

GENERIC STATUS OF THE AMERICAN PIPISTRELLES (VESPERTILIONIDAE) WITH DESCRIPTION OF A NEW GENUS

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Although traditionally placed in the genus *Pipistrellus*, studies since the mid-1900s have shown that the western pipistrelle (*P. hesperus*) and eastern pipistrelle (*P. subflavus*), the only 2 representatives of *Pipistrellus*-like bats in the Western Hemisphere, do not share a most recent common ancestry with true *Pipistrellus* or each other. More than 20 years ago, authors recommended taxonomic revision for the American pipistrelles by placing *subflavus* in a separate genus called *Perimyotis*, and *hesperus* in a another separate genus called “*Parastrellus*.” Recently, a comprehensive study of the molecular phylogenetics of vespertilionid bats affirmed these suggested revisions. However, the name “*Parastrellus*” is currently unavailable according to the *International Code of Zoological Nomenclature* because no formal description of the genus has been provided. In this study, we provide additional morphological and genetic data demonstrating the marked divergence among *hesperus*, *subflavus*, *Pipistrellus*, and other *Pipistrellus*-like genera, and provide a formal description of a new generic name for the nominal species *P. hesperus*.

Key words: classification, cytochrome *b*, morphology, *Perimyotis subflavus*, phylogenetics, *Pipistrellus hesperus*, 12S ribosomal RNA, Vespertilionidae

Hoofer and Van Den Bussche (2003) examined higher-level phylogenetic relationships in the cosmopolitan bat family Vespertilionidae (vesper bats) based on DNA sequence variation in mitochondrial ribosomal genes (12S and 16S ribosomal RNA). Their study provided well-supported resolution to many relationships and the 1st explicit test of monophyly for many traditional groupings in the family, including all taxa with cosmopolitan distributions. An important trend emerging from the study was that the zoogeographic history of vesper bats is far less complex than thought traditionally, especially regarding transoceanic dispersal events, and that many of the similar phenotypes and life-history strategies found across biogeographic regions have resulted from repeated episodes of convergent evolution. Based on their findings, coupled with bacular and karyotypic evidence in the literature, Hoofer and Van Den Bussche (2003) offered a new classification for vespertilionoid bats examined in their study that in many respects reflects traditionally held views of relationship but that

also suggests several changes, at various taxonomic levels (Table 1).

Two of the changes concern the western pipistrelle (*hesperus*) and eastern pipistrelle (*subflavus*), the only 2 representatives of *Pipistrellus*-like bats in the Western Hemisphere. Although traditionally placed in the genus *Pipistrellus*, phylogenetic analyses confirm previous contentions that the American pipistrelles do not share a most recent common ancestry with true *Pipistrellus* or with each other (Fig. 1). To avoid polyphyletic taxa, Hoofer and Van Den Bussche (2003) recognized *hesperus* and *subflavus*, each in separate genera. They recognized *subflavus* in *Perimyotis*, a genus Menu (1984) described 20 years earlier to include only the species *subflavus*.

The situation with *hesperus* is more complex because, at about the same time as Menu's (1984) description, Horáček and Hanák (1985, 1985–1986) published an abstract and a paper in which they proposed a new genus, “*Parastrellus*,” for the nominal species *hesperus*. Although they discussed the anatomical characters examined, they did not provide a formal description for the name. Under the rules of the *International Code of Zoological Nomenclature* (International Commission on Zoological Nomenclature 1999), the name “*Parastrellus*” is nomen nudum in both of their publications, and it still remains unavailable for *hesperus*.

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TABLE 1.—Classification of Hoofer and Van Den Bussche (2003) for vespertilionoid bats examined in their study as amended by the present study.

Superfamily Vespertilionoidea	Genus <i>Scotomanes</i>
Family Natalidae	Genus <i>Eptesicus</i>
Family Molossidae	Subgenus <i>Cnephaeus</i> ^f
Family Miniopteridae	Subgenus <i>Eptesicus</i> ^g
Genus <i>Miniopterus</i>	Subgenus <i>Histiotus</i>
Family Vespertilionidae	Tribe Pipistrellini
Subfamily Vespertilioninae	Genus <i>Pipistrellus</i> ^h
Genus <i>Otonycteris</i> ^a	Genus <i>Scotoecus</i>
Genus <i>Parastrellus</i> , new genus ^{a,b}	Tribe Vespertilionini
Genus <i>Perimyotis</i> ^{a,c}	Genus <i>Vespertilio</i>
Tribe Antrozoini ^d	Unnamed Genus ⁱ
Genus <i>Antrozous</i>	Genus <i>Neoromicia</i> ^j
Genus <i>Bauerus</i>	Genus <i>Laephotis</i>
Genus <i>Baodon</i>	Genus <i>Nycticeinops</i> ^k
Genus <i>Rhogeessa</i>	Genus <i>Hypsugo</i> ^l
Tribe Lasiurini ^d	Genus <i>Tylonycteris</i>
Genus <i>Lasiurus</i>	Genus <i>Vespadelus</i>
Tribe Plecotini ^d	Genus <i>Chalinolobus</i>
Genus <i>Barbastella</i>	Genus <i>Nyctophilus</i>
Genus <i>Corynorhinus</i>	Subfamily Myotinae
Genus <i>Euderma</i>	Genus <i>Myotis</i>
Genus <i>Idionycteris</i>	Subgenus <i>Aeorestes</i> ^m
Genus <i>Plecotus</i>	Subgenus <i>Myotis</i> ⁿ
Tribe Scotophilini ^d	Subfamily Kerivoulinae
Genus <i>Scotophilus</i>	Genus <i>Kerivoula</i>
Tribe Nycticeiini	Subfamily Murininae
Genus <i>Glauconycteris</i>	Genus <i>Harpiocephalus</i>
Genus <i>Lasionycteris</i>	Genus <i>Murina</i>
Genus <i>Nycticeius</i> ^e	

^a Placed incertae sedis within Vespertilioninae.

^b *Parastrellus* includes only *P. hesperus*.

^c *Perimyotis* includes only *P. subflavus*.

^d Tribes Antrozoini, Lasiurini, Plecotini, and Scotophilini are sedis mutabilis.

^e *Nycticeius* includes only *N. humeralis*.

^f Subgenus *Cnephaeus* includes *E. hottentotus* and *E. serotinus*.

^g Subgenus *Eptesicus* includes *E. brasiliensis*, *E. diminutus*, *E. furinalis*, and *E. fuscus*.

^h *Pipistrellus* includes *Nyctalus*.

ⁱ We allocate (*Hypsugo*) *nanus* and (*Neoromicia*) *brunneus* and *rendalli* to a separate, as yet unnamed, genus.

^j *Neoromicia* includes only *N. somalicus*.

^k *Nycticeinops* includes *N. eisenrauti* and *N. schlieffeni*.

^l *Hypsugo* includes only *H. savii*.

^m Subgenus *Aeorestes* includes all sampled New World species of *Myotis*.

ⁿ Subgenus *Myotis* includes all sampled Old World species of *Myotis*.

Our purpose in this paper is 3-fold: to verify identifications of the specimen of *hesperus* and the specimen of *subflavus* examined in Hoofer and Van Den Bussche (2003) through comparisons of DNA sequences of 12S ribosomal RNA and cytochrome-*b* genes between them and additional individuals of both *hesperus* and *subflavus* and among representatives of *Hypsugo*, *Pipistrellus*, and other vespertilionid genera; to discuss some of the taxonomic problems and solutions associated with the large complex of *Pipistrellus*-like bats; and to provide a formal description of a new genus to include the nominal species *P. hesperus* as warranted by mitochondrial DNA analysis (Hoofer and Van Den Bussche 2003) and other lines of evidence.

