genera and approximates the mean TMRCA of the 24 genera analyzed. Opponents of Baird *et al.'s* taxonomy argued that these three lineages should be considered as subgenera to avoid changing scientific names for purpose of nomenclatural stability and ease of conducting a literature search and because the three deep lineages are all monophyletic. That argument ignores the biological reality that these lineages are morphologically distinct, and that they are genetically as distinct from one another as other genera of vespertilionid bats; there is ample precedent in the mammalian literature to use values of TMRCA as a metric to maintain consistency of higher taxonomic categories such as genus. We encourage other mammalogists to utilize taxonomy to its maximum descriptive potential, while taking into account phylogenetic relationships of the taxa of interest.

La historia taxonómica de murciélagos del tribu Lasiurini (Chiroptera: Vespertiliónidae) muestra grandes cambios significativos con el tiempo. Varios autores han reconocido diferentes números de géneros y subgéneros dentro del tribu. La taxonomía mas recién propone cambios a nivel de géneros (sugeriendo que existen tres géneros y no solamente uno). Este punto de vista ha sido debatiado en la literatura. Hemos revisado los trabajos que tratan de la taxonomía de estos murciélagos, notando que algunos autores aceptan la nueva taxonomía y otros autores no. Hemos revisado la bibliografía desde 1942, y por lo general, subraya la taxonomía fluida de estos murciélagos. La bibliografía muestra que solamente los estudios recientes que reconocen los 3 grupos de murciélagos como tres géneros distintos pueden diferenciar filogenéticamente el tribu del género o géneros. Considerando el tiempo del ancestro en común mas recién (TMRCA) de 24 géneros de vespertiliónidos muestra que *Lasiurus*, si incluye el total de Lasiurini, es un caso aparte. En este trabajo apoyamos el reconocimiento de tres géneros distintos y notamos como describe la evolución de los Lasiurini cuando se comparen géneros de Lasiurini con géneros de los vespertiliónidos con respeto a las divergencias evolucionarias y distancias genéticas. Si consideramos que los Lasiurini efectivamente está descrito solamente por el género *Lasiurus*, tal género va a tener el TMRCA mas grande, y comparable solamente con la subfamilia Kerivoulinae. Sin embargo, si reconocmos los tres géneros muy divergidos (murciélagos rojos, amarillos, canosos) como géneros hace sus TMRCA comparables a los otros géneros y a los otros 24 géneros analizados. Los que difieren con nosotros piden estabilidad de nomenclatura porque hace mas fácil la búsqueda de información bibliográfica y porque cada lineaje es monofilética. Ese argumento ignora la realidad biológica que estas lineas son tan distintas una del otra que de los otros géneros de vespertiiónidos. Recomendamos que mastozoólogos utilicen la taxonomía que tiene el máximo poder explicativa e incluye las relaciones filogenéticas del tribu, es decir los valores de TMRCA como una medida más para describir las categorías mas altas, como género, de la taxonomía.

Keywords: Genus; lasiurine bats; phylogeny; subgenus; taxonomy.

Introduction

Recent studies on the evolutionary history of lasiurine bats (Chiroptera: Vespertilionidae: Lasiurini; Baird *et al.* 2015, 2017) have spurred discussion in the mammal literature regarding the broader implications of taxonomic revisions to long-standing nomenclature. Baird *et al.* (2015, 2017) recommended the separation of lasiurines into three genera: *Lasiurus* (red bats), *Aeorestes* (hoary bats), and *Dasypterus* (yellow bats). Until Baird *et al.* (2015, 2017), the vespertilionid tribe Lasiurini had been considered monotypic, comprised solely of the monophyletic genus, *Lasiurus*. At the time, some authors also recognized two subgenera: *Dasypterus* (yellow bats) and *Lasiurus* (red + hoary bats; Figure 1A). In the more distant past, other authors recognized each of these groups (red, hoary, and yellow bats) as separate genera. Throughout the taxonomic history of these bats, their status has been in flux (Figure 2). The purpose of this paper is to review the relevant literature regarding generic and subgeneric taxonomy within the Lasiurini and to address the concerns expressed by Ziegler *et al.* (2016), Novaes *et al.* (2018), and Teta (2019).

