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Nuclear introns support the subtribe Laephotina and recently proposed genera of African Vespertilionidae

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The widespread family Vespertilionidae constitutes the largest family of bats with 533 described species. However, systematic relationships within this family remain unresolved for many clades among the pipistrelle-like bats of the tribes Vespertilionini and Pipistrellini. In this study, we focus on the recently proposed endemic African subtribe Laephotina (Vespertilionini) and African representatives of the Pipistrellini. Recent revisionary systematics utilizing mitochondrial, morphological, and morphometric data has clarified relationships and species limits in Laephotina (*Laephotis*, *Neoromicia*, *Afronycteris*, *Pseudoromicia*), correcting genus assignments and describing two new genera. However, genetic data from independent nuclear loci have been lacking to date. Using four independent nuclear introns to generate gene trees and species trees, we establish strong support for the monophyly of the four Laephotina genera and the sister relationship of *Laephotis* + *Neoromicia*. However, the relationships of *Afronycteris* and *Pseudoromicia* remain unresolved. Our results are consistent with mitochondrial, karyotypic, and bacular morphological data previously used to delimit Laephotina. We found strong support for *Nycticeinops* + *Afropipistrellus* as sister to Laephotina. Deep divergence between *Nycticeinops* and *Afropipistrellus* in nuclear introns adds to dental and bacular evidence for their recognition as separate genera.

Key words: Africa, Afrotropics, bats, phylogeny, species tree, taxonomy, Vespertilionini

INTRODUCTION

Bats comprise fully 20% of the mammal species of the world, one of three vertebrate groups capable of powered flight, and are uniquely adapted to exploit nocturnal habitats using echolocation. Despite the diversification of living bats into 21 families, more than a third of all species belong to the cosmopolitan family Vespertilionidae, colloquially known as vesper bats. The vesper bats are generally insectivorous and range in size from 2 to 91 g, although most weigh less than 20 g (Moratelli and Burgin, 2019). They have relatively simple faces, rather typical wings, and comparatively unspecialized dentitions. Although they are more speciose than the Neotropical family Phyllostomidae, their morphological and ecological disparity is lower (e.g., Rossoni *et al*., 2024), most sharing a conservative bauplan and lifestyle. However, vesper bats as a group have features such as highly variable chromosomal complements (Sotero-Caio *et al*., 2017) and extreme modifications of the inner ear cochlea (Sulser *et al*., 2022) that may enhance their evolvability (see Houle and Rossoni, 2022).

Africa and Madagascar are home to 12 families and 332 recognized bat species, including vespers, which make up more than a third of the total (124 species — Mammal Diversity Database, 2024). Three of the four vesper subfamilies are present, but most of the species belong to Vespertilioninae (103 species): 36 species of Vespertilionini, 21 of Pipistrellini, 18 of Eptesicini, seven Plecotini, and 20 of Scotophilini (tribes sensu Simmons and Cirranello, 2024). Strikingly, half of all recognized African and Malagasy species of Vespertilionini belong to species or genera first described in the 21st century. Knowledge of systematic interrelationships has understandably not kept pace with this remarkable

taxonomic flux. Recently, Monadjem *et al*. (2021) presented a mitochondrial (cytochrome-*b* — cytb) phylogeny of the African pipistrelle-like bats of the genera *Neoromicia*, *Hypsugo* and *Pipistrellus* (sensu Monadjem *et al*., 2013). Using genetic, bacular and craniodental morphology, they allocated members of *Neoromicia* sensu lato into four genera — *Neoromicia*, *Laephotis*, and the newly described *Afronycteris* and *Pseudoromicia* (Monadjem *et al*., 2021). Members of the lately described *Parahypsugo* (Hutterer *et al*., 2019) were recovered with *Nycticeinops* and treated in this genus by Monadjem *et al*. (2021), despite the long-recognized morphological distinctions of *Nycticeinops schlieffenii*. Benda *et al*. (2022) argued that these were better treated as species of *Afropipistrellus*. Most recently, citing karyotypic synapomorphies of *Neoromicia*, *Laephotis*, *Afronycteris*, and *Pseudoromicia*, as well as earlier evidence for genetic and bacular differentiation, Volleth *et al*. (2023) proposed that this group of genera constituted a new subtribe of Vespertilionini, the Laephotina, endemic to Africa.

The goal of our study was to investigate the phylogenetic relationships of the Laephotina and related African vespertilionines using a broader set of genetic characters, specifically unlinked nuclear intron sequences. Volleth *et al*. (2023) interpreted the shared distribution of three Robertsonian fusions (7/11, 8/9, and 10/12) among the karyotypes of seven species in four genera as synapomorphous, given their strong agreement with the mitochondrial phylogeny of Monadjem *et al*. (2021). The rationale for recognizing the subtribe also noted prior evidence from penis and bacular morphology (Kearney *et al*., 2002; Fasel *et al*., 2020) for the close relationship of the four genera, as well as evidence from genetic supertrees (Amador *et al*., 2018; Upham *et al*., 2019). Our first objective was to evaluate whether the interpretations of karyotypic and bacular relationships are supported by a new phylogeny based on nuclear sequences. A secondary objective was to test whether the nuclear phylogeny confirms the sister-pair relationships of *Afronycteris*-*Pseudoromicia* and *Laephotis*-*Neoromicia* indicated by the cytb tree of Monadjem *et al*. (2021).

Materials and Methods

Taxon Sampling

To assess nuclear support for the existing mitochondrial phylogeny of these African vespers (Monadjem *et al*., 2021), we utilized the same selection of taxa. Where possible, multiple species to represent the four focal genera (*Afronycteris*, *Laephotis*, *Neoromicia*, and *Pseudoromicia*) and *Nycticeinops* and *Afropipistrellus* were sampled. We also used multiple species of the tribe Pipistrellini (*Pipistrellus*, *Scotoecus*, and *Vansonia*), which is robustly recovered as the sister to the Vespertilionini (Amador *et al*., 2018; Upham *et al*., 2019). An African species of the vesper subfamily Myotinae (*Myotis tricolor*) was used as an outgroup. The provenance of all specimens and sequences used are listed in the Appendix.