MATERIALS AND METHODS

Specimens examined.—Specimens examined are listed in Appendix I, including information associated with museum vouchers and

GenBank accession numbers. We generated complete 12S ribosomal RNA sequences and the first 400 base pairs (bp) of the cytochrome-*b* gene for 2 new specimens each of *P. hesperus* and *P. subflavus*. We generated cytochrome-*b* data for the same 2 specimens of *P. hesperus* and *P. subflavus* examined by Hoofer and Van Den Bussche (2003), 1 specimen of *Lasiurus cinereus*, and 1 specimen of *L. ega*. From GenBank, we retrieved 8 12S ribosomal RNA sequences that were originally generated by Hoofer and Van Den Bussche (2003) and 5 cytochrome-*b* sequences that were originally generated by Benda et al. (2004), Ruedi and Mayer (2001), Stadelmann et al. (2004), and Sudman et al. (1994). We also expanded upon the morphological comparisons made by Horáček and Hanák (1985–1986) by examining dental, cranial, penial, bacular, and external features among >200 specimens representing >75 species of *Pipistrellus*-like bats.

Molecular methods and data analysis.—We extracted genomic DNA from skeletal muscle or organ tissue samples with standard phenol methods (Longmire et al. 1997). We followed the methods of Van Den Bussche and Hoofer (2000) to amplify and sequence the 12S ribosomal RNA gene (approximately 1.2 kilobases).

We amplified the 1st two-thirds of the cytochrome-*b* gene (800 bp) by polymerase chain reaction (PCR) using primers Myo-7L (5'–CGT TGT ATT TCA ACT RTA AGA–3') and Myo-16 (5'–TAR AAA GTA TCA YTC TGG TT–3'), and sequenced the first 400 bp using primers Myo-7L and MVZ 04 (Smith and Patton 1993). For polymerase chain reaction, we used a 50-μl reaction, and added approximately 300–500 ng of DNA, 0.30 μM of each primer, 2.5 mM of MgCl₂, 0.16 mM of deoxynucleoside triphosphates, 1× final buffer concentration, and 1.25 U of *Taq* DNA polymerase (Promega Corp., Madison, Wisconsin). We used the following thermal profile: 94°C for 4-min initial denaturation, followed by 35 cycles of 94°C for 40 s, 50°C for 40 s, and 72°C for 1 min, and a final extension at 72°C for 10 min.

We purified double-stranded polymerase chain reaction amplicons by using a QIAquick PCR Purification Kit (Qiagen, Inc., Chatsworth, California) and sequenced both strands by using Big-Dye version 3.1 chain terminators, followed by electrophoresis on a 3100-Avant Genetic Analyzer (Applied Biosystems, Inc., Foster City, California). We used AssemblyLIGN 1.0.9 software (Oxford Molecular Group PLC 1998) to assemble resulting, overlapping fragments.

We performed multiple sequence alignments for both data sets in Clustal X software (Thompson et al. 1997) with default parameters for costs of opening and extending gaps. We viewed alignments in MacClade software (version 4.0—Maddison and Maddison 2002) to ensure there were no insertions, deletions, or stop codons in the cytochrome-*b* sequences and to inspect gap placement in the 12S ribosomal RNA sequences. We coded nucleotides as unordered, discrete characters, gaps as missing data, and multiple states as polymorphisms. In PAUP* software (test version 4.0b10—Swofford 2002), we calculated uncorrected ("p") distances for all pairwise comparisons in each data set.

RESULTS

Complete 12S ribosomal RNA sequences were 961 bp for the 2 new specimens of *P. hesperus* (TK 20347 and TK 26039) and 956 bp for the 2 new specimens of *P. subflavus* (TK 84525 and TK 90667). These were identical to the sequence lengths for each species reported in Hoofer and Van Den Bussche (2003). Alignment of these, along with 12S ribosomal RNA sequences from GenBank, resulted in 977 characters. The first 400 bp of the cytochrome-*b* gene obtained for 8 vespertilionids

contained no insertions or stop codons; therefore, we assumed a mitochondrial DNA origin for all sequences. We submitted all sequences generated in this study to GenBank and list accessions numbers in Appendix I.

Pairwise comparisons of percentage sequence distance (uncorrected “p”) for both data sets verify that the specimens of *P. hesperus* and *P. subflavus* examined by Hoofer and Van Den Bussche (2003) were identified correctly (Table 2; Bradley and Baker 2001). Distances averaged 0.21% (12S ribosomal RNA) and 0.17% (cytochrome-*b*) among the 3 specimens of *P. hesperus*, and averaged 0.14% (12S ribosomal RNA) and 0.83% (cytochrome-*b*) among the 3 specimens of *P. subflavus*. Between *P. hesperus* and *P. subflavus*, distances averaged 9.89% (12S ribosomal RNA) and 18.17% (cytochrome-*b*). For 12S ribosomal RNA sequences, distances among all species examined ranged from 9.61% (*Hypsugo savii* compared to *P. pipistrellus*) to 16.01% (*H. savii* compared to *Lasiurus cinereus*), with an average of 12.16%, and for cytochrome-*b* sequences, ranged from 17.00% (*P. subflavus*–1 compared to *Eptesicus fuscus*) to 23.75% (*P. subflavus*–1 compared to *L. cinereus*), with an average of 20.11% (Table 2).

Results of morphological comparisons are detailed in the subsequent description section. Here, we list some penial characters for which *hesperus* differs from other vespertilionid bats (Fig. 2): baculum is rooflike in section, elongated (length = 1.80–2.15 mm, $n = 3$; i.e., about one-third of the penis length) and inflexed ventrally; distal end terminates in a dorsally oriented tuberosity that forms a bony support for large and distinct trilobate globular bodies of accessory cavernous tissue; trilobate globular bodies markedly expand the dorsal wall of glans penis; urethra nozzle is extremely broad and folded, apparently enlarging into a funnellike structure during penial erection; the entire distal complex of accessory cavernous bodies is further attached to the lateral margins and proximal base of the baculum via distinct laterally paired, musclelike cavernous structures; praeputium is thin-walled and lacks cavernous tissue; proximal base of praeputium is attached along proximal base of baculum about one-fifth of its length; and praeputial vestibulum is particularly expanded, apparently in response to lateral erectile enlargement of glans structures. Most of these characters, and particularly their combination, are apparently unique for *hesperus*.

DISCUSSION

The Pipistrellus problem.—Systematics and taxonomy of the genus *Pipistrellus* have proven to be extremely difficult and complex. Traditionally, *Pipistrellus* includes the short-eared, short-faced vesper bats (family Vespertilionidae) lacking any striking character but retaining the 2nd upper premolar (Tate 1942). Approximately 70 species from all biogeographic regions are included under this definition (Hill and Harrison 1987; Nowak 1999). Yet, morphologists have questioned the validity of traditional *Pipistrellus* for decades, noting that, in the context of other vespertilionid phenotypes, the true phyletic relationships may run across traditional generic lines (Hill and Topál 1973; Horáček and Hanák 1985–1986; Koopman 1975;

Kuzyakin 1950; Menu 1984; Sokolov 1973; Tate 1942; Wallin 1969). In addition, several “nonclassical” studies of presumably less adaptive features (e.g., bacula, chromosomes, allozymes, and DNA sequences) have documented the polyphyletic origin of *Pipistrellus* (reviewed in Hoofer and Van Den Bussche 2003).

In an attempt to help solve the dilemma of a confused pipistrelloid classification, Heller and Volleth (1984) and Horáček and Hanák (1985–1986) outlined the usefulness of a more diverse classification stressing each case of documented (or suspected) paraphyly so that current taxonomy better reflects actual phyletic relationships rather than adaptive similarity. Accordingly, several suggested revisions of traditional *Pipistrellus* began appearing in the literature. The Palearctic *Hypsugo*, Ethiopian *Neoromicia*, Australian *Vespadelus*, and Indomalayan *Arielulus* and *Falsistrellus* all have been considered generically distinct from *Pipistrellus* at one time or another during the past 25 years (Adams et al. 1987a, 1987b; Csorba and Lee 1999; Heller and Volleth 1984; Hoofer and Van Den Bussche 2003; Horáček 1991; Horáček and Hanák 1985–1986; Kitchener et al. 1986; Ruedi and Arlettaz 1991; Volleth et al. 2001; Volleth and Heller 1994a, 1994b; Volleth and Tidemann 1991).

