PHYLOGENY OF PLECOTINE BATS: REEVALUATION OF MORPHOLOGICAL AND CHROMOSOMAL DATA

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Recent systematic studies of the tribe Plecotini have generated two alternative phylogenetic hierarchies: (*Barbastella* (*Corynorhinus* (*Plecotus* (*Idionycteris Euderma*)))); and (*Euderma* [including *Idionycteris*] (*Barbastella* (*Plecotus Corynorhinus*))). To test these hypotheses we examined 44–45 morphological and 11 karyological characters of 10 plecotine species, including *Otonycteris hemprichii.* Character states for the hypothetical ancestor were inferred by evaluation of selected outgroup taxa: *Rhogeessa tumida, Nycticeius humeralis, Eptesicus fuscus, Myotis lucifugus, M. ciliolabrum,* and *Miniopterus schreibersi.* The most parsimonious trees, identical in topology but different in character-state optimization, were congruent with the systematic hierarchy of Plecotini suggested by the first hypothesis. *Otonycteris* branched off before *Corynorhinus.* These results strongly support separation of *Corynorhinus* as an independent genus and limitation of *Plecotus* to Palaearctic species. The two highly derived taxa, *Idionycteris phyllotis* and *Euderma maculatum,* seem to be sufficiently different from each other to be regarded as generically distinct. It is proposed that the tribe Plecotini originated in the eastern hemisphere.

Key words: Plecotini, plecotine bats, morphology, karyology, phylogenetic systematics, biogeography

The tribe Plecotini (Chiroptera: Vespertilionidae) is distributed throughout the Holarctic and consists of 11 or 12 species of mostly long-eared bats (Corbet and Hill, 1991, 1992; Koopman, 1993; Yoshiyuki, 1991). Numerous systematic studies have evaluated phylogenetic affinities within the tribe at generic, subgeneric, and specific levels (e.g., Frost and Timm, 1992; Handley, 1959; Leniec et al., 1987; Qumsiyeh and Bickham, 1993; Tumlison and Douglas, 1992; Williams et al., 1970); however, no consistent phylogeny has emerged. Handley (1959) first examined morphological relationships among plecotines and concluded that the genera *Plecotus* (including subgenera *Plecotus, Corynorhinus,* and *Idionycteris*) and *Euderma* shared a common ancestor after divergence from *Barbastella* in the Miocene. Based on karyological data, Williams et al. (1970) suggested the phylogeny (*Barbastella* ((*Euderma Idionycteris*) (*Plecotus Corynorhinus*))). Leniec et al. (1987), also using karyological data, proposed that the tribe's only short-eared bats, genus *Barbastella,* are derived from the long-eared plecotines in the arrangement ((*Euderma Idionycteris*) (*Barbastella Plecotus Corynorhinus*)).

Results from two of the most recent phylogenetic studies of the Plecotini indicate two quite different topologies. Tumlison and Douglas (1992) suggested the phylogeny (*Barbastella* (*Corynorhinus* (*Plecotus* (*Idionycteris Euderma*)))). However, Frost and Timm (1992) proposed the cladistic relationship of (*Euderma* [including *Idionycteris*] (*Barbastella* (*Plecotus Corynorhinus*))). This discrepancy might be due to the fact that Tumlison and Douglas (1992) used only morphological traits, and Frost and Timm (1992) included both morphological and karyological characters. As substantiation, one of the four alternate trees of Frost and Timm (1992), based only on morpho-

logical characters, is identical in topology to the tree of Tumlison and Douglas (1992).