DNA Extraction, Amplification, and Sequencing

Genomic DNA from frozen tissue samples was extracted using the DNeasy Blood and Tissue Kit (Qiagen). Specimens were sequenced for four unlinked autosomal nuclear introns: ABHD11 intron 5 (ABHD11), ACOX2 intron 3 (ACOX2), COPS7A intron 4 (COPS7A — Salicini *et al*., 2011), and STAT5B (Matthee *et al*., 2001). Information on these four primer pairs is described in Demos *et al*. (2018). The PCR mixture included 12.5 µL of OneTaq Quick-Load 2X Master Mix (New England Biolabs, Ipswich, MA, USA), 8.5 µL of water, 1 µL of each 10 µmol/L primer solution, and 2 µL of template DNA. Thermal conditions for ABHD11, ACOX2, COPS7A, and STAT5B consisted of an initial denaturing step at 95°C for 3 min; 1 cycle of 95°C for 15 s, 65°C for 30 s, and 72°C for 1 min; followed by 1 cycle each at annealing temperature in 1°C decrements from 60°C (64−56°C); 32 cycles of 95°C for 30 s, 55°C for 30 s, and 72°C for 1 min; followed by a final extension step of 5 min at 72°C. Polymerase chain reaction product was purified using ExoSAP-IT (Thermo Scientific, Waltham, MA, USA). Sequencing was conducted on an ABI 3100 thermocycler (Applied Biosystems, Bedford, MA, USA) at the Pritzker Laboratory for Molecular Systematics and Evolution (FMNH). Chromatograms were edited and assembled in GENEIOUS PRIME v.2024.0.5 (Biomatters Ltd.). Sequence alignments were made using MUSCLE (Edgar, 2004) with default settings in GENEIOUS.

The sequence alignments used in this study have been deposited on the Mendeley Data repository (doi: 10.17632/ypx4kdw2nv.1). Newly generated sequence data have been deposited in GenBank under accession numbers (PQ537188–PQ537314) and are listed in the Appendix.

Phylogenetic Analyses

Maximum likelihood estimates of the concatenated alignment of the four partitioned introns and each individual intron were made using the program IQ-TREE v.2.3.2 (Minh *et al*., 2020) on the CIPRES portal (Miller *et al*., 2010). The TESTNEW option was implemented using extended model selection that included the FreeRate model and was immediately followed by tree reconstruction using the best-fit model found. The FreeRate model generalizes the gamma (+G) model by relaxing the assumption of Gamma-distributed rates and generally fits data better than the +G model (Soubrier *et al*., 2012). The UltraFast bootstrap algorithm (UFBS) and SH-aLRT (Shimodaira-Hasegawa-like approximate likelihood ratio test) support were implemented using 1000 replicates.

PopART v.1.7 (Leigh and Bryant, 2015) was used to construct median-joining networks of intron haplotypes for the four Laephotina genera and their species. Relative haplotype frequencies and haplotype relationships within genera were depicted in the networks. PopART trims alignments to the shortest sequence length because it excludes positions with gaps and

ambiguous characters. As a result, network relationships are not always identical to maximum likelihood and Bayesian tree reconstructions when sequences of different lengths are included in an alignment.

Phylogenetic reconstruction by Bayesian inference (BI) of the concatenated alignment of the four partitioned introns was conducted in MRBAYES v.3.2.7 (Ronquist *et al*., 2012) on the CIPRES portal. Two replicate MRBAYES analyses were conducted using four Markov chains and 1×10^8 generations with default heating values and sampling every 10,000th generation and a burn-in of 25%. The HKY + Gamma substitution model was chosen and applied to each locus. Stationarity and mixing of MRBAYES results were assessed in Tracer v1.7.2 (Rambaut *et al*., 2018).

We estimated a coalescent-based species-tree implemented in StarBEAST3 (Ogilvie *et al*., 2017), an extension of BEAST v2.7.7 (Bouckaert *et al*., 2019) using four nuclear intron alignments. Substitution, clock, and tree models were unlinked across all loci. A strict clock model was applied under a Yule tree model. The Tamura-Nei + Gamma substitution model was applied to ABHD11 and ACOX2, the HKY + Gamma substitution model was applied to COPS7A, and the HKY substitution model was applied to STAT5B. Four independent replicates were run with random starting seeds and chain lengths of 1×10^8 generations and parameters were sampled every 10,000 steps. Evidence for convergence and stationarity of posterior distributions of model parameters was assessed based on ESS values >200 and examination of trace files in Tracer v.1.7.2. The burn-in was set at 10% and separate runs were assembled using LOGCOMBINER v.2.7.7 and TREEANNOTATOR v.2.7.7 (Rambaut *et al*., 2018). Tree files in the Nexus format are archived on Mendeley Data (doi:10.17632/ypx4kdw2nv.1).