Methods

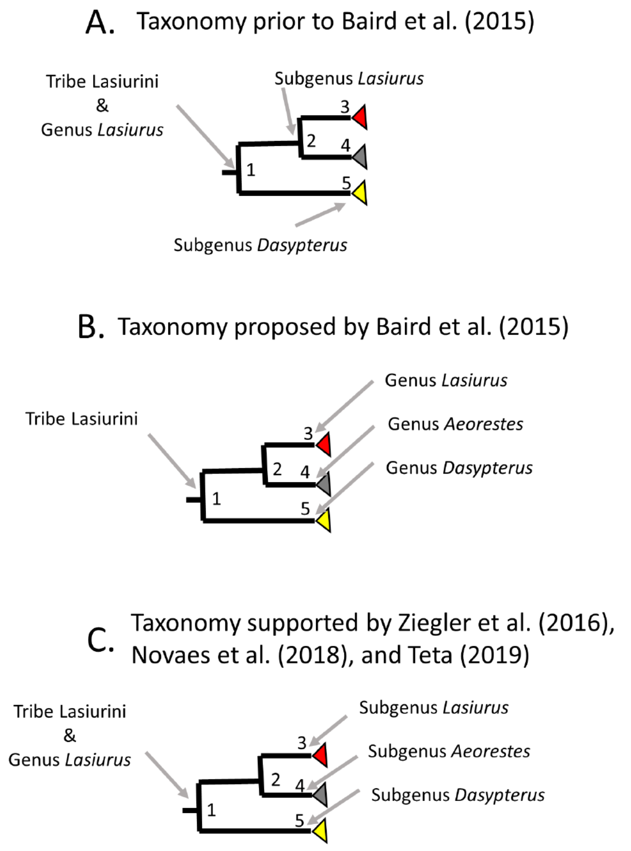
We reviewed the literature beginning with Tate (1942) who first recognized the Tribe Lasiurini and included the bats commonly referred to as red bats, hoary bats, and yellow bats. The literature of this group is extensive, but we restrict our assessment to 13 papers that we consider most influential for taxonomy (Figure 2), represent all the various taxonomic proposals, and are illustrative of the numerous changes, back and forth, between recognizing one or two genera over the course of nearly 80 years. We use this information to address the criticisms of our proposed arrangement of three genera of lasiurine bats (Baird *et al.* 2015, 2017) by Ziegler *et al.* (2016), Novaes *et al.* (2018), and Teta (2019).

Additionally, times to most recent common ancestor (TMRCA) for vespertilionid bat groups were estimated from the data provided in Amador *et al.* (2016). We recorded all estimated TMRCA for vespertilionid genera, tribes, and subfamilies for those taxa that were monophyletic. Two exceptions were *Hypsugo/Falistrellus* and *Eptesicus/Histiotus*. Genera represented by a single specimen in Amador *et al.* (2016) were not included in our analysis. Finally, dates for the TMRCA within Lasiurini were obtained from the estimates of Baird *et al.* (2017) because Amador *et al.* (2016) did not include multiple specimens of all lineages within Lasiurini. Those dates were not all specified in the Baird *et al.* (2017) paper, but they were extracted from the original analysis. The date for Lasiurini and the monotypic *Lasiurus* were included in the dates obtained from Amador *et al.* (2016). We sorted the TMRCA for each taxon by date and plotted them as a histogram using R.