Published descriptions of karyotypes of the genera of Plecotini have been inconsistent. Several taxa were distinguished based on different chromosome banding qualities, and misinterpretations of the standard numbering system have been indicated (revised by Volleth and Heller, 1994*a*). In addition, a study using G-banded chromosomes indicated that the large long-eared bat *Otonycteris hemprichii* is also a member of the tribe Plecotini, with Qumsiyeh and Bickham (1993) inferring the phylogeny ((*Euderma Idionycteris*) (*Otonycteris Barbastella Plecotus Corynorhinus*)). The karyotype of *Otonycteris* shows an extensive similarity with karyotypes of *Plecotus, Corynorhinus,* and *Barbastella* (Qumsiyeh and Bickham, 1993; Zima et al., 1992). Tumlison and Douglas (1992), Qumsiyeh and Bickham (1993), and Bogdanowicz and Owen (1996) also have suggested that problems in the intepretations of some morphological characters from works such as Handley (1959) may have led to questionable conclusions. Phenetic results, based on cranial geometric morphometrics, indicated that *Otonycteris* was the most divergent species of the Plecotini (Bogdanowicz and Owen, 1996) and has undergone extensive adaptive changes (Horáček, 1991).

Our objectives were to resolve the taxonomic status of *Idionycteris* and *Corynorhinus,* determine the validity of *Otonycteris* as a member of the tribe, and establish phylogenetic relationships of all genera and subgenera of plecotine bats. This research was accomplished by cladistic analysis of morphological and karyological characters.

Materials and Methods

The ingroup was composed of 10 species representing the 6 genera (or subgenera) of the Plecotini (including *Otonycteris*; Appendix I). A hypothetical ancestor for the Plecotini was inferred from multiple outgroup analysis, and all character states were polarized using the outgroup comparison method of Maddison et al. (1984). Outgroups were chosen and arranged based on probable relationships among the ingroup and outgroups following the karyology-only cladogram of the Vespertilionidae (Volleth and Heller, 1994*b*). In our study, they were formed by the sister groups "Nycticeiini" (*Nycticeius humeralis* and *Rhogeessa tumida*) and Eptesicini (*Eptesicus fuscus*), the tribe Myotini (*Myotis lucifugus* and *M. ciliolabrum*), and the subfamily Miniopterinae (*Miniopterus schreibersi*). Chromosome banding indicates that the Miniopterinae is the first subfamily to diverge from the common Vespertilionidae stem (Volleth and Heller, 1994*b*).

Nixon and Carpenter (1993) suggested that characters should not be polarized prior to an analysis, rather that polarity should be determined a posteriori through rooting the cladogram between ingroup and outgroup taxa. However, this is a reasonable procedure only when there is absolutely no uncertainty concerning the relationship of the ingroup to the putative outgroup taxa (i.e., certainty of ingroup monophyly). In many systematic analyses, including this one, there may be certainty concerning most taxa and uncertainty concerning a few putative ingroup or outgroup taxa. Using the method of Maddison et al. (1984), position of these taxa may be examined, particularly by using multiple character sets or subdividing characters being examined, as we have done.

Characters (i.e., individual hypotheses of taxic homology) were compiled from the literature and examination of zoological material. The 61 skin, skull, and chromosomal characters for which primitive states could be inferred, were determined for each species (Table 1, Appendix II). Five characters, however, were autapomorphic either for *Idionycteris* or *Euderma,* and one character (biarmed chromosome, arm combination 11/14) presented an obvious synapomorphic feature of the tribe (Appendix II). Thus, these six characters were phylogenetically uninformative and were omitted from final analyses. Character states for polymorphic taxa (sensu Swofford, 1991) were intepreted as uncertain. Characters were not weighted. Because karyological data were taken from the literature and were not our direct observations, a second analysis was performed on a data matrix containing only morphological characters, which we scored directly.