Results

The ML and BI analyses of the concatenated four nuclear intron alignments had similar topologies and the ML analysis is presented here (Fig. 1). Samples from all posterior parameter values of the MRBAYES and StarBEAST3 analyses using the four intron nuclear data set had ESS values > 200 apart from tree distance parameters for the StarBEAST3 analyses. The monophyly of the four genera comprising the subtribe Laephotina is confirmed with 100% UFBS support and 1.0 PP support in the ML and BI trees, respectively. *Nycticeinops* is recovered as strongly supported sister to the Laephotina (USBS = 100, PP = 1.0) and the monophyly of *Nycticeinops* (sensu lato) is strongly supported. The sister relationship of *Laephotis* and *Neoromicia* is strongly supported (UFBS = 100, PP = 1.0). The relationship of *Afronycteris* to *Laephotis* + *Neoromicia* and to *Pseudoromicia* is unresolved. Finally, the monophyly of Laephotina is confirmed with UFBS = 99 and PP = 1.0. In

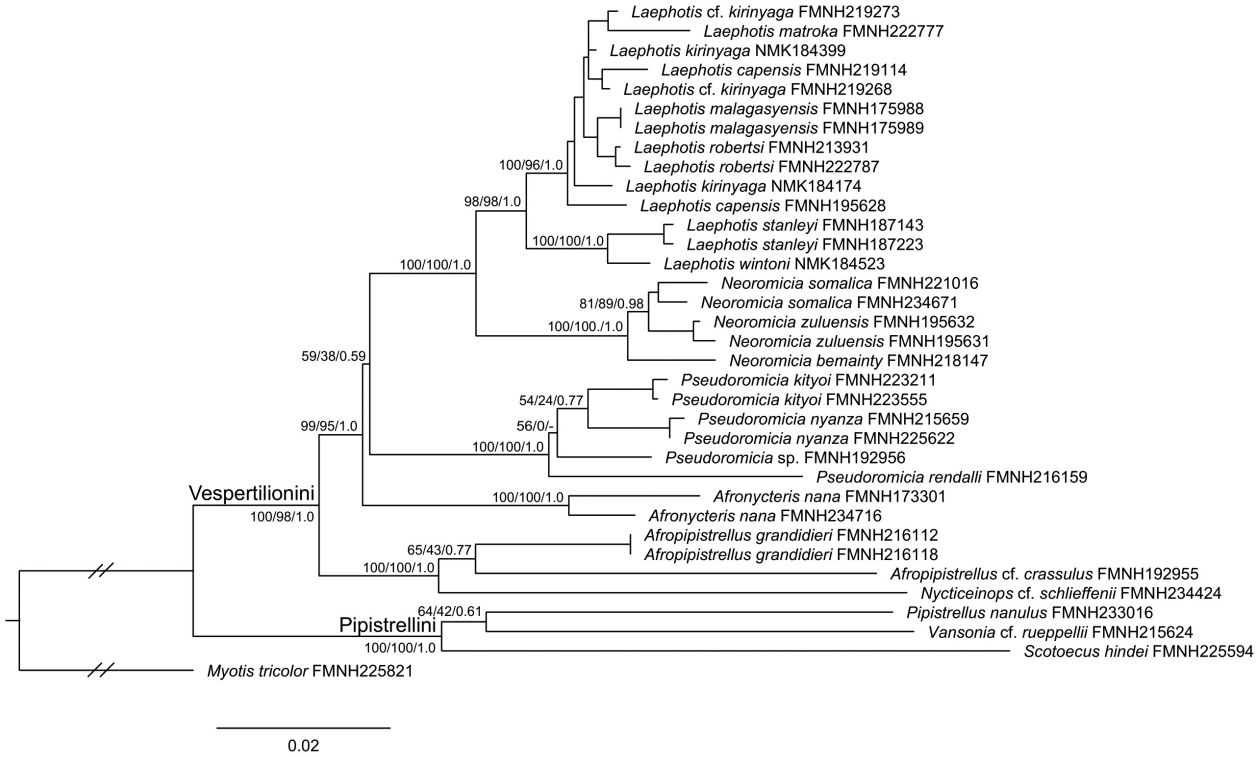
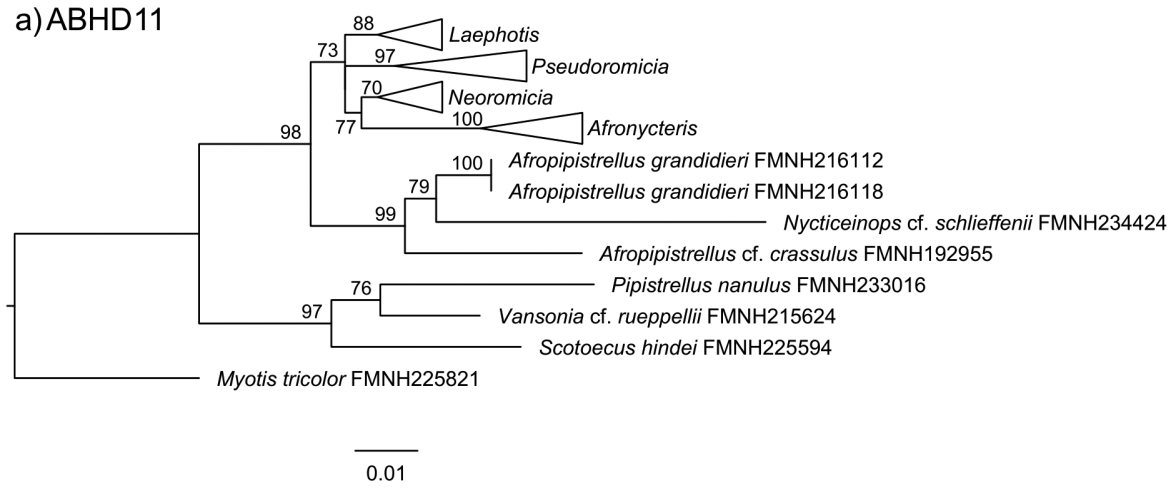
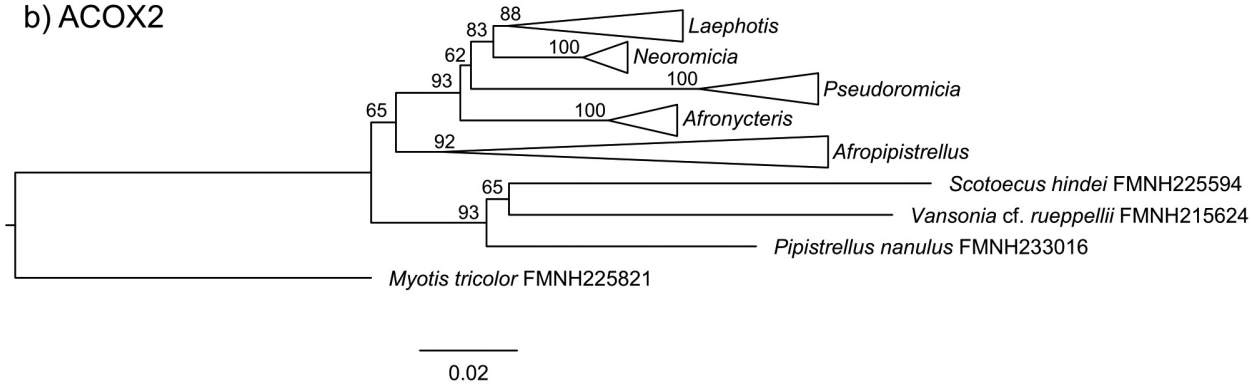
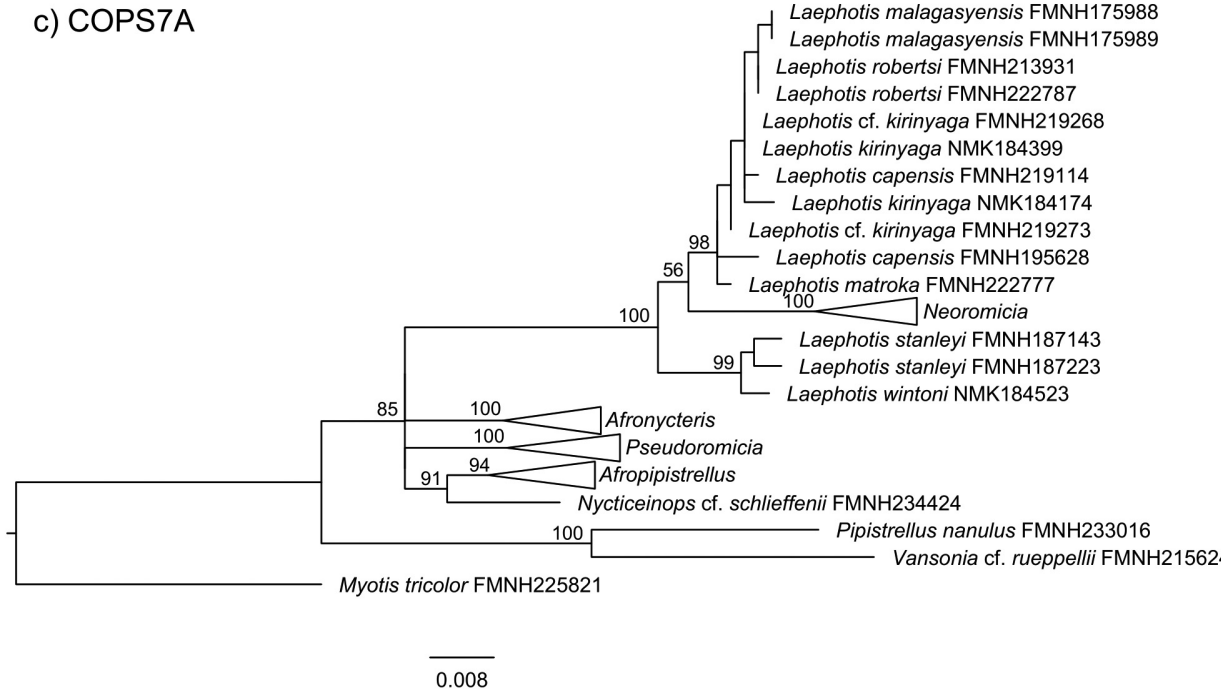