Results

Phylogenetic relationships of the major groups of Lasiurini and the various generic and subgeneric taxonomic arrangements are shown in Figure 1. The taxonomic changes proposed by Baird *et al.* (2015, 2017, Figure 1B), who recognized three genera of lasiurine bats instead of the single genus *Lasiurus*, have been accepted by many authors (Alurralde *et al.* 2017; Amador *et al.* 2016; Best and Hunt 2020; Schmidly and Bradley 2016; Decker *et al.* 2020; Espinosa-Martínez *et al.* 2016; Geluso and Bogan 2018; Gimenez and Giannini 2017; Krejsa *et al.* 2020; Lew and Lim 2019; Tirira 2018); however, others have not followed our taxonomy including Upham *et al.* (2019) who report the most extensive phylogeny of mammals. Ziegler *et al.* (2016), Novaes *et al.* (2018), and Teta (2019) have argued that changes to the taxonomy of Lasiurini are not warranted because *Lasiurus* was a monophyletic genus. They all suggest recognizing the red, yellow, and hoary bats as different subgenera of *Lasiurus* (Figure 1C).

Table 1 shows the estimated Time to Most Recent Common Ancestor (TMRCA) for 24 genera, five tribes, and four subfamilies of vespertilionid bats. Figure 3 shows a histogram of these estimates and illustrates how the subdivision of Lasiurini into three genera changes the monotypic *Lasiurus* from an outlier among genera to three genera having approximately average vespertilionid TMRCAs.


A. Taxonomy prior to Baird et al. (2015)

B. Taxonomy proposed by Baird et al. (2015)

C. Taxonomy supported by Ziegler et al. (2016), Novaes et al. (2018), and Teta (2019)

Figure 1. Phylogenetic relationships of the major groups of lasiurine bats according to Baird *et al.* (2015, 2017). The taxonomy proposed by Baird *et al.* (2015, 2017) in B differentiates the phylogenetic node that demarcates the tribe from the node, or nodes, that demarcates the genus or genera. In the taxonomies shown in A and C, node 1 demarcates both the tribe and genus.

Discussion

Teta (2019) asserted that a "main goal of the zoological nomenclature is to promote nomenclatural stability." Nomenclatural stability also is a key point raised by Ziegler *et al.* (2016) and Novaes *et al.* (2018). We agree that it is good to strive for stability; however, we reject the idea that stability is the main purpose of nomenclature. The history of nomenclature is one of frequent change and this is true for lasiurine bats (Figure 2). With the current rapid rate of change in technology, including increasing computing capacity and the increased speed and decreased cost of genetic sequencing, it is inevitable that change will be rapid in our understanding of biosystematics and consequently in taxonomy. Zoological nomenclature is a powerful tool that should be utilized to its maximum descriptive potential, not simply conserved because of the status quo and to make the lives of scientists, and online searches, easier. When used to its potential, nomenclature should convey evolutionary relationships, diversity, divergence, and the potential to clarify conservation priorities. Teta (2019) promoted the use of subgenera in cases such as Lasiurini where a monophyletic genus contains multiple distinct lineages. This was considered herein, but for reasons outlined below it is apparent that full generic recognition of the lineages is warranted due to their genetic and morphological distinction, and to keep them consistent with other vespertilionid genera. Having a distinct tribe comprised of a single genus containing three morphologically diverse lineages that are genetically as distinct and old as other vespertilionid genera does not adequately reflect the true biodiversity or history of the tribe.

Table 1. Time to most recent common ancestor (TMRCA) of vespertilionid taxa as estimated from the genetic data discussed herein. Dates are rounded to the nearest million years. Taxa with asterisks (*) follow the taxonomy of Lasiurini proposed by Baird *et al.* 2015.