The most important survey of vespertilionid taxonomy appearing by the end of the 20th century was that of Hill and Harrison (1987), who examined bacular features in all named species of *Pipistrellus*-like bats. They provided an extensive rearrangement of vespertilionid classification and, contrary to earlier suggestions (Heller and Volleth 1984; Horáček and Hanák 1985–1986), advocated a lumped concept of the genus *Pipistrellus*, in which they even included the Australian and African species traditionally arranged in *Eptesicus* (Tate’s *E. pumilus* group, and the *E. capensis* and *tenuipinnis* groups). Hill and Harrison (1987) subdivided *Pipistrellus* into several subgenera, partly covering the respective species groups of Tate (1942) and Koopman (1975): *Pipistrellus*, *Vespadelus*, *Perimyotis*, *Hypsugo*, *Falsistrellus*, *Neoromicia*, and *Arielulus*. It is important to recognize that their classification implies not only a most recent common ancestry for the subgroups, but also an extremely complex biogeographic history requiring numerous transcontinental dispersal events. Essentially, this concept of *Pipistrellus* has been the standard or conservative view of relationships in the genus (e.g., Koopman 1994).

Hoofer and Van Den Bussche (2003) examined the molecular phylogenetics of the Vespertilionidae through mitochondrial DNA analysis of more than 50 *Pipistrellus*-like bats and 78 other vespertilionids. Results from their study affirm the often-discussed polyphyletic origin of traditional *Pipistrellus*, and correspond well with previous multilined classifications of *Pipistrellus* based on detailed studies of morphologic, biochemical, and especially, karyotypic data (Adams et al. 1987a, 1987b; Csorba and Lee 1999; Horáček and Hanák 1985–1986; Kearney et al. 2002; Kitchener et al. 1986; McBee et al. 1987; Menu 1984; Ruedi and Arlettaz 1991; Volleth 1987, 1989; Volleth et al. 2001; Volleth and Heller 1994a; Volleth and Tidemann 1989, 1991). The classification of Hoofer and Van Den Bussche (2003) partitions *Pipistrellus*-like bats into 3 tribes, Pipistrellini, Vespertilionini, and Nycticeini; the latter

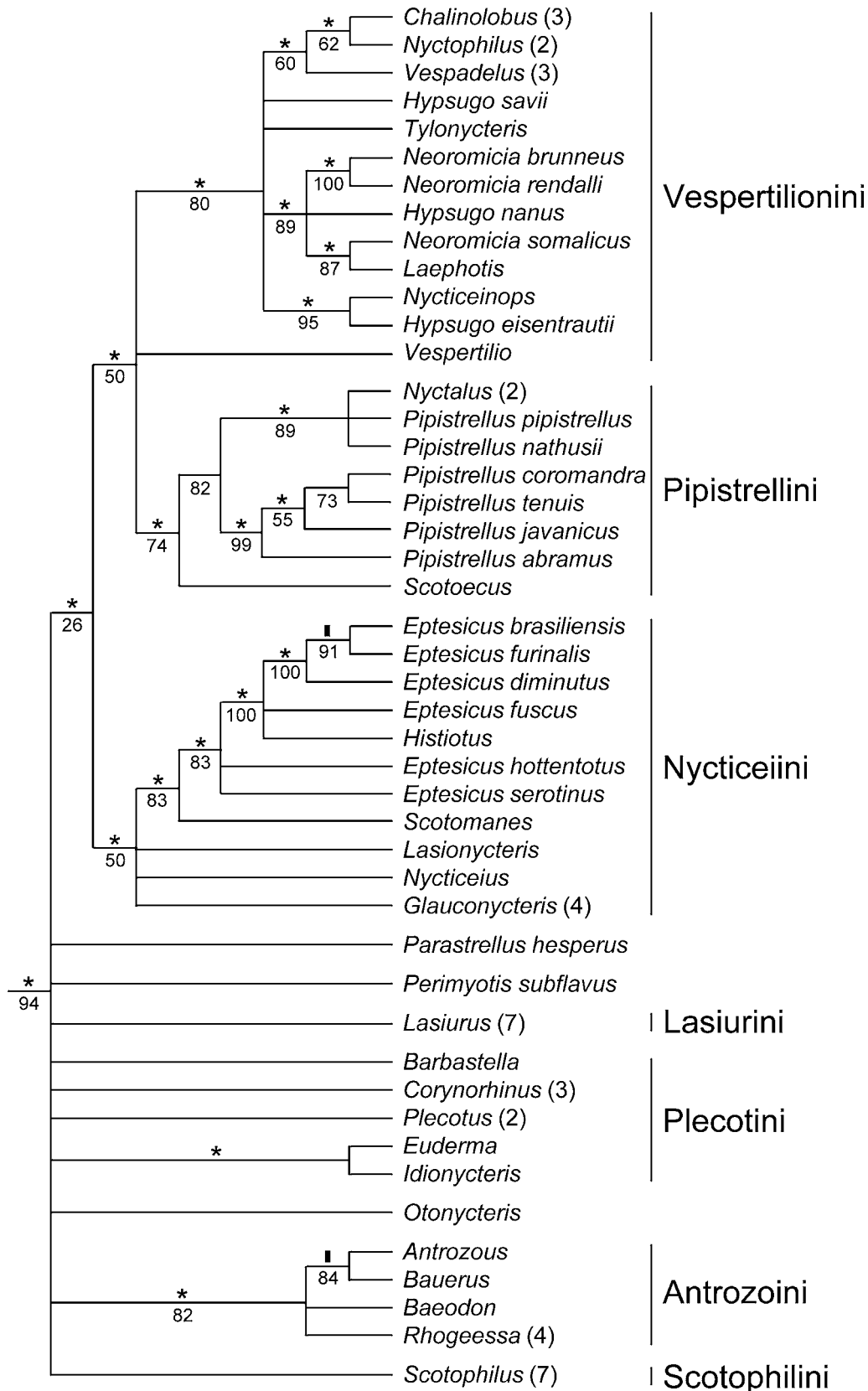


FIG. 1.—Cladogram from Hoofer and Van Den Bussche (2003:27, figure 6) that summarizes relationships within their other figures (figures 3:14 and 4:19) for subfamily Vespertilioninae. Their figure legend read as follows: “Only relationships that were supported strongly by either or both Bayesian and Parsimony analyses are depicted. Symbols above branches indicate Bayesian posterior probabilities (P) averaged conservatively over all multiple, independent analyses that employed various outgroup taxa and two different sequence alignments. *, $P = 1.0$ in

TABLE 2.—Pairwise comparisons of percentage sequence distance (uncorrected “p”) in the first 400 base pairs of the cytochrome-*b* gene (below the diagonal) and the entire 12S ribosomal RNA gene (above the diagonal). *Parastrellus hesperus*–3 and *Perimyotis subflavus*–3 specimens also were examined by Hooper and Van Den Bussche (2003).

Taxon ^a	1	2	3	4	5	6	7	8	9	10	11	12	13
1 <i>Lasiurus cinereus</i>		0.0971	0.1601	0.1345		0.1569	0.1473	0.1291	0.1291	0.1270	0.1366	0.1387	0.1377
2 <i>L. ega</i>	0.1775		0.1366	0.1227		0.1419	0.1398	0.1355	0.1355	0.1334	0.1281	0.1259	0.1270
3 <i>Hypsugo savii</i>	0.1950	0.2175		0.0961		0.1217	0.1313	0.1270	0.1270	0.1259	0.1259	0.1259	0.1249
4 <i>Pipistrellus pipistrellus</i> –1	0.2225	0.2225	0.1900			0.1174	0.1078	0.1067	0.1067	0.1057	0.0993	0.0993	0.0982
5 <i>P. pipistrellus</i> –2	0.2225	0.2225	0.1900	0.0000									
6 <i>Nycticeius humeralis</i>	0.2275	0.2175	0.2075	0.2175	0.2175		0.1291	0.1355	0.1355	0.1345	0.1227	0.1217	0.1217
7 <i>Eptesicus fuscus</i>	0.2175	0.1975	0.2225	0.1925	0.1925	0.1975		0.1302	0.1302	0.1291	0.1174	0.1153	0.1163
8 <i>Parastrellus hesperus</i> –1	0.2250	0.2025	0.2125	0.2225	0.2225	0.2125	0.1800		0.000	0.0032	0.0982	0.1003	0.0993
9 <i>P. hesperus</i> –2	0.2225	0.2000	0.2100	0.2200	0.2200	0.2100	0.1775	0.0025		0.0032	0.0982	0.1003	0.0993
10 <i>P. hesperus</i> –3	0.2225	0.2000	0.2100	0.2200	0.2200	0.2100	0.1775	0.0025	0.0000		0.0971	0.0993	0.0982
11 <i>Perimyotis subflavus</i> –1	0.2375	0.2000	0.2000	0.1950	0.1950	0.1925	0.1700	0.1850	0.1825	0.1825		0.0021	0.0011
12 <i>P. subflavus</i> –2	0.2300	0.1925	0.1950	0.1900	0.1900	0.1800	0.1675	0.1825	0.1800	0.1800	0.0125		0.0011
13 <i>P. subflavus</i> –3	0.2300	0.1925	0.1950	0.1900	0.1900	0.1850	0.1625	0.1825	0.1800	0.1800	0.0075	0.0050	