Cladograms were constructed using the

TABLE 1.—*Distribution of states for 45 morphological and 11 karyological characters of the plecotine bats and their hypothetical ancestor. See Appendix II for character descriptions.*

	Character number									
	1 11111 11112 22222 22223 33333 33334 44444 44445 55555 5									
Taxon	12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 6									
Ancestor	00000 00000 00000 00001 00000 00000 00001 00000 00000 00000 00000 0									
Barbastella barbastellus	10110 01000 00000 00000 10001 00000 00010 00120 10100 10110 01100 0									
Barbastella leucomelas	10110 01000 00000 00000 10001 00000 00010 00120 10100 10110 01100 0									
Corynorhinus mexicanus	10110 11000 21111 11011 01111 00000 10001 11121 00101 ????? ????? ?									
Corynorhinus rafinesquii	10110 11000 21111 11011 01111 00000 10001 11121 00101 ????? ????? ?									
Corynorhinus townsendii	10110 11000 21111 11011 01111 0?000 10001 11121 00101 10110 01100 0									
Euderma maculatum	01002 00111 11211 11101 00100 11100 11210 11101 11000 01001 10011 1									
Idionycteris phyllotis	01001 00111 11211 10112 00100 11000 11210 11101 11010 01001 10011 1									
Otonycteris hemprichii	00100 20100 00100 00001 00100 01011 10002 00111 00000 10110 01100 0									
Plecotus auritus	11100 21101 11110 11111 00000 00111 10101 00011 11010 10110 01100 0									
Plecotus austriacus	11100 21101 11110 11111 00000 00111 10101 00011 11010 10110 01100 0									

branch-and-bound method (Hendy and Penny, 1982) included in the PAUP package version 3.0 (Swofford, 1991). Separate analyses were performed under the assumption of additivity (ordered morphoclines permitted) and under the assumption of non-additivity (ordered morphoclines not permitted), allowing for assessment of differences based solely on the assumption of additivity instead of being based on simple character matching (Frost and Timm, 1992). Two character optimization algorithms were used (ACCTRAN and DELTRAN; Swofford and Maddison, 1987) and enabled us to find characters with an ambiguous distribution on a tree. ACCTRAN (accelerated transformation) favors reversals over parallelisms; DELTRAN (delayed transformation) assumes that the opposite is more likely. Reliability of branches on the most parsimonious tree was estimated using a 1,000 iteration bootstrap analysis, i.e., the random sampling of *N* characters from the entire data set with replacement (Felsenstein, 1985). Because bootstrap analyses perturbate the original data and consistency and retention indices are sensitive to higher numbers of states per character (Naylor and Kraus, 1995), the stability of the tree also was evaluated using a type of branch-support index, specifically the number of additional steps (added tree length) needed to collapse a branch of the most-parsimonious tree (Bremer, 1994).

RESULTS

Unbracketed statistics refer to data analysis in which all character-state matches were regarded as additive (ordered). Bracketed results were derived from analyses in which multistate characters were treated as non-additive (unordered). There was no difference between the tree topology resulting from additive and nonadditive analyses, and the only departure from character congruence was in the placement of multistate characters 5, 6, 11, 33, and 39 (Appendix II). Character 5 was informative only under an assumption of additivity. Eight traits (1, 7, 8, 15, 28, 36, 37, and 44) were dependent on character-optimization methodology employed (i.e., ACCTRAN or DELTRAN). These characters could not be placed unambiguously and therefore were not considered to be evidence of relationship.

Analysis of the entire data matrix produced one most parsimonious tree (Fig. 1), which has a length of 97 [94], consistency index (CI) of 0.660 [0.660], rescaled consistency index (RC) of 0.512 [0.509], and retention index (RI) of 0.776 [0.771]. Ideally, this data matrix required 64 [62] steps, so 33 [32] steps must be attributed to reversals and parallelisms. Regardless of character optimization or assumptions about character additivity, the Plecotini formed a monophyletic clade supported by seven synapomorphies (character number in parentheses): relatively narrow braincase (3); second phalanx of third digit much lon-