Name	Taxonomic Level	TMRCA (Ma)
Harpiocephalus	Genus	2
Laephotis	Genus	3
Nyctophilus	Genus	6
Vespertilio	Genus	8
Otonycteris	Genus	8
*Lasiurus**	Genus	9
Nyctalus	Genus	11
*Aeorestes**	Genus	11
Chalinolobus	Genus	11
Corynorhinus	Genus	11
Vespadelus	Genus	12
Hypsugo + Falistrellus	Genus	12
*Dasypterus**	Genus	12
Scotophilus	Genus	14
Neoromicia	Genus	14
Scotophilini	Tribe	14
Barbastella	Genus	15
Rhogeessa	Genus	16
Glauconycteris	Genus	17
Murina	Genus	17
Eptesicus + Histiotus	Genus	17
Arielulus	Genus	19
Plecotus	Genus	19
Pipistrellus	Genus	19
Myotis	Genus	19
Lasiurus (monotypic)	Genus	20
Lasiurini	Tribe	20
Kerivoula	Genus	20
Kerivoulinae	Subfamily	20
Pipistrellini	Tribe	20
Murininae	Subfamily	21
Myotinae	Subfamily	22
Antrozoini	Tribe	23
Vespertilionini	Tribe	24
Plecotini	Tribe	27
Vespertilioninae	Subfamily	34

Novaes *et al.* (2018) also argued against the splitting of the vespertilionid genus *Lasiurus* into three distinct genera (*Aeorestes*, *Dasypterus*, and *Lasiurus*), as proposed by Baird *et al.* (2015, 2017). The first argument made by Novaes *et al.* (2018) is that genetic distance, and divergence times calculated from genetic distance, is not a useful character for defining genera because it is not comparable between different groups. They cite the examples of primate genera, *Tarsius* and *Homo*, which have vastly different divergence times from their respective sister taxa. Although this is certainly true for widely divergent taxa, Baird *et al.* (2015, 2017, and references therein) stated that divergence times and genetic distance among genera within Vespertilionidae are generally consistent, with the notable exception of *Lasiurus*.

Splitting the clades within *Lasiurus* into three distinct genera aligns their divergence times and genetic distances more closely to most other splits within Vespertilionidae. Examples of vastly different divergence times in other mammalian taxa, such as those in Primates cited by Novaes *et al.* (2018), are irrelevant to the discussion of lasiurine taxonomy because those discrepancies are not seen to the same degree in vespertilionids. Evidence of the relative consistency in age of vespertilionid taxa can be seen in Figure 3 and Table 1. The TMRCA of Lasiurini, and of *Lasiurus* prior to our subdivision of the genus, is 20 MYA making this the oldest genus in the family (tied with *Kerivoula* of the monotypic subfamily Kerivoulinae). The three genera recognized by Baird *et al.* (2015, 2017) have TMRCA estimates that range from 9 to 12 MYA and which are close to the mean TMRCA of 12.58 calculated for the 24 genera in Figure 3 and Table 1 (not including the monotypic Kerivoulinae, *Kerivoula*, and Lasiurini, *Lasiurus*, which are clear outliers).

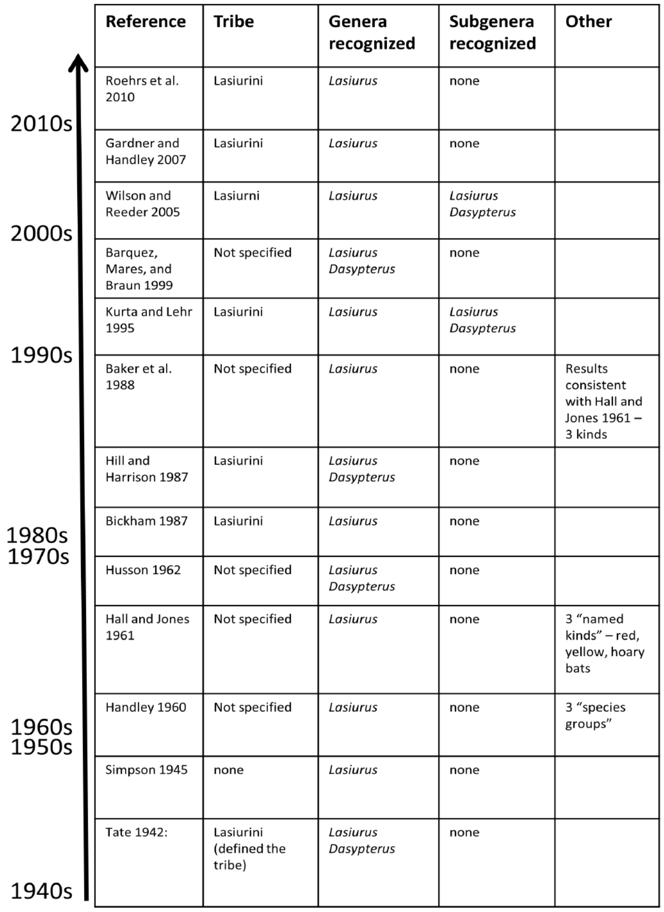
The equivalence of taxonomic categories at the same rank and the decision as to what appropriate taxonomic level a group of species should be included have long been issues that have vexed taxonomists. Schaefer (1976, p. 2) recommended a clear and logical solution: "Should a natural group of species, clearly distinct from other groups, be treated as a genus, tribe, or family? The answer of course appears to lie in comparing the group with other genera, tribes, and families in the higher category to which the group in question belongs." This is precisely what was done by Baird *et al.* (2015, 2017).