Fig. 1. Maximum likelihood (ML) gene tree of Vespertilionini and Pipistrellini species based on a concatenated alignment of four nuclear intron loci. The phylogeny was inferred in IQ-TREE and the topology is nearly identical to the phylogeny inferred under a Bayesian model in MRBAYES. Values at each node represent UF bootrap/SH-aLRT/posterior probabilities in order


a) ABHD11
88
Laephotis
73
97
Pseudoromicia
70
Neoromicia
77
100
Afronycteris
98
100
Afropipistrellus grandidieri FMNH216112
79
Afropipistrellus grandidieri FMNH216118
99
Nycticeinops cf. schlieffenii FMNH234424
Afropipistrellus cf. crassulus FMNH192955
76
Pipistrellus nanulus FMNH233016
97
Vansonia cf. rueppellii FMNH215624
Scotoecus hindei FMNH225594
Myotis tricolor FMNH225821
0.01


b) ACOX2
88
83
Laephotis
100
62
Neoromicia
100
93
Pseudoromicia
65
100
Afronycteris
92
Afropipistrellus
65
Scotoecus hindei FMNH225594
93
Vansonia cf. rueppellii FMNH215624
Pipistrellus nanulus FMNH233016
Myotis tricolor FMNH225821
0.02


c) COPS7A
Laephotis malagasyensis FMNH175988
Laephotis malagasyensis FMNH175989
Laephotis robertsi FMNH213931
Laephotis robertsi FMNH222787
Laephotis cf. kirinyaga FMNH219268
Laephotis kirinyaga NMK184399
Laephotis capensis FMNH219114
Laephotis kirinyaga NMK184174
Laephotis cf. kirinyaga FMNH219273
98
Laephotis capensis FMNH195628
56
Laephotis matroka FMNH222777
100
Neoromicia
100
Laephotis stanleyi FMNH187143
99
Laephotis stanleyi FMNH187223
Laephotis wintoni NMK184523
85
100
Afronycteris
100
Pseudoromicia
94
91
Afropipistrellus
Nycticeinops cf. schlieffenii FMNH234424
100
Pipistrellus nanulus FMNH233016
Vansonia cf. rueppellii FMNH215624
Myotis tricolor FMNH225821
0.008