tribe corresponds closely with the tribe Eptesicini of Volleth and Heller (1994a), and thus is defined quite differently than the traditionally recognized Nycticeiini of Koopman (1994) and Tate (1942). Furthermore, to avoid polyphyletic taxa, their classification recognized generic status for several *Pipistrellus* subgroups (Fig. 1; Table 1).

The American pipistrelles.—Affinities of the American pipistrelles, the western pipistrelle (*hesperus*) and eastern pipistrelle (*subflavus*), also have been debated. A half-century ago, Hamilton (1949:101) reported “very great dissimilarity” between bacular characteristics of the 2 species, leading him to suggest “generic, or at least subgeneric differences” for the only 2 representatives of *Pipistrellus* in the Western Hemisphere. Baker and Patton (1967:281), in their study of karyotypic systematics, likewise documented “extremely significant” differences between *hesperus* and *subflavus*. They doubted a close relationship between them, “for such would necessitate the complete loss of a major chromosome in the evolution of *P. hesperus* from *P. subflavus* or a common ancestor.”

Subsequent morphologic study of both species agreed with these early assertions, providing more evidence of important differences not only between the American forms but also between them and Old World forms of *Pipistrellus* as well. Based on comparative study of dental, skeletal, and bacular characters in vespertilionine bats, Menu (1984) considered *subflavus* generically distinct from both *hesperus* and *Pipistrellus*. He placed *subflavus* in a new genus that he called *Perimyotis*, in reference to the *Myotis*-like tragus and dentition of *subflavus*.

Horáček and Hanák (1985–1986), in a study of 30 cranial characters in 52 species of *Pipistrellus*-like bats, demonstrated that Tate’s (1942) diagnosis of *Pipistrellus* should actually be looked upon more as a common grade of vespertilionid

organization rather than a proof of phyletic proximity. In addition to providing revised diagnoses for *Eptesicus*, *Hypsugo*, and *Pipistrellus*, they found that *subflavus* and *hesperus* differed in essential characters from each of those genera and each other. Horáček and Hanák (1985–1986) recognized *Perimyotis*, and furthermore considered *hesperus* generically distinct from other vespertilionids. They offered “*Parastrellus*” as a new generic name for *hesperus*, but never formally described the name under the rules of the *International Code of Zoological Nomenclature* (International Commission on Zoological Nomenclature 1999).

Hoofer and Van Den Bussche (2003) provided the 1st cladistic assessment of molecular data for *hesperus*, *subflavus*, and several other *Pipistrellus*-like bats. Their analysis documented marked genetic divergence between *hesperus* and *subflavus*, and between them and the 3 tribes of *Pipistrellus*-like bats (Nycticeiini, Pipistrellini, and Vespertilionini), further justifying recognition of *subflavus* within *Perimyotis* and *hesperus* within “*Parastrellus*” (Fig. 1). Therefore, to solve the nomen nudum status of the name “*Parastrellus*,” below we provide a formal description of the genus.

Parastrellus, new genus

Scotophilus (partim): H. Allen, 1864:43; not *Scotophilus* Leach, 1821.

Vesperugo (partim): True, 1884:62; not *Vesperugo* Keyserling and Blasius, 1839.

Pipistrellus (partim): Miller, 1897:88; not *Pipistrellus* Kaup, 1829.

Parastrellus Horáček and Hanák, 1985:62; nomen nudum.

Parastrellus Horáček and Hanák, 1985–1986:15; nomen nudum.

Pipistrellus (*Hypsugo*) (partim): Hill and Harrison, 1987:246; not *Pipistrellus* Kaup, 1829; not *Hypsugo* Kolenati, 1856.

←

all analyses regardless of alignment; ■, $0.95 \leq P < 1.0$ in all analyses regardless of alignment. Numbers below branches are bootstrap support values (percentages of 200 iterations) from Parsimony analysis, also averaged conservatively over all analyses. Numbers following some genera (in parentheses) indicate number of species included in phylogenetic analysis.”

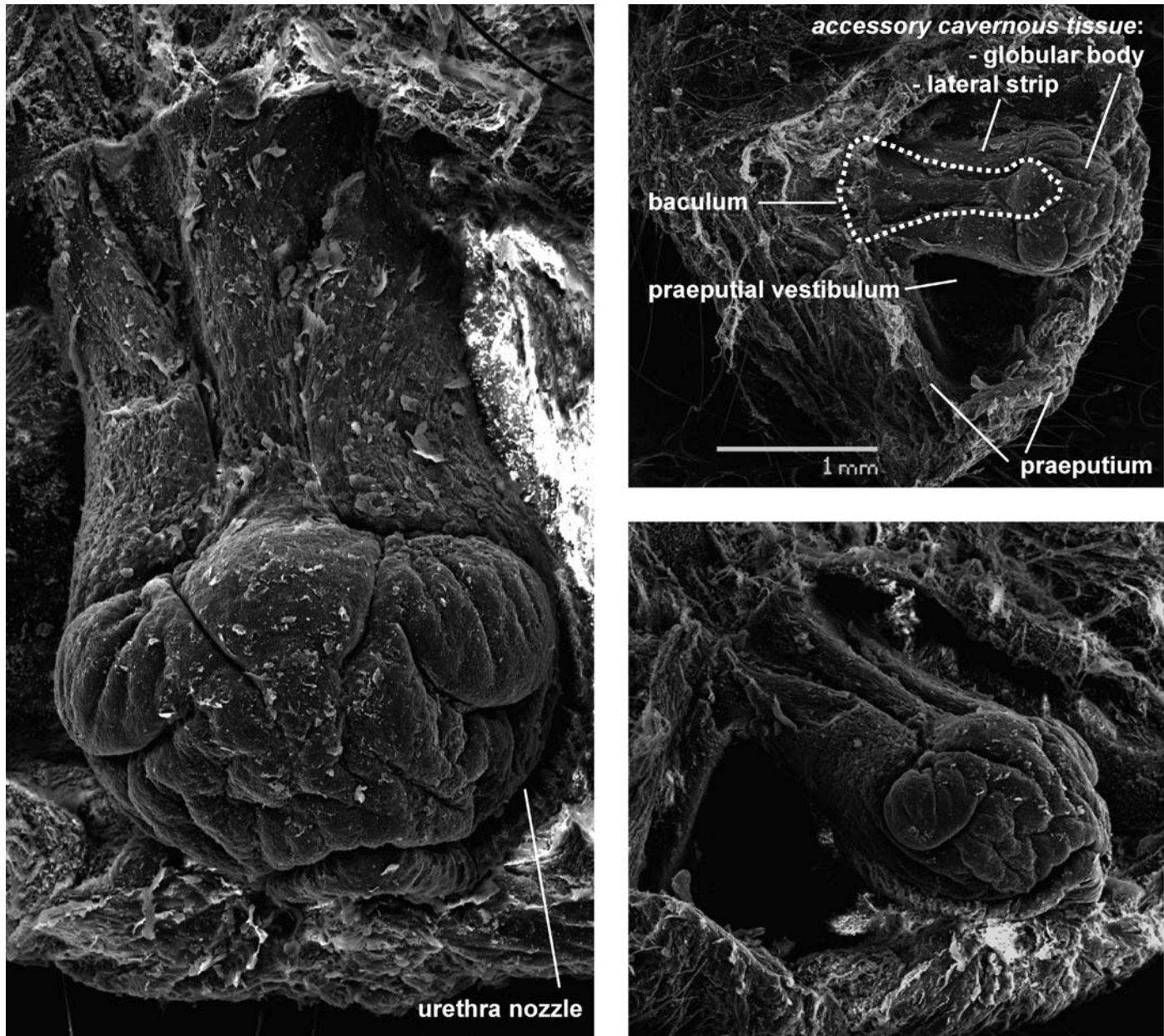


FIG. 2.—Penial structures in *Parastrellus hesperus* (TTU 357): glans penis, baculum (dotted line demarcates complete ossified bone), and separate bodies of accessory cavernous tissue at the tip of glans penis. Note also the extremely broad urethra nozzle.