Secondly, Novaes *et al.* (2018) disputed that morphological differences distinguish *Aeorestes*, *Dasypterus*, and *Lasiurus* and thus stated that the taxonomic arrangement of Baird *et al.* "attributes unnecessary weight to clades whose phenotypic distinction is merely superficial". The most obvious morphological difference among the three genera is pelage color, which has given rise to the colloquial names of each group: the hoary, yellow, and red bats. *Aeorestes* (the hoary bats) are characterized by grayish pelage, *Dasypterus* (yellow bats) by yellowish pelage, and *Lasiurus* (red bats) by reddish pelage. Moreover, members of *Dasypterus* have only one premolar on each side of the upper jaw (Hall and Jones 1961) compared to two in *Lasiurus* and *Aeorestes*. *Aeorestes* species generally are larger in size than the other two genera. Other diagnostic characters of *Aeorestes* include multiple unique dental and skeletal features (Shump and Shump 1982). Although Handley (1960) considered the differences among the three "species groups" (as he referred to them) insufficient to warrant their distinction as different genera, he nonetheless provided a table of distinguishing characteristics for each (see Table 3 in Handley 1960).

The final point made by Novaes *et al.* (2018) was that vernacular names "cannot be used as an argument to take (sic) taxonomic decisions." There is a reason that the vernacular names red bats, hoary bats, and yellow bats exist: it is because the names reflect morphological distinction among the groups. We do not support changing taxonomy simply because vernacular names exist; it is the basis for their existence that supports the taxonomic change.

Characters in support of taxonomic revision. Novaes *et al.* (2018) admitted that separating a monophyletic group into different genera can be supported if "well-marked phenotypic discontinuities are detected among them" and "if supported by a suite of consistent characters, preferably from multiple datasets." But their bias towards the use of morphology in making taxonomic decisions is evident from the first part of the title of their paper. "Separation of monophyletic groups into distinct genera should consider phenotypic discontinuities." We argue that the split of Lasiurini into three distinct genera is supported by both morphology and, more importantly, genetics. Lasiurine bats are among the most easily distinguishable group of vespertilionids, even by those who are not experts in vespertilionid morphology. It is trivial to identify most species to genus from some distance away, without having to measure skull characters, etc. Moreover, given the new taxonomy proposed by Baird *et al.* (2015), it would be useful to have a morphological revision of the tribe that could provide morphological diagnoses of the genera and, importantly, include species that were unavailable to Baird *et al.* (2015) for genetic analysis. As for the "suite of consistent characters" required by Novaes *et al.* (2018) to define genera, Baird *et al.* (2015, 2017) certainly have defined a suite of characters that consistently group the three genera into reciprocally monophyletic groups and can be used to define them. Those characters are genetic data from multiple mtDNA and nuclear loci.