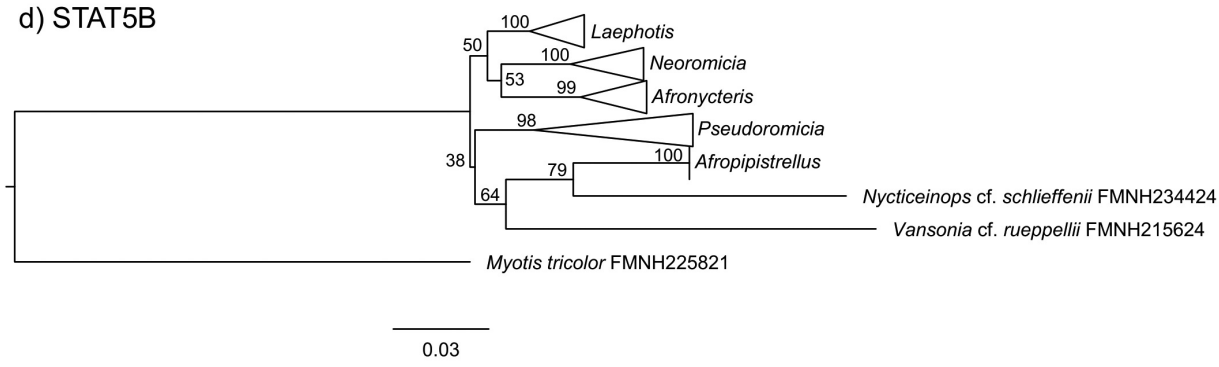


FIG. 2. Maximum likelihood (ML) gene trees of Vespertilionini and Pipistrellini species based on four nuclear intron loci. The phylogeny was inferred in IQ-TREE. Values at each node represent UF bootstrap probabilities. a) ABHD11, b) ACOX2, c) COPS7A, d) STAT5B

comparison, the individual intron ML trees did not recover support for intergeneric relationships, although the monophyly of most genera were supported (Fig. 2).

The individual intron haplotype networks (Fig. 3) support the close relationship between *Laephotis* + *Neoromicia*, in contrast to the more ambiguous relationship between *Afronycteris* and *Pseudoromicia*. Among the six genera in the haplotype network analyses, the deep divergence of *Afropipistrellus* from *Nycticeinops* is evidenced by the number of mutational steps separating these genera.

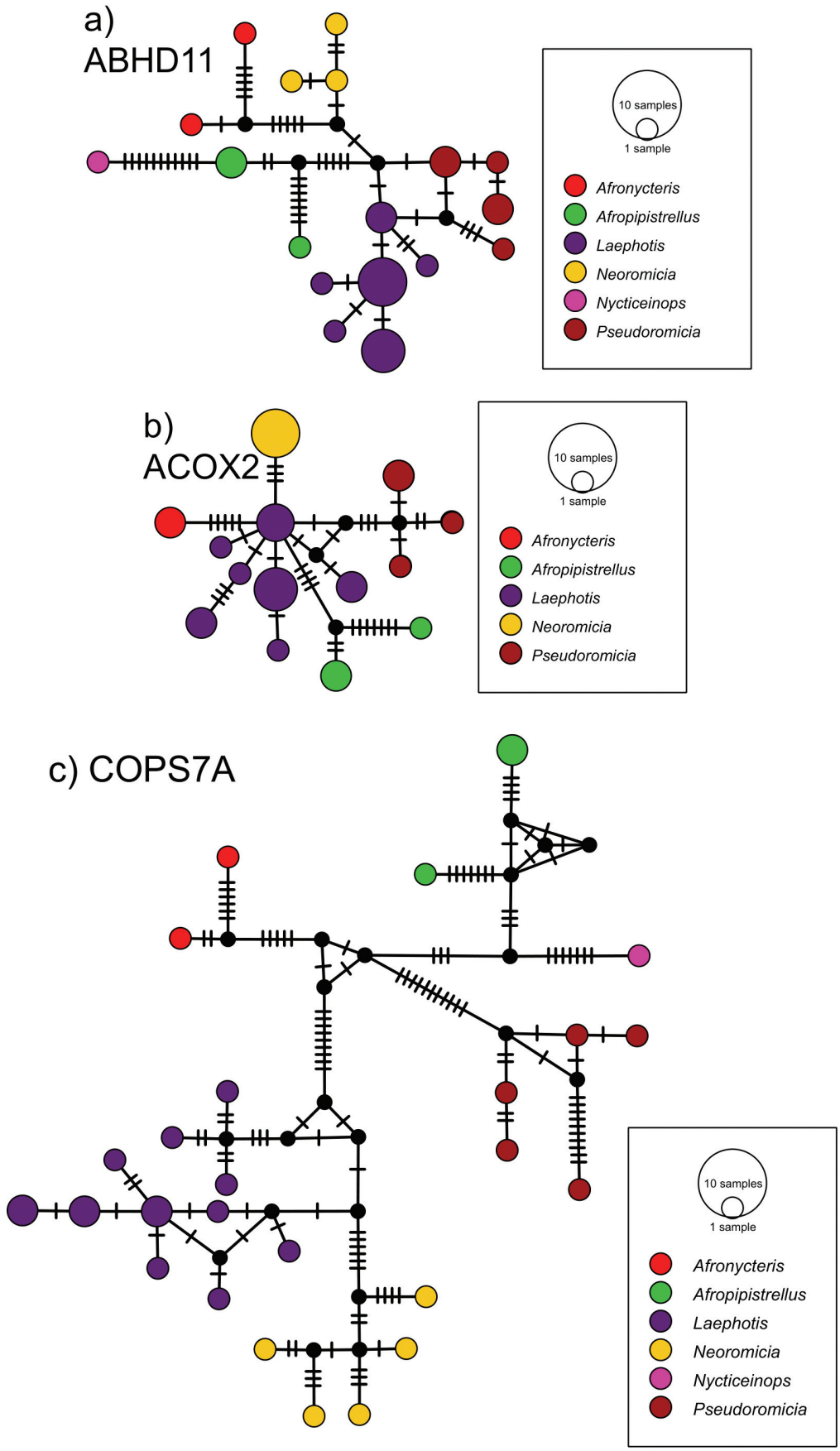
Species-tree analyses using StarBEAST3 resulted in a topology that was moderately supported with 12 of 21 nodes having PP ≥ 0.95 (Fig. 4). The monophyly of Laephotina (*Afronycteris*, *Laephotis*, *Neoromicia*, *Pseudoromicia*) is strongly supported (PP = 1.0) as is the monophyly of the Pipistrellini species included in our study (species of *Pipistrellus*, *Vansonia*, and *Scotoecus*).