Type species.—*Scotophilus hesperus* H. Allen, 1864:43.

Description.—Smallest North American bat (total length 60–86 mm, tail 26–36 mm, forearm 26–33 mm, mass 2–6 g); dorsal and ventral pelage with 2 color bands (basal band dark, blackish brown, terminal band varies from pale yellowish to pale orange-yellow or smoky gray-brown); muzzle, ears, forearms, legs, feet, and flight membranes blackish, contrasting sharply with pelage; ears short; tragus blunt, slightly curved, and usually half the height of ear; hind foot short, less than half the length of tibia; calcar keeled; wing membrane attaches at side of foot near base of toes; dorsum of uropatagium thinly furred on basal one-third; braincase low, but broad and elongated; postorbital region wide; supraorbital area slightly widened; rostrum short, not conspicuously

expanded, and with a shallow median depression where rostrum merges with frontals; slight lateral–rostral depressions just above anteorbital foramina; cranial profile almost straight, slightly depressed above anterior root of zygomata; premaxillae not shortened; zygomata slender, a little widened anteriorly, and lacking any jugal eminence; interdental palate about as wide as long; maxillary toothrows convergent; short bony postdental palate; mesopterygoid fossa broad; no basisphenoid pits; basioccipital narrow; cochlear bullae inflated. Parts of the above description were modified from Hill and Harrison (1987:246).

A unique combination of dental characters define *Parastrellus* (Fig. 3): (1) myotodont lower molars with (2) extremely thin-walled trigonids, (3) narrow and deep trigonid

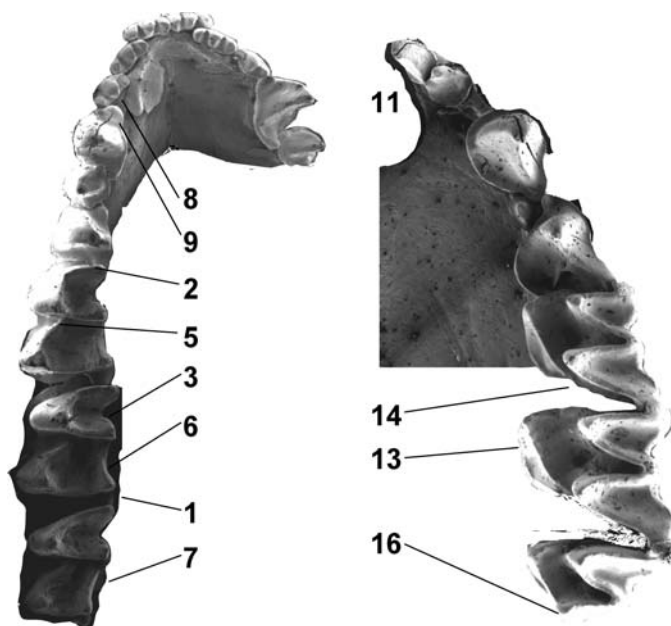


FIG. 3.—Mandibular (left) and maxillary (right) tooththrows of *Parastrellus hesperus* (ISZ 333). Numbers correspond to text in description of the genus.

basin, and (4) spacious talonids with (5) high crista obliqua and (6) sharp entoconid crest; (7) unreduced m3 with long talonid; (8) 3 lower incisors in nearly serial position, all trilobed; i3 smaller than i1 and i2, and in contact with canine; (9) lower canine often with a distinct mesiolingual cingular cusp and extensive distolingual cingular extension interlocked with (10) a moderately reduced p3 that is aligned in the tooththrow (c and p4 not in contact); (11) 2 upper incisors (I2 and I3), both small and unicuspid (secondary cusps indistinct or missing); 2nd (I3) about equal in crown size to 1st (I2), but its crown about half as high; 2nd (I3) separated from upper canine by a small to moderate gap about as wide as its crown width; (12) P3 small to minute, at best slightly less in crown area than 2nd upper incisor (I3), and located in recess between canine and 2nd upper premolar (P4), which is in or near contact with the canine; (13) M1 and M2 with a narrow protoconal basin and a deep fossa without hypocone or any hypoconal undulation, with (14) a complete protocrista passing from palatal base of protostyle to palatal base of metastyle without any interruption even in a zone of distal fossal sweep (the completeness of protocrista is retained even in old adult individuals with considerably worn molars), and with (15) complete absence of para- and metalophes; (16) M3 unreduced with well-developed and distally extending metacone. Dental formula is i 2/3, c 1/1, p 2/2, m 3/3, total 34.

Unique penial characters further distinguish the genus (Fig. 2): (17) tip of baculum inflated dorsally, forming (18) a broad, rooflike support for (19) an extensive distal enlargement of glans penis (with trilobate globular bodies); (20) urethra nozzle extremely broad and folded; and (21) entire distal complex of accessory cavernous bodies is attached to

the lateral margins and proximal base of the baculum via distinct laterally paired, musclelike cavernous structures.

Karyotype ($2n = 28$, $FN = 46$) is with 9 pairs of medium-sized to large metacentrics and submetacentrics, 1 pair of small submetacentrics, 3 pairs of small acrocentrics, a medium-sized submetacentric X, and a small acrocentric Y (Baker and Patton 1967).

Diagnosis and comparisons.—Despite considerable degree of correspondence in external characters, *Parastrellus* is distinguished from *Pipistrellus*, *Hypsugo*, *Perimyotis*, and other *Pipistrellus*-like bats by its distribution, cranial and dental characteristics, penial and bacular characteristics, karyotype, and degree of genetic divergence. Regarding specific dental characteristics (listed above), *Parastrellus* differs in character 1 from all nyctalodont genera (*Pipistrellus* sensu stricto; including *Nyctalus* and *Glischropus*), as well as in characters 2, 11, 13, and, particularly, 14 and 15; resembles *Hypsugo*, *Neoromicia*, *Arieulus*, and *Eptesicus* in characters 1, 4, 10, 12, and 15, but differing markedly by 2, 11, 13, and 14; resembles *Laephotis* in most dental characters, including the design of molars and characters 1, 8, 9, 11, and 14 (the latter being unusual among vespertilionids), but not in 13 or external characters (e.g., auricle); similar to *Plecotus* and *Barbastella* in 2, 3, 13, and 15 but markedly different in the other 12 characters; differs from *Perimyotis* in having robust canines, a compressed unicuspid row, and in general design of molars, including characters 13, 14, and 15. Regarding specific penial characteristics, *Parastrellus* resembles *Hypsugo* and *Neoromicia* in having an enlarged rooflike baculum and the perpendicular orientation of the urethra nozzle (20 partly), but differs in 17, 18, 19, and 21; resembles *Otonycteris* in 17, 18, and 20 (partly for each) but not in 19 or 21, or in the orientation of urethra nozzle (axial in *Otonycteris*).