Despite the historical importance of morphological characters in taxonomy, we are now on the cusp of the genomics age in mammalogy (Baird *et al.* 2019), and molecular markers, not morphology, are the current gold standard for conducting phylogenetic analysis. Since it is generally agreed that taxonomy must reflect phylogeny, then it follows that genetic characters are the most useful in taxonomy as well. But morphology will continue to be used to diagnose taxa because those characters are useful for identification of specimens. In fact, morphological characters are useful to diagnose living and extinct taxonomic groups *because* they are characters with a genetic basis. If they were not, they could not be used. Nonetheless, they are not the best genetic-based characters available to us. DNA sequences are easily understood, discrete, and quantifiable.



Reference	Tribe	Genera recognized	Subgenera recognized	Other
Roehrs et al. 2010	Lasiurini	*Lasiurus*	none	
Gardner and Handley 2007	Lasiurini	*Lasiurus*	none	
Wilson and Reeder 2005	Lasiurni	*Lasiurus*	*Lasiurus* *Dasypterus*	
Barquez, Mares, and Braun 1999	Not specified	*Lasiurus* *Dasypterus*	none	
Kurta and Lehr 1995	Lasiurini	*Lasiurus*	*Lasiurus* *Dasypterus*	
Baker et al. 1988	Not specified	*Lasiurus*	none	Results consistent with Hall and Jones 1961 – 3 kinds
Hill and Harrison 1987	Lasiurini	*Lasiurus* *Dasypterus*	none	
Bickham 1987	Lasiurini	*Lasiurus*	none	
Husson 1962	Not specified	*Lasiurus* *Dasypterus*	none	
Hall and Jones 1961	Not specified	*Lasiurus*	none	3 "named kinds" – red, yellow, hoary bats
Handley 1960	Not specified	*Lasiurus*	none	3 "species groups"
Simpson 1945	none	*Lasiurus*	none	
Tate 1942:	Lasiurini (defined the tribe)	*Lasiurus* *Dasypterus*	none	

Figure 2. Studies showing the various generic and subgeneric taxonomic relationships of the Tribe Lasiurini prior to Baird *et al.* (2015, 2017).

Novaes *et al.* (2018) "agree that clades may be separated into different genera if well-marked phenotypic discontinuities are detected among them." Their condemnation of our decision to recognize three well differentiated lasiurine genera is based in part on a vague and undefinable metric of morphological divergence. What exactly is a well-marked phenotypic discontinuity? No such scale exists. They went on to say that "the decision will always be arbitrary." Our decision, however, was *not* arbitrary. It was based on our use of genetics to estimate percent sequence divergences and divergence time estimates based on multiple genetic loci. These metrics were compared to other genera of vespertilionid bats and determined to be comparable. Consequently, we concluded that not only are *Aeorestes*, *Dasypterus*, and *Lasiurus* easy to distinguish based on morphology, there is also no doubt that they are distinct, highly divergent, and easily definable groups based on genetics.

Taxonomy and Phylogeny. Prior to Baird *et al.* (2015), the tribe Lasiurini was a monophyletic group consisting of a single, monophyletic genus. Therefore, the same node on the tree defined both a tribe and a genus (Node 1 in Figure 1A). The only taxonomic status given to the divergent clades within the tribe were the subgenus *Lasiurus* (node 2 in Figure 1A) and subgenus *Dasypterus* (node 5 in Figure 1A); however, the subgeneric taxonomy was not recognized by many authors (Figure 2). Even the authors who recognized subgenera would not normally use those names when referencing a particular group of lasiurines; they only used the genus name, which references node 1 in Figure 1A.

The taxonomic change proposed by Baird *et al.* (2015) maintains the monophyletic tribe defined by one node (node 1 in Figure 1B), but shifts the generic levels to their own nodes on the tree (nodes 3–5 in Figure 1B). This arrangement maximizes the use of taxonomy to describe the variation present in the lasiurine tree. The old arrangement (Figure 1A) did not assign taxonomic status to several important nodes in the lasiurine phylogeny. In using the Baird *et al.* (2015) taxonomy, researchers can now reference specific parts of the lasiurine tree by utilizing a genus name.