DISCUSSION

Both the cytb phylogeny of Monadjem *et al*. (2021) and our intron trees based on a concatenated alignment (Fig. 1) offer strong support for the integrity of the Laephotina. The cytb tree recovered *Nycticeinops* + *Hypsugo* (sensu stricto) as sister to the Laephotina, whereas our nuclear intron gene tree analyses (which lacked *Hypsugo*) has *Nycticeinops* and *Afropipistrellus* in that position. Both datasets also confirm the membership of the African vespers *Pipistrellus*, *Scotoecus*, and *Vansonia* in the tribe Pipistrellini, but differ in the topology of that group. The mtDNA tree of Monadjem *et al*. (2021) recovers ((*Pipistrellus*, *Scotoecus*), *Vansonia*) whereas their relationships in the intron dataset are unresolved. In comparison, Dool and Puechmaille (2024) inferred *Scotoecus* as sister to the Pipistrellini genera *Pipistrellus*, *Nyctalus*, *Vansonia*, and an Asian clade *Pipistrellus*, in a six nuclear intron Bayesian phylogeny that also recovered strong support for the paraphyly of *Pipistrellus*.

The only African genus of Vespertilionini not sampled was *Mimetillus*, which is poorly represented in museum collections. In an analysis of 3,300 bp of four nuclear genes (Hassanin *et al*., 2018), this genus was recovered well outside the pair *Chalinolobus neocaledonicus-Laephotis angolensis*, suggesting that its inclusion in our analysis would not have altered group integrity or relationships.

The cytb phylogeny of Monadjem *et al*. (2021) had strong support for *Laephotis* and *Neoromicia* as sisters and moderate support for the sister relationship of *Afronycteris* and *Pseudoromicia*. The nuclear intron gene trees in this study strongly confirm the sister-group relationship of *Laephotis* and *Neoromicia* but offer different views on the positions of *Afronycteris* and *Pseudoromicia*. The concatenated intron analysis recovers *Afronycteris* as sister to *Laephotis* + *Neoromicia* and an unresolved node subtending *Pseudoromicia*. Like the concatenated intron alignment gene trees, the species tree (Fig. 4) also failed to resolve phylogenetic relationships of *Pseudoromicia* and *Afronycteris*. *Nycticeinops* and *Afropipistrellus* were strongly supported as sister to the subtribe. The monophyly of the African Pipistrellini in the study was strongly supported, although as in Laephotina, intergeneric relationships were not resolved. The lack of resolution for parts of the species tree is not unexpected for phylogenies


a)
ABHD11
10 samples
1 sample
Afronycteris
Afropipistrellus
Laephotis
Neoromicia
Nycticeinops
Pseudoromicia
b)
ACOX2
10 samples
1 sample
Afronycteris
Afropipistrellus
Laephotis
Neoromicia
Pseudoromicia
c) COPS7A
10 samples
1 sample
Afronycteris
Afropipistrellus
Laephotis
Neoromicia
Nycticeinops
Pseudoromicia

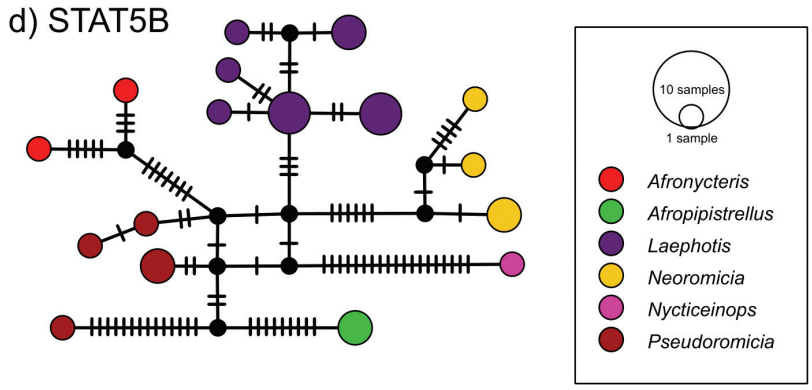


FIG. 3. Median-joining networks of intron haplotypes inferred using POPART. Colored circles represent different sampled haplotypes and black circles indicate missing or unsampled states. Hatch marks represent mutational steps between haplotypes. Because POPART excludes positions with gaps and ambiguous characters, network relationships are not identical to maximum likelihood and Bayesian tree reconstructions. a) ABHD11 network, b) ACOX2 network, c) COPS7A network, d) STAT5B network

with small internal branch lengths as exhibited by the lack of support for the node subtending *Pseudoromicia*. This may be due to the effect of incomplete lineage sorting (ILS) on gene tree discordance, where discordance at a locus can occur because not every gene sampled from a species will share an ancestral branch with other genes (Bryant and Hahn, 2020), although introgressive hybridization cannot be ruled out.