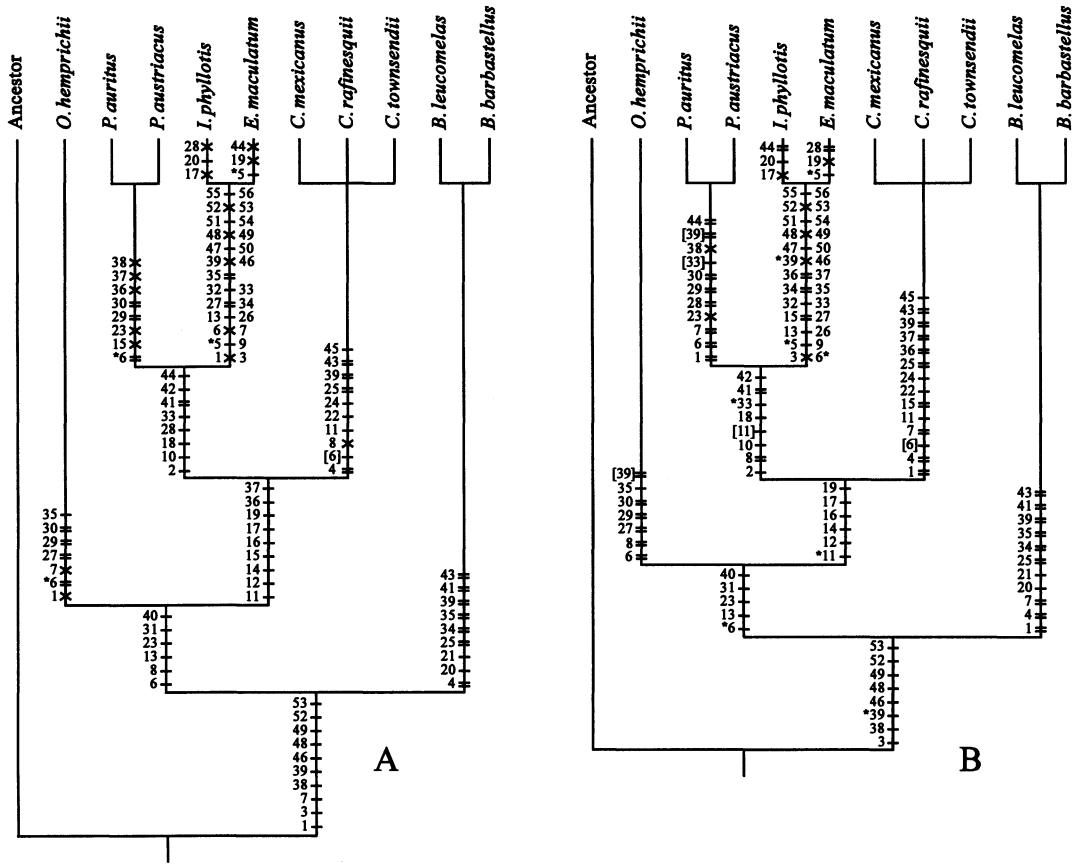

FIG. 1.—The most parsimonious cladogram of 45 [44] morphological and 11 karyological features for plecotine bats assuming A) accelerated character transformation and B) delayed character transformation. Asterisks and brackets denote alternative changes under the assumption of character additivity and nonadditivity, respectively. Bars represent synapomorphies, double lines represent parallelisms, and crosses represent reversals.

ger than the first (38); and fused chromosomal arms No. 7 and 19 (46), 8 and 21 (48), 9 and 12 (49), 10 and 15 (52), and 13 and 18 (53). All of these presumed synapomorphies were reversed in some terminal taxa, except for *Barbastella, Otonycteris,* and *Corynorhinus* species. The karyological synapomorphies were reversed only in *E. maculatum* and *I. phyllotis.*

Barbastella was first to diverge from the common plecotine stem, being the sister taxon to *Otonycteris, Corynorhinus, Plecotus, Euderma,* and *Idionycteris. Otonycteris* was placed within traditional Plecotini, as the sister taxon of *Corynorhinus, Plecotus, Euderma,* and *Idionycteris. Otonycteris* and traditional Plecotini are linked as a monophyletic group unambiguously by four synapomorphies: enlarged and slightly elongated auditory bullae (13), but with an additional multistate change in *Euderma* and *Idionycteris*; convex medial roof of pharynx (23); straight angle of dentary (31); and extremely enlarged auricles (40). Within the long-eared bats, *Corynorhinus, Plecotus, Idionycteris,* and *Euderma* were united as a monophyletic clade by at least five synapomorphies: zygomatic arch bowed dorsally (12); anterior border of auditory bullae rounded (14); hamulus straight and parallel with longitudinal axis of skull (16); pterygoid walls vertical (17);