Critics of the Baird *et al.* (2015) taxonomy, including Ziegler *et al.* (2016), Novaes *et al.* (2018), and Teta (2019), all supported the following taxonomy: Tribe Lasiurini and Genus *Lasiurus*, with subgenera *Lasiurus*, *Aeorestes*, and *Dasypterus*. As shown in Figure 1C, this arrangement does not help resolve the issue of having the Tribe and Genus both defined by the same node on the phylogeny (*i.e.*, both the genus and the tribe still reference node 1 in Figure 1C). Although the subgenera would clarify the specific part of the phylogeny, researchers do not generally use subgenera, and therefore this proposed taxonomy does not meet our criteria of maximizing the potential of taxonomy to reflect phylogenetic divergence. Naming each of the major nodes within the lasiurine phylogeny is the most powerful way to utilize taxonomy.

The fact that the three critical papers all suggested that the recognition of three subgenera of *Lasiurus* would be appropriate, indicates that all three studies do in fact recognize these lineages as being distinct, and that we are only arguing about the taxonomic level at which they should be recognized. Patterson and Norris (2016) faced a similar dilemma in that all chipmunks were placed in a monophyletic genus *Tamias,* but it included three distinct lineages recognized as subgenera. Patterson and Norris (2016) elevated the subgenera to genera based on 1) the degree of genetic differentiation among the subgenera being comparable to other genera of ground squirrels, 2) the chipmunk lineages are older than the ground squirrel lineages as indicated in the fossil record, and 3) morphological distinction. Thus, we now have three genera of chipmunks despite the original genus *Tamias* being monophyletic. As with the lasiurine bats addressed here, the key metric to determine if the lineages represent genera or subgenera was the level of genetic differentiation and TMRCA of the lineages as compared to others in their taxonomic group.

Novaes *et al.* (2018), Teta (2019), and Ziegler *et al.* (2016) supported the status quo of recognizing a single, monophyletic genus, *Lasiurus*, within the tribe Lasiurini. They suggested that the names *Aeorestes* and *Dasypterus* should be used as subgenera (Figure 1C). Although we agree that splitting a monophyletic genus should not be done without strong evidence, we do not think that sub-generic taxonomy is the best way to handle the lasiurine situation. If, as Ziegler *et al.* (2016), Novaes *et al.* (2018), and Teta (2019) suggested, one were to recognize *Aeorestes* and *Dasypterus* as subgenera of *Lasiurus*, it would not solve the problem of having a single node on the tree defining both a genus and a tribe, thus still rendering the taxonomy ambiguous and lacking in resolution (Figure 1C). Additionally, and more importantly, it does not reflect the true degree of differentiation of these three highly distinctive lineages that are comparable in age and genetic distance to average vespertilionid generic lineages (Table 1, Figure 3).

Finally, Novaes *et al.* (2018) concluded their paper by wrongly suggesting that the taxonomic arrangement of Baird *et al.* (2015, 2017) has not been widely accepted. Multiple papers cited above have followed Baird *et al.* (2015), but it is especially worthwhile to note Amador *et al.* (2016). This is a comprehensive molecular systematic review of bats based on a study of 796 species using 9 nuclear and mitochondrial genetic markers. They report data for 270 species from 48 genera of vespertilionid bats. Notably, they report no subgenera.

We encourage other mammalogists to view taxonomy as we have outlined here. It should be a tool used to convey evolutionary relationships and biodiversity. A taxonomic arrangement is a hypothesis; therefore, it is subject to change when better data are available. The taxonomy of Baird *et al.* (2015, 2017) is a hypothesis that will be tested in future studies as better methods and more samples become available. Future studies may support or falsify the