Volleth *et al*. (2023) used comparative karyotype data to delineate chromosomal homologies and shared chromosomal characters and then mapped them on the comprehensive mitochondrial phylogeny of Monadjem *et al*. (2021). Karyotypic data revealed three derived chromosomal fusions that were shared by seven species in the four African Vespertilionini genera *Afronycteris*, *Laephotis*, *Neoromicia*, and *Pseudoromicia*. These synapomorphies, and

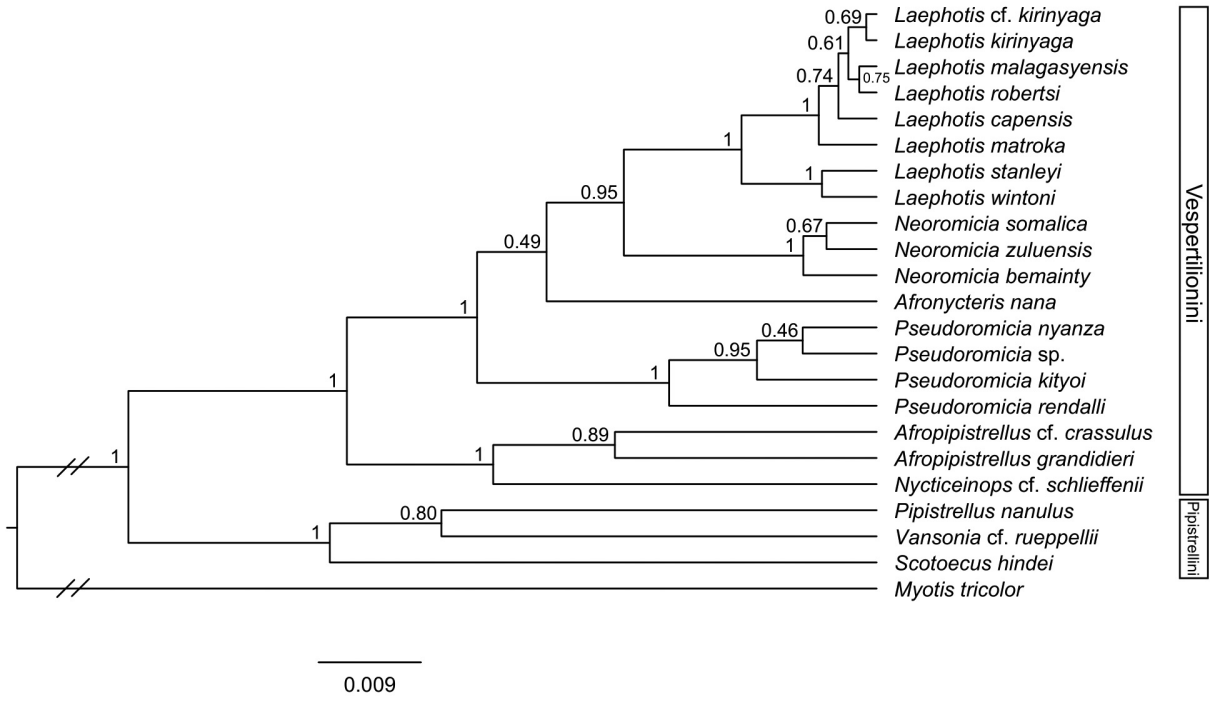


FIG. 4. Species tree for Vespertilionini and Pipistrellini species inferred using four nuclear intron loci in StarBeast3. Nodes are labeled with posterior probabilities

their congruence with phylogenetic analyses of the pipistrelle-like vespertilionids (Pipistrellini and Vespertilionini) in Monadjem *et al*. (2021), as well as broader chiropteran phylogenies (Amador *et al*., 2018; Upham *et al*., 2019), formed the basis for the newly proposed subtribe Laephotina (Volleth *et al*., 2023). Bacular morphology also supports the close relationship of the members of the Laephotina (Kearney *et al*., 2002; Fasel *et al*., 2020; Monadjem *et al*., 2021) as discussed in Volleth *et al*. (2023). As in the phylogenetic analyses of this study, the close relationship of *Laephotis* and *Neoromicia* was supported by a shared chromosomal fusion product. The mitochondrial sequence data of Monadjem *et al*. (2021) also supported a close relationship between *Afronycteris* and *Pseudoromicia*, but Volleth *et al*. (2023) did not find chromosomal character support for this relationship. The nuclear introns used in our study were unable to resolve the phylogenetic relationship of these two genera.

For those *Laephotis* species represented by multiple specimens in this study, the reciprocal monophyly of *L. capensis*, *L. kirinyaga*, and *L*. cf. *kirinyaga* was not evident in the intron dataset, despite strong support for reciprocal monophyly in earlier mitochondrial analyses (Monadjem *et al*., 2021). Volleth *et al*. (2023) found nearly identical 2n = 32 karyotypes for *L. capensis* and *L. kirinyaga*, but different chromosomal numbers for *L. stanleyi* (2n = 40) and *L. wintoni* (2n = 34). The close relationship of *L. capensis*, *L. kirinyaga*, and *L*. cf. *kirinyaga* was inferred in the cytb phylogeny of Monadjem *et al*. (2021), where these three species and *L. matroka* formed a well-supported clade, whose interrelationships were moderately or poorly supported. In this study, the haplotype networks for *Laephotis* exhibit fewer mutational steps than *Afronycteris*, *Neoromicia*, *Nycticeinops*, and *Pseudoromicia* (Fig. 3). The limited variation of these loci in *Laephotis*, as well as the short internode branch lengths in the intron gene trees, may account for their paraphyly in the nuclear trees.

The mitochondrial analyses of Monadjem *et al*. (2021) recovered several species formerly included in *Pipistrellus* in closer association with *Nycticeinops* than with any other African genus. All were consequently treated as members of *Nycticeinops* in their revised classification. Our intron analyses strongly support the association of these bats but raise questions concerning their nomenclature. As noted by Benda *et al*. (2022), Thorn *et al*. (2007) erected *Afropipistrellus* as a subgenus in recognition of the distinctive dental and bacular morphology of *N. grandidieri* (genus type). These species and their relatives (*N. happoldorum*, *N. bellieri*, and *N*. cf. *crassulus*) all occupy moist forests in Sub-Saharan Africa, whereas *N. schlieffenii* (type locality in Cairo, Egypt) occupies a drier savanna mosaic. Deep divergence between the included species of *Nycticeinops* (Figs. 1 and 4) and numerous substitutions in their median-joining networks (Fig. 3) support the suggestion that the forest clade (currently all species except *N. schlieffenii*) should be recognized in the genus *Afropipistrellus*.