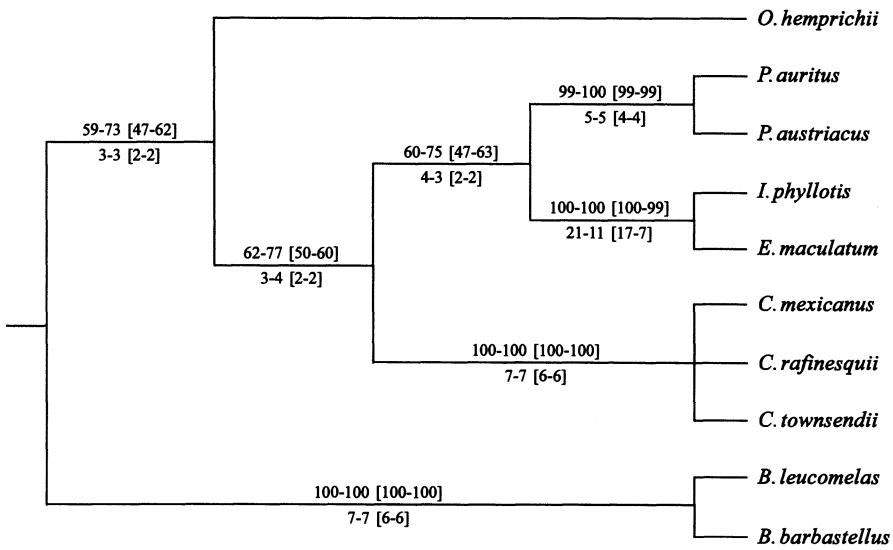

FIG. 2.—Topology of the single-most parsimonious tree generated by the branch-and-bound algorithm, hypothesizing phylogenetic relationships among plecotines with and without (in brackets) the assumption of character additivity. Numbers above branches reflect the percentage of 1,000 bootstrap iterations in which each clade was detected. Branch-support values are given below branches. Numbers are arranged after the type of the data matrix used (entire, 1st and 3rd value, or morphology-only, 2nd and 4th).

and posterior parapterygoid foramen anterior to hamulus (19) but with a reversal in the last two characters in *Idionycteris* and *Euderma,* respectively. The two members of the genus *Plecotus* formed the sister group to the clade comprising monotypic genera *Idionycteris* and *Euderma.* These three genera shared at least four synapomorphies: greatest braincase breadth located anteriorly (2); zygomatic arch relatively thick and strong (10); shelf-like process on lateral wall of pterygoids (18); and a paddle-like tragus with a prominent constriction near the base (42). The sister-group relationship of the highly derived *Idionycteris* and *Euderma* were indicated by at least four morphological (9, 13, 26, 32) and six karyological synapomorphies (47, 50, 51, 54, 55, 56), and several chromosomal reversals (3, 46, 48, 49, 52, 53; Appendix II). Analysis of the entire data matrix using Nixon and Carpenter's (1993) revised outgroup algorithm led to the complete separation of the ingroup and outgroup, resulting in trees of identical topology (and very similar in character transformational polarity) to those based on the Maddison et al. (1984) method.

Parsimony analysis of the morphology-only matrix showed topologies identical to those based on the entire data set, both with and without the assumption of additivity. A single most-parsimonious cladogram was 81 [78] steps long, with CI = 0.654 [0.654], RC = 0.514 [0.511], and RI = 0.786 [0.782]. In terms of homoplasy, these were similar values to those in the first analysis. Ideally, this matrix required 53 [51] steps, so 28 [27] steps must be attributed to reversals and parallelisms.