Parastrellus hesperus is similar to the African *Hypsugo musciculus* in both overall appearance and more detailed cranial and dental characters, including 1, 2, 3, 6, 7, 8, 10, 12, 13, and 15. The 2 species differ in other respects. In *H. musciculus*, the protoconal complex of the upper molars is more robust and even narrower in mesiodistal direction than in *P. hesperus*; the base of the fossa is not as deep as in *P. hesperus*, and the postprotocrista terminates with a protoconal distal sweep similar to that found in *Eptesicus* or *Neoromicia* (i.e., without passing along base of metacone). P4 in *H. musciculus* has a well-developed, sharp, mesiopalatal cusp but lacks distal emargination, contrasting with a flat base of the tooth and distal emargination in *P. hesperus*. Slight but clear differences in shape of canines and upper incisors also exist between the 2 species. In any case, apparent similarities between *musciculus* and *hesperus*, stressed already in classifications proposed by Koopman (1973, 1994), deserve further study to determine whether they result from convergent evolution or reflect actual phyletic proximity; the latter possibility would be particularly interesting with respect to the paleobiogeographic history of *Parastrellus*. Unfortunately, *H. musciculus* is rather poorly known, reported from few records in Cameroon and Gabon (Simmons 2005), and no modern redescription or molecular data are available.

Distribution.—Southwestern North America. Coastal states from Washington to Guerrero (Mexico), eastward to Colorado, western Oklahoma, and Texas, and southward to Morelos (Mexico).

Content.—Monotypic, includes only *Parastrellus hesperus* (H. Allen, 1864). Allocated taxa, either as valid subspecies or as synonyms, include *apus* Elliot, 1904; *australis* Miller, 1897; *hesperus* Burt, 1936; *maximus* Hatfield, 1936; *merriami* Dobson, 1886; *oklahomae* Glass and Morse, 1959; *potosinus* Dalquest, 1951; and *santarosae* Hatfield, 1936.

Etymology.—From the Greek word *para*, meaning beside or aside from, and *strellus*, referring to *Pipistrellus*, the Latinized form of pipistrello, the Italian word meaning bat.

Remarks.—The description of *Scotophilus hesperus* by H. Allen (1864) was fairly detailed and accurate. Among other things, it suggested that "... the first premolar is very small, wedged between the canine and the second premolar, which is large, as in other species of *Scotophilus* (*Vesperugo*) ... the skull is eminently Scotophiloid, being flat and broad This bat resembles the *S. pipistrellus* of Europe in the contour of the head, the shape of the ear and tragus, the smallness and shape of the thumb and nail" Further generic placement of *Scotophilus hesperus* was established in a monograph by Dobson (1878), who provided perhaps the 1st nearly complete classification of all the then-known chiropteran species. He arranged all short-eared vespertilionids with a robust, shortened, and moderately reduced dentition into a large genus *Vesperugo* Keyserling and Blasius, 1839, which he separated from *Scotophilus* Leach, 1822, based on dental and cranial characters (2 upper incisors and flattened skull in the former instead of 1 upper incisor and conical rostrum in the latter). Dobson (1878) placed pipistrelles together with members of the current genera *Arielulus*, *Hypsugo*, *Nyctalus*, *Philetor*, and *Tylonycteris* in the nominate subgenus *Vesperugo*.

Dobson (1878:228–229, footnote) treated the North American *hesperus* as a typical member of the genus, quite close to Old World "*abramus*"—a name applied then in a very broad sense different than its current meaning. H. Allen (1864) demonstrated separate generic status for other subgenera of Dobson's (1878) *Vesperugo* and confirmed identity of both the American species with *Vesperugo* in a restricted sense. Later, Miller (1897) accepted this conclusion, but replaced the name *Vesperugo* with *Pipistrellus* Kaup, 1829 (type species *Vespertilio pipistrellus* Schreber, 1774), because of priority over *Vesperugo* Keyserling and Blasius, 1839. Miller (1907) later split Dobson's (1878) interpretation of *Vesperugo* into 10 genera and supplemented them with an additional 5 genera described based on newly discovered species (*Ia*, *Mimetillus*, *Rhinopterus*, *Philetor*, and *Baeodon*). He explicitly fixed the position of *hesperus* in the genus *Pipistrellus* (then covering about 40 species) based on its dental formula, shape of upper incisors, shortened auricle, and small body size. The subsequent taxonomic comparisons (e.g., Koopman 1973, 1975; Tate 1942) entirely respected Miller's (1907) concept of *Pipistrellus*, although they refined it by definitions of several species groups within the genus. In contrast to Tate (1942), who did not comment on *hesperus*, Koopman (1975) arranged

hesperus together with the African *musculus* Thomas, 1913, in a separate "*hesperus* group."

Horáček and Hanák (1985–1986) suggested generic distinction for *hesperus* because of a lack of congruence between the characters of *hesperus* and the diagnostic criteria (dental, cranial, phallus, and chromosomal specificities) of the genera supposedly related to it. The phenetic cranial data analyzed by Horáček and Hanák (1985–1986) clustered *hesperus* near several species of *Hypsugo*, *Nycticeinops*, *Eptesicus*, and *Vespertilio* (not with *Pipistrellus* sensu stricto). Hill and Harrison (1987) disagreed; they recognized *hesperus* within *Pipistrellus*, arranged alone in the *hesperus* subgroup, 1 of 7 subgroups (the others are *eisentrautii*, *imbricatus*, *lophurus*, *nanus*, *pulveratus*, and *savii*) within the *savii* group in subgenus *Hypsugo*. They stated (Hill and Harrison 1987:260), "*P. hesperus* should evidently be referred to *P. (Hypsugo)* with which it has close bacular and dental similarities, although recently generic separation (Horáček and Hanák 1985, 1985–1986) has been proposed for it."

Although most subsequent classifications honored the arrangement of Hill and Harrison (1987) of *hesperus* (e.g., Koopman 1993, 1994; McKenna and Bell 1997; Nowak 1999; Simmons 2005), the above-listed dental specificities of *hesperus*, especially characteristics 2, 13, and 14, mark it as clearly distinct from *Hypsugo*; in contrast, those dental characters are all nearly homogenous among several species of *Hypsugo* examined (*affinis*, *alaschanicus*, *anchietae*, *arabicus*, *bodenheimeri*, *pulveratus*, and *savii*). Furthermore, the baculum in *Hypsugo* species is flat-roofed, almost straight in lateral view, and has a cartilaginous or partly ossified apical (mostly lateral) extension at distal tip, whereas in *hesperus* the baculum is markedly curved in lateral view and terminates with a well-ossified trapezoid tuberosity reminiscent of the highly derived condition characteristic of *Lasiurus* (terminal tuberosity) or *Otonycteris* (dorsal inflexion of the tip). In *hesperus*, the design of penial soft tissues and morphology of glans penis also are unique (Fig. 2). In contrast to examined species of *Hypsugo* (*savii*, *alashanicus*, *pulveratus*, and *ariel*), *Neoromicia* (*somalicus*) and *Otonycteris*, *hesperus* does not have a separate body of accessory cavernous tissue at the base of penis. Further, *hesperus* is distinguished by the presence of unique globular structures situated at dorsal and lateral walls of the glans penis, and along a broad and laterally enlarged urethra nozzle. In most vespertilionid genera (including *Hypsugo*, *Neoromicia*, and *Otonycteris*) there is no erectile tissue at the dorsal roof of the baculum. The above penial characters of *hesperus*, therefore, can be looked upon as autapomorphies of the genus.

The cladistic assessment of Hofer and Van Den Bussche (2003) documented marked genetic divergence between *hesperus* and *Hypsugo*, further justifying generic distinction for *hesperus*. They recognized *hesperus* within a new, as yet unnamed, genus with incertae sedis placement within the subfamily Vespertilioninae, rather than within any of the 3 tribes of *Pipistrellus*-like bats. Hofer and Van Den Bussche (2003:34) noted that whether or not *hesperus* "shared a common ancestry with *Pipistrellus*-like bats or [has] closer affinities with other vespertilionine tribes [was] clearly un-

resolved in [their] study.” Analysis of additional, independent data sets will be necessary to resolve the phylogenetic affinities of *Parastrellus* within the Vespertilioninae.