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Author Contribution Statement

TD: research concept and design, collection and/or assembly of data, data analysis and interpretation, writing, critical revision, and final approval of the article; PWW: collection and/or assembly of data, critical revision and final approval of the article; AM: collection and/or assembly of data, writing, critical revision, and final approval of the article; BDP: research concept and design, collection and/or assembly of data, data analysis and interpretation, writing, critical revision, and final approval of the article.

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Appendix

Catalog No.	Species	Country	Latitude	Longitude	ABHD11	ACOX2	COPS	STAT5B
FMNH173301	*Afronycteris nana*	DRC	-2.2160	28.8638	PQ537190	PQ537223	PQ537256	PQ537289
FMNH234716	*A. nana*	Kenya	-1.0190	38.3260	PQ537189	PQ537224	PQ537257	PQ537290
FMNH192955	*Afropipistrellus* cf. *crassulus*	Tanzania	-1.0942	31.5154	PQ537209	PQ537244	PQ537277	
FMNH216112	*A. grandidieri*	Kenya	-3.3000	39.9951	PQ537211	PQ537245	PQ537279	PQ537307
FMNH216118	*A. grandidieri*	Kenya	-3.3033	39.9989	PQ537212	PQ537246	PQ537280	PQ537308
FMNH195628	*Laephotis capensis*	South Africa	-25.3600	31.7600	PQ537191	PQ537225	PQ537258	
FMNH219114	*L. capensis*	Tanzania	-7.7071	34.0305	PQ537192	PQ537226	PQ537259	PQ537292
FMNH219268	*L.* cf. *kirinyaga*	Tanzania	-7.7071	34.0305	PQ537193	PQ537227	PQ537260	PQ537291
FMNH219273	*L.* cf. *kirinyaga*	Tanzania	-7.7071	34.0305	PQ537194	PQ537228	PQ537261	PQ537293
NMK184174	*L. kirinyaga*	Kenya	2.3204	37.9940	PQ537195	PQ537229	PQ537262	PQ537294
NMK184399	*L. kirinyaga*	Kenya	2.3090	38.0001	PQ537196	PQ537230	PQ537263	
FMNH175988	*L. malagasyensis*	Madagascar	-22.4867	45.3783	PQ537197	PQ537231	PQ537264	PQ537295
FMNH175989	*L. malagasyensis*	Madagascar	-22.3167	45.2933	PQ537198	PQ537232	PQ537265	PQ537296
FMNH222777	*L. matroka*	Madagascar	-18.4047	47.9349	PQ537199	PQ537233	PQ537266	
FMNH213931	*L. robertsi*	Madagascar	-18.8157	48.4272	PQ537201	PQ537234	PQ537267	PQ537297
FMNH222787	*L. robertsi*	Madagascar	-18.4100	47.9400	PQ537200	PQ537235	PQ537268	PQ537298
FMNH187143	*L. stanleyi*	Tanzania	-3.7979	36.0688	PQ537202	PQ537236	PQ537269	PQ537299
FMNH187223	*L. stanleyi*	Tanzania	-3.7979	36.0688	PQ537203	PQ537237	PQ537270	PQ537300
NMK184523	*L. wintoni*	Kenya	0.2013	37.1299	PQ537204	PQ537238	PQ537271	PQ537301
FMNH225821	*Myotis tricolor*	Kenya	-0.25157	36.0548	PQ537188	PQ537222	PQ537255	PQ537288
FMNH218147	*Neoromicia bemainty*	Madagascar	-20.0700	44.6700	PQ537205	PQ537239	PQ537272	PQ537302
FMNH221016	*N. somalica*	Kenya	-2.7055	37.2661	PQ537206	PQ537240	PQ537273	PQ537303
FMNH234671	*N. somalica*	Kenya	0.1863	37.0849		PQ537241	PQ537274	PQ537307
FMNH195631	*N. zuluensis*	South Africa	-25.3613	31.7629		PQ537242	PQ537275	PQ537304
FMNH195632	*N. zuluensis*	South Africa	-25.3613	31.7629	PQ537208	PQ537243	PQ537276	PQ537305
FMNH234424	*Nycticeinops* cf. *schlieffenii*	Kenya	-1.6975	38.4673	PQ537210		PQ537278	PQ537306
FMNH233016	*Pipistrellus nanulus*	Uganda	2.0945	31.8679	PQ537213	PQ537247	PQ537281	
FMNH223211	*Pseudoromicia kityoi*	Uganda	0.4451	32.8888	PQ537214	PQ537248	PQ537282	PQ537309
FMNH223555	*P. kityoi*	Uganda	0.4451	32.8888	PQ537215	PQ537249	PQ537283	PQ537310
FMNH215659	*P. nyanza*	Kenya	-0.6517	34.3434	PQ537216		PQ537284	PQ537311
FMNH225622	*P. nyanza*	Kenya	-1.3306	34.9941	PQ537217	PQ537250	PQ537285	PQ537312
FMNH216159	*P. rendalli*	Kenya	-3.3033	39.9989	PQ537218		PQ537286	PQ537313
FMNH192956	*Pseudoromicia* sp.	Tanzania	-1.0942	31.5154	PQ537219	PQ537252		
FMNH225594	*Scotoecus hindei*	Kenya	-1.33058	34.99414	PQ537220	PQ537253		
FMNH215624	*Vansonia* cf. *rueppellii*	Kenya	-0.1096	34.7459	PQ537221	PQ537254	PQ537287	PQ537314