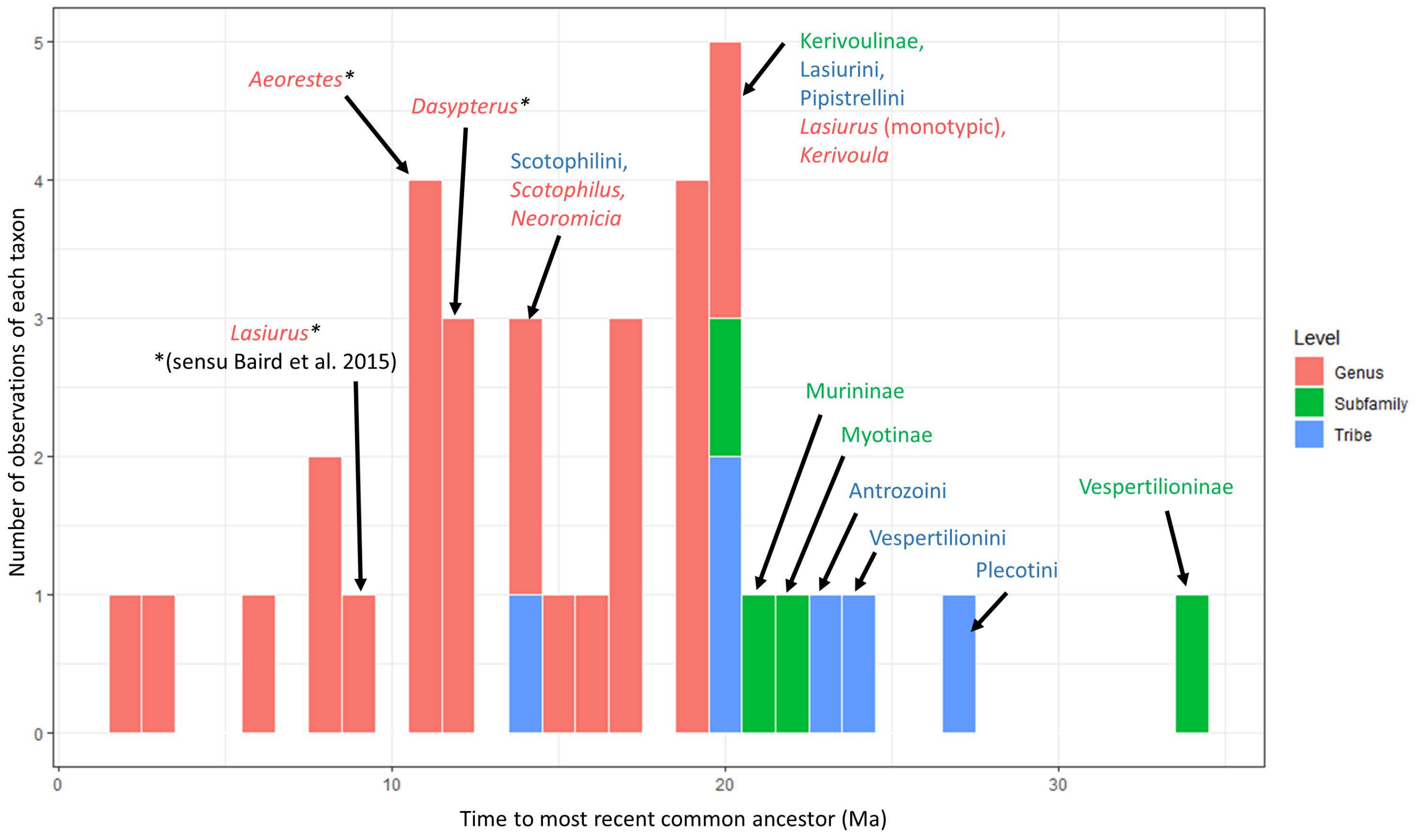


Figure 3. Observations of time to most recent common ancestors (TMRCA) of vespertilionid taxa. The data used to create this figure are detailed in Table 1.

hypothesis of three genera, but as it stands now, Baird *et al.* (2015, 2017) is the most complete and modern analysis of phylogeny and taxonomy of lasiurine bats ever conducted. Thus, their phylogenetic and taxonomic hypotheses should be accepted pending studies presenting data and analyses that falsify them.

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