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APPENDIX I

Specimens examined.—Voucher specimens are housed in the following institutions: The Natural History Museum (formerly the British Museum [Natural History]; BM), London, United Kingdom; Carnegie Museum of Natural History (CM), Pittsburgh, Pennsylvania; Department of Zoology, Charles University (ISZ), Prague, Czech Republic; Louisiana State University, Museum of Natural Science (LSUMZ), Baton Rouge, Louisiana; Muséum d'Histoire Naturelle de Genève (MHNG), Geneva, Switzerland; Museum für Naturkunde an die Humboldt Universität (MNB), Berlin, Germany; Museum of Texas Tech University (TTU), Lubbock, Texas; Museum of Vertebrate Zoology, University of California (MVZ), Berkeley, California; National Museum Praha (NMP), Prague, Czech Republic; Naturhistorisches Museum Wien (NMW), Vienna, Austria; Senckenberg Natural History Museum (SMF), Frankfurt, Germany; Universidad Nacional Autónoma de México City (UNAM), México City, México; Zoological Museum Alexander Koenig (ZMB), Bonn, Germany; and Zoological Museum at Lomonosov State University (ZMM), Moscow, Russia. Specimens used in morphological and genetic comparisons are listed separately. Museum catalog numbers are missing for vouchers that are housed but not yet cataloged or the number is unknown.

Daggers (†) denote type specimens. For genetic comparisons, 2 numbers in square brackets separated by a comma identify each specimen: tissue number, museum catalog number. GenBank accession numbers for the cytochrome-*b* gene (*Cytb*) or 12S ribosomal RNA gene (12S), or both, are given in parentheses after the catalog numbers.

“DQ” GenBank accession numbers distinguish the sequences generated in this study. Specimens of *Parastrellus hesperus*, *Perimyotis subflavus*, and *Pipistrellus pipistrellus* used in genetic comparisons are numbered (1, 2, or 3) to correspond with Table 2.

Morphological Comparisons

Arielulus circumdatus.—INDONESIA: Java (BM 7.1.1.401); MALAYSIA: Pahang, Fraser Hill (BM 73.618). *Arielulus cupro-*—MALAYSIA: Borneo, Sabah, Sepilok (BM 84.1989).

Eptesicus bobrinskoi.—KAZAKHSTAN: Kyzylorda, 65 km S Aralsk, Kolodec Tjulek, Kara-Kum (ZMM S5091†); Kyzylorda, Kazalinsk (ZMM S-5081; ZMM S-5091; ZMM S5092). *Eptesicus brasiliensis*.—BRAZIL: (NMW 21694). *Eptesicus dimissus*.—INDONESIA: Bandung (BM 529.13). *Eptesicus floweri*.—SUDAN: Kanisa Janu (BM 15.3.6.69). *Eptesicus furinalis*.—BRAZIL: (NMW 32148; ZMM 32151; ZMM 21695). *Eptesicus matroka*.—MADAGASCAR: Fianarantsoa, Betsileo (NMW 27455). *Eptesicus nasutus*.—AFGHANISTAN: Nangahar, Bisut (ISZ AF569); IRAN: Khuzestan, Ahwaz, Karun River (BM 5.10.4.6); SAUDI ARABIA: (SMF 20086); Makkah, near Jeddah (BM 48.350).

Falsistrellus tasmaniensis.—AUSTRALIA: Tasmania (BM 51.7.24.3; “*P. krefftii*”); SW Australia, King River (BM 6.8.1.20).

Glauconycteris argentata.—ZAIRE: Netona (SMF 2516†). *Glauconycteris poensis*.—CAMEROON: Victoria (SMF 28245). *Glauconycteris variegata*.—TANZANIA: Kiswawe (ZMB 22.8.60).

Glischropus tylopus.—MALAYSIA: Selangor (SMF 18298).

Hesperoptenus blandfordi.—MALAYSIA: Borneo Island, Sabah (BM 84.1996). *Hesperoptenus tickelli*.—INDIA: Andaman and Nicobar Islands, Middle Andaman, Long Island (BM 67.196); SRI LANKA: Kalutara, Bentona (BM 66.5531). *Hesperoptenus tomesi*.—SRI LANKA: (NMW 28758).

Hypsugo affinis.—NEPAL: Nagarkot (BM 37.3.14.3); INDIA: Kotagiri, Nelghiris (BM 92.4.7.2; BM 92.4.7.1). *Hypsugo alaschanicus*.—CHINA: Manchuria, Jablonija (ZMM S83943–ZMM S83947); MONGOLIA: Dzhungar Gobi (ZMM S40126); NORTH KOREA: Vechi (ZMM S94785); RUSSIA: Vladivostok (ZMM S2808†; type of *velox*). *Hypsugo arabicus*.—OMAN: Wadi Sahtan (BM 2.10052). *Hypsugo ariel*.—EGYPT: E Desert (BM 4.11.4.6). *Hypsugo bodenheimeri*.—ISRAEL: Wadi Araba (BM 67.1229); YEMEN: Socotra, Suk (BM 6.7.1255). *Hypsugo cadornae*.—MYANMAR: (BM 76.1266); Upper Burma, Tasa Khu (BM 50.408). *Hypsugo eisen-trauti*.—CAMEROON: Rumysi Hilus (ZMB 50.498†); Mount Kupe (ZMB 50.198). *Hypsugo imbricatus*.—INDONESIA: Java (BM 9.1.5.315); Java, Bandung (SMF 29079); Sumatra (SMF 52031). *Hypsugo joffrei*.—MYANMAR: 50 km W Kindat (BM 16.3.26.84). *Hypsugo kitcheneri*.—INDONESIA: Central Borneo, Kalimantan, Boentoh, Barito River, (BM 10.4.5.154). *Hypsugo macrotis*.—INDONESIA: NW Sumatra, Sabang (BM 23.10.2.12); MALAYSIA: Selangor (BM 84.1990). *Hypsugo musciculus*.—CAMEROON: Ja River, Bitye (BM 19.11.1.2; BM 23.1.22.26). *Hypsugo pulveratus*.—CHINA: Fukien (SMF 42384; NMW MAK50.257); Shaowu, Fujian (ZMB 50.266; ZMB 50.299). *Hypsugo savii*.—AZERBAIJAN: (ISZ Az73; ISZ Az76; ISZ Az90; ISZ Az92); BULGARIA: Karlukovo (ISZ B0234; ISZ B0249; ISZ B0443–ISZ B0459); LEBANON: Ainab (BM 61.393; BM 61.394); UKRAINE: Crimea (ZMM S96375†; type of *tauricus*); SPAIN: Gran Canaria, Las Palmas (BM 13.7.26.6); Cape Verde Islands, St. Fillipe (BM 5.12.6.2). *Hypsugo vordermanni*.—INDONESIA: Borneo, Kalimantan, 2°N, 109°32'E (BM 82.547).

Laephotis angolensis.—ZAIRE: Musonge, 68 km E Elisabethville (BM 57.435). *Laephotis botswanae*.—ZAIRE: (SMF 16868). *Laephotis wintoni*.—ETHIOPIA: Shoa, Koka (BM 72.4398).

Lasiurus cinereus.—UNITED STATES: California (SMF 58303).

Mimetillus moloneyi.—TANZANIA: Liwale (BM 64.1786); UGANDA: Moyo, W Nile (SMF 39436).

Neoromicia brunneus.—GABON: Benito River, 15 km from mouth (BM 98.5.4.18). *Neoromicia capensis*.—ETHIOPIA: Taflu River, 30 km W Degek Bur (SMF 49589); ZAMBIA: Mazabuka, Boma (BM 55.1123). *Neoromicia guineensis*.—NIGERIA: Umuaha (BM 53.29); SUDAN: Nzara (SMF 33275); Rheika, Kordofan (SMF 33276). *Neoromicia nanus*.—ZAIRE: Netona (SMF 2524; lectotype); Kakondo (ISZ 16873). *Neoromicia rendalli*.—ZAMBIA: Naleza, Blue Lagoon (BM 68.1011). *Neoromicia somalicus*.—ETHIOPIA: Gamu Gofa, Lake Chamo (SMF 47867); MADAGASCAR: Majunga (NMW 19654; as *E. humblotii*). *Neoromicia zuluensis*.—ZIMBABWE: Bulaways (BM 8.8.16.2).

Nyctalus azoreum.—PORTUGAL: Azores Islands (SMF 54809).

Nycticeinops schlieffeni.—CONGO: Inhumane (BM 6.11.8.20).