A bootstrap analysis with 1,000 iterations also resulted in a single most-parsimonious tree identical to that found in the analysis of the entire data matrix (Fig. 1). A high degree of confidence can be placed, however, in only the intrageneric branching order. Intrageneric clades were detected in ≥99% of the bootstrap iterations (Fig. 2). Repeatability of intergeneric clades, except the clade comprising *Euderma* and *Idionyc-*

teris (99–100%), was lower than the intrageneric clades and never exceeded 77% regardless of data matrices and character additivity. Bootstrap values agreed with results of branch-support analysis. All intrageneric branches of the most-parsimonious tree were well supported and at least four steps were needed to lose them in the consensus. In contrast, intergeneric branches required a minimum of two, and usually up to four, additional steps (but up to 21 steps for the clade comprised of *Euderma* and *Idionycteris*) to be collapsed (Fig. 2). In general, both methods showed better branch support or higher branch repeatability for morphology-only matrices than for the entire data set. Similar generalizations about character additivity favored ordered over unordered characters (Fig. 2).

Discussion

In general, our phylogenetic arrangement of plecotine bats was similar to that proposed by Tumlison and Douglas (1992) and contrasted with that of Frost and Timm (1992). In analysis of the entire data set, including *Otonycteris,* the most parsimonious tree suggested by Frost and Timm (1992) required four steps more than our most parsimonious tree under the assumption of additivity (length = 101; CI = 0.634; RI = 0.748) and three steps more without this assumption [length = 97; CI = 0.639; RI = 0.750]. Analysis of the entire data matrix without *Otonycteris* showed topologies similar to those based on the complete data set but with less homoplasy (length = 89 [85]; CI = 0.708 [0.718]; RI = 0.805 [0.808]). If this matrix is forced onto the tree chosen by Frost and Timm (1992), resulting statistics are: length = 92 [87], CI = 0.685 [0.701], and RI = 0.782 [0.792]. Similar analyses based on the morphology-only data matrix, including and excluding *Otonycteris,* are even more indicative.

The tree suggested by Frost and Timm (1992) fared particularly poorly, requiring 8–9 steps more under the assumption of additivity and 7–8 steps more without this assumption, being ca. 10% longer than our most parsimonious cladogram. For this group of bats, this is not surprising because morphological data appear to be at variance with karyological evidence (Qumsiyeh and Bickham, 1993). This conclusion also is supported by a bootstrap analysis (Fig. 2). The number of times out of 1,000 iterations that each clade was detected is much higher in the case of the morphology-only data matrix than with the most parsimonious topology based on the entire data set. In addition, ancestral character states in Frost and Timm's (1992) analyses were inferred from examination of an outgroup represented by several species of only one genus, *Myotis.* This approach excludes any chance to detect characters possibly derived in all *Myotis* taxa (cf. Tumlison and Douglas, 1992).

One key question concerning taxonomy of Plecotini is the systematic position of *O. hemprichii.* Miller (1907) believed that similarity of *Otonycteris* to the plecotine bats was superficial, and until quite recently, this species was considered to be either a member of Nycticeiini (e.g., Koopman, 1994) or Eptesicini (cf. Menu, 1987). Based on bacular morphology, Hill and Harrison (1987) proposed a taxonomic arrangement of Plecotini that included *Rhogeessa* (along with *Baeodon*), *Nycticeius,* and *Otonycteris* within the tribe. Nevertheless, this arrangement has been criticized for its subjectivity and lack of discussion of character transformational polarity (Frost and Timm, 1992). Recent studies based on G-banded karyotypes indicated, however, that *Otonycteris* was a plecotine bat (Qumsiyeh and Bickham, 1993; Zima et al., 1992). Karyologically, *Otonycteris, Barbastella, Plecotus,* and *Corynorhinus* appear to form one lineage of Plecotini, while the other is comprised of *Euderma* and *Idionycteris* (Qumsiyeh and Bickham, 1993; Volleth and Heller, 1994*a*; Zima et al., 1992). Placement of *Otonycteris* within traditional plecotines also was confirmed in our study, al-

though its sister relationships at least to *Barbastella* were not supported by our data. This may be because proposed karyological trees (e.g., Qumsiyeh and Bickham, 1993) have included only centric fusion events as synapomorphies. Such conditions may produce misleading phylogenies if the possibility of synapomorphic fissions is not considered (Qumsiyeh et al., 1987).