Parastrellus hesperus.—UNITED STATES: Arizona, Coconino County, Kwagunt Canyon (ISZ 333; ISZ 334; ISZ 340); Arizona, Coconino County, Round Rock Lake (ISZ 370; ISZ 372); Texas, Brewster County, 5 miles S Terlingua (TTU 357); Texas, Brewster County, Big Bend National Park, Harte Ranch Mountain Lodge (TTU 59970); Texas, Hudspeth County, 0.5 mile S, 4.8 miles W Guadalupe Peak, Guadalupe Mountain (TTU 23275).

Perimyotis subflavus.—UNITED STATES: Arkansas, Maddison County (NMP 92625); Pennsylvania (ISZ 325).

Philetor brachypterus.—PHILLIPINES: Mindanao (SMF 31341).

Pipistrellus abramus.—CHINA: (NMW MAK836); central part of country (NMW 17849); Jiangxi, Nandang (NMW 17846); JAPAN: (SMF 51213). *Pipistrellus ceylonicus*.—PAKISTAN: western part of country (BM 73.761). *Pipistrellus collinus*.—NEW GUINEA: eastern part of country (SMF 18873). *Pipistrellus coromandra*.—AFGHANISTAN: Nangahar, Jalalabad (ISZ AF713); BURMA: Rhakine (NMW 27504; NMW 27505). *Pipistrellus inexpectatus*.—UGANDA: Kampala (BM 66.1171). *Pipistrellus javanicus*.—AUSTRALIA: (BM 47.7.21.18); INDIA: Andaman and Nicobar Islands, Nicobar Islands (NMW 30472); INDONESIA: West Java, Bogor (NMW 28327; NMW 28328; NMW 28391; NMW 28438; NMW 30477); Java (BM 9.1.5.295). *Pipistrellus kuhlii*.—GREECE: Halkidiki, Petralona (ISZ Gr06); IRAQ: Amara (SMF 34380); ITALY: Trieste (ISZ Flor01). *Pipistrellus maderensis*.—SPAIN: Canary Islands, Tenerife (SMF 5363). *Pipistrellus mordax*.—INDONESIA: Java (MNB 2559†). *Pipistrellus nanulus*.—EQUATORIAL GUINEA: Fernando Po (ZMB 106). *Pipistrellus nathusii*.—CZECH REPUBLIC: Karlstejn, Beroun (ISZ 18/74); TURKEY: Demürköy, Thrace (ISZ T93/05). *Pipistrellus papuanus*.—PAPUA NEW GUINEA: (SMF 57203). *Pipistrellus patreculus*.—INDIA: Assam, Khasi Hills (NMW 30484; NMW 30486; NMW 30487). *Pipistrellus pipistrellus*.—CZECH REPUBLIC: Doubice, N Bohemia (ISZ M120); KYRGYSTAN: Bishkek (ISZ CT84/01–ISZ CT84/10); Osh: Sasyk-Ungur Cave (ISZ CT84/283–ISZ CT84/288); SLOVAKIA: Ernya cave, Roznava (NMP 90016–NMP 90022). *Pipistrellus pygmaeus*.—CZECH REPUBLIC: Lednice, Breclav (NMP 90139); GREECE: Ilia, Simopoulo (NMP 49016). *Pipistrellus rueppellii*.—KENYA: Gan Gafe (SMF 45023); UGANDA: Kaborole, Semliki Valley (BM 75.2567); SUDAN: (ZMB 50.157; ZMB 50.168). *Pipistrellus rusticus*.—ETHIOPIA: (ZMB 79.233; SMF 44830). *Pipistrellus stenopterus*.—SUMATRA: (SMF 52033; SMF 44258; NMW AB78/29–NMW AB78/35). *Pipistrellus tenuis (mimus)*.—INDIA: Madras (SMF 59577); Khasi Hills, Assam (NMW 30485); NEPAL: Birguns (ISZ Ob 81/59; ISZ Ob 81/91). *Pipistrellus tramatus*.—VIETNAM: Hanoi (ISZ PS18–ISZ PS21).

Scotoecus albigula.—KENYA: Rift Valley, Kitale, N Hoys bridge (BM 75.2594). *Scotoecus pallidus*.—INDIA: Bihar, Darbhanga, Bahgoumie (BM 23.4.8.4). *Scotoecus hindei*.—ETHIOPIA: Gamu

Gofa (SMF 49136); KENYA: southwestern part of country (SMF 48673).

Scotozous dormeri.—INDIA: Hazaribagh, SW Bengal (BM 15.4.3.28); Madurai, Tamilnadu (SMF 61410).

Tomopeas ravus.—PERU: Jayan (BM 0.3.1.101†).

Tylonycteris robustula.—INDONESIA: Medan, northern Sumatra (SMF 39688); Sumatra (SMF 12389). *Tylonycteris pachypus*.—INDONESIA: Sumatra (SMF 39674; SMF 39455).

Vespadelus pumilus.—AUSTRALIA: SW Australia, Kings River (BM 6.8.1.7); W Australia, Bewin Lake (BM 6.10.5.4).

Genetic Comparisons

Eptesicus fuscus.—UNITED STATES: California, Solano County, 1 mile SW Vacaville, 38.346516°N, 121.996563°W [FC 1433, MVZ 148681 (*Cytb* AF376835)]; West Virginia: Hampshire County, 1.5 miles N, 3.1 miles W Kirby, Nathaniel Mountain Public Hunting and Fishing Area, 39°12'N, 78°47'W [SP 844, CM 102826 (12S AF326092)].

Hypsugo savii.—SWITZERLAND: Valais, Fully, 46°13'N, 7°1'E [IZEA 3407, MHNG 1805.007 (*Cytb* AJ504450)]; Valais [IZEA 3586, MHNG 1804.100 (12S AY495475)].

Lasiurus cinereus.—UNITED STATES: Texas, Jeff Davis County, Mount Livermore Preserve, Universal Transverse Mercator: 13-580697 E 3392220 N [TK 78926, TTU (12S AY495482)]; Texas, Lubbock County, Lubbock [TK 18855, TTU 77985 (*Cytb* DQ421825)]. *Lasiurus ega*.—ECUADOR: Guayas, Reserva Ecológica Manglares Charute, Guardiania Principal del Parque, 2°27'16.9"S,

79°37'38.6"W [TK 134649, TTU (*Cytb* DQ421826)]; MEXICO: Michoacan, Aquila, near Colola [TK 43132, UNAM (12S AY495483)].

Nycticeius humeralis.—UNITED STATES: Louisiana, De Soto Parish, Denson, off highway 512 [LSUMZ 23913, LSUMZ 23913 (*Cytb* L19727)]; Texas, Real County, Leakey [TK 26380, TTU 49536 (12S AF326102)].

Parastrellus hesperus.—UNITED STATES: New Mexico, Lincoln County, 1 mile N, 3 miles W Carrizozo [specimen 1—TK 20347, TTU 38402 (*Cytb* DQ421824, 12S DQ421815)]; Texas, Brewster County, Black Gap Wildlife Management Area [specimen 3—TK 78703, TTU 79269 (*Cytb* DQ421822, 12S AY495522)]; Texas, Culberson County, 23 miles ENE Van Horn [specimen 2—TK 26039, TTU 45844 (*Cytb* DQ421823, 12S DQ421816)].

Perimyotis subflavus.—UNITED STATES: Texas, Cass County, White Oak Creek Wildlife Management Area [specimen 2—TK 90667, TTU 80676 (*Cytb* DQ421820, 12S DQ421817); specimen 3—TK 90671, TTU 80684 (*Cytb* DQ421821, 12S AY495523)]; Texas, Leon County, Keechi Creek Wildlife Management Area [specimen 1—TK 84525, TTU 80754 (*Cytb* DQ421819, 12S DQ421818)].

Pipistrellus pipistrellus.—GREECE: Stereá Eláda, Mount Parnass, Corycian Grotta [specimen 2—M 812, MHNG 1807.055 (12S AY663799)]; Thessalía, Píli, Prespa Lake, 39°15'N, 21°75'E [specimen 1—M 699, MHNG 1807.052 (12S AJ504443)]; SPAIN: Barcelona, S Andreu de la Barca [IZEA 3403, MHNG 1806.032 (*Cytb* AF326105)].