Furthermore, our study indicates that *Corynorhinus* is a valid generic designation and that *Plecotus* should be limited to species of the Palaearctic. Interestingly, removal of *Corynorhinus* from synonymy within *Plecotus* recently was suggested by Menu (1987), Frost and Timm (1992), and Tumlison and Douglas (1992), although that point of view was not accepted by Corbet and Hill (1991), Qumsiyeh and Bickham (1993), or Koopman (1993, 1994). Recent findings of *Corynorhinus* from the upper Miocene of Polgárdi, Hungary (Topál, 1989) demonstrated that this genus, currently restricted to the Nearctic, occurred in Eurasia as early as ca. 6.0×10^6 years ago. This taxon disappeared from Europe during the Betfian substage of the lower Pleistocene (Topál, 1989). Historically, *Plecotus* probably entered Europe later than *Corynorhinus,* but this speculation was based on little more than negative evidence. The first known occurrence of *Plecotus* in Eurasia dates to the lower Pliocene of Hungary (Topál, 1989). Additional support for distinction between the two genera can be found in karyological data. The karyotypes of *Corynorhinus* species include an acrocentric chromosome X and only nine pairs of autosomal metacentrics, whereas *Plecotus* species have karyotypes in which the X chromosome is submetacentric and all 10 pairs of autosomes are metacentric (López-W. et al., 1995).

Both Frost and Timm (1992) and Tumlison and Douglas (1992) found *Euderma* and *Idionycteris* to be sister taxa. However, these two revisions offered different taxonomic treatments of the two genera. Frost and Timm (1992) synonymized *Idionycteris* with *Euderma* because of their sister-taxa status and few autapomorphies. Tumlison and Douglas (1992) considered each generically distinct, following Williams et al. (1970) and Nader and Hoffmeister (1983). Although the decision ultimately is arbitrary, we concur with Tumlison and Douglas (1992) that these two highly derived taxa are sufficiently different from each other to be regarded as generically distinct (Fig. 1). This is especially evident when our data are coupled with bacular (e.g., Hill and Harrison, 1987; Nader and Hoffmeister, 1983) and additional chromosomal information (Qumsiyeh and Bickham, 1993). In fact, all the plecotine genera, including *Idionycteris,* are characterized by distinctive bacular morphology (Nader and Hoffmeister, 1983; Strelkov, 1989; Wassif and Madkour, 1972). The baculum of *Idionycteris* is two to three times as long as those of *Barbastella* and *Euderma* (N. J. Czaplewski, in litt.).

Based on phylogenetic evidence (Fig. 1), the tribe probably originated in the eastern Hemisphere. The plecotine taxa that are the most basally positioned in our cladograms (*B. barbastellus, B. leucomelas,* and *O. hemprichii*) are known from northern Africa, Europe, and a large part of Asia (Corbet and Hill, 1992; Gharaibeh and Qumsiyeh, 1995; Koopman, 1993; Rydell and Bogdanowicz, 1997). If our hypothesized topology is correct, it also would suggest that North America was invaded by a plecotine bat at least twice, probably first by *Corynorhinus* and then later by a more *Plecotus*-like ancestor of the highly derived *Euderma/Idionycteris* clade. Current geographic distributions of these genera and dates and distributions of fossil collections may indicate distinct immigration routes into both eastern (*Corynorhinus*) and western (*Euderma/Idionycteris* ancestor) North America. Present data are not sufficient to speculate further concerning place of origin, time of emergence, or probable colonization routes of these bats. Assuming the specific validity of *P. taivanus* and *P. te-*

neriffae, the following should be recognized as the appropriate and current taxonomic arrangement for plecotine bats:

Tribe Plecotini Dobson, 1875
- *Barbastella* Gray, 1821
  - *B. barbastellus* (Schreber, 1774)
  - *B. leucomelas* (Cretzschmar, 1830)
- *Otonycteris* Peters, 1859
  - *O. hemprichii* Peters, 1859
- *Corynorhinus* H. Allen, 1865
  - *C. rafinesquii* (Lesson, 1827)
  - *C. townsendii* (Cooper, 1837)
  - *C. mexicanus* G. M. Allen, 1916
- *Plecotus* E. Geoffroy Saint-Hilaire, 1818
  - *P. auritus* (Linnaeus, 1758)
  - *P. austriacus* (Fischer, 1829)
  - *P. teneriffae* Barrett-Hamilton, 1907
  - *P. taivanus* Yoshiyuki, 1991
- *Euderma* H. Allen, 1892
  - *E. maculatum* (J. A. Allen, 1891)
- *Idionycteris* Anthony, 1923
  - *I. phyllotis* (G. M. Allen, 1916)

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APPENDIX I
Specimens Examined

Specimens examined are arranged by species and country. Museum acronyms are defined in the Acknowledgments. Numbers in parentheses after the species name indicate the number of males and females examined, respectively. Preparations of specimens examined were as follows: skin and skull (s/sk); skin and skeleton (s/sb); alcoholic and skull (al/sk); alcoholic only (al); skin only (s); skull only (sk); skeleton only (sb).

Ingroup Taxa

Barbastella barbastellus (8, 3)—England: HZM 5.579 (s/sk), 7.606 (s/sk), 9.608 (s/sk) 10.703 (s/sk), 11.832 (s/sk). Germany: MCZ 37000–37001 (s/sk). Poland: AMNH 212187–89 (s/sk), the former USSR: TTU 38959 (s/sk).

Barbastella leucomelas (4, 5)—China: AMNH 44562 (s/sk). India: FMNH 34768 (al/sk), 48573 (s/sk), 82737–38 (s/sk), AMNH 163074 (s/sk). Iran: HZM 2.4415 (s/sk), the former USSR: TTU 38960 (sk), 38961 (s).

Corynorhinus mexicanus (10, 12)—Mexico: TTU 25367 (s/sk), 37939 (s/sk), 57065 (sb), KU

29848–60 (s/sk), 29890–91 (s/sk), 29915 (s/sk), 29918 (s/sk), 29923 (s/sk), 29888 (s/sk).

Corynorhinus rafinesquii (23, 27)—United States: TTU 6443 (s/sk), 9834 (s/sk), 11880–84 (s/sk), 45372 (s/sb), 45373 (sb), 45374–81 (sk), 45382 (s/sb), 45383 (s/sk), 45385 (s/sk), 45391–92 (s/sb), 45393 (s/sk), 45394–95 (s/sb), 45396–98 (s/sk), 45399 (s/sb), 45400 (s), LSUMZ 0054 (s/sk), 1395–96 (s/sk), 6258 (s/sk), 6263 (s/sk), 6792 (s/sk), 6795 (s/sk), 8733–34 (s/sk), 9305 (s/sk), 19793–94 (s/sk), 20390–91 (s/sk), 20393 (s/sk), 20396 (s/sk), 21927 (s/sb), 23793 (s/sb), 25225 (s/sb), 28462 (s/sk).

Corynorhinus townsendii (31, 30)—United States: TTU 0195 (s), 0196 (s/sk), 0198 (s/sk), 0199 (s), 0200–202 (s/sk), 0204 (s/sb), 0205 (s), 2038 (s), 3959 (s/sk), 6149 (s/sb), 6428 (s/sb), 6464 (s/sb), 6548–49 (s/sb), 6921 (s/sk), 7473 (s/sk), 8390 (s), 9148 (s/sb), 9161 (s/sb), 9835 (s/sk), 10175–76 (sb), 11555 (s/sb), 14068 (sb), 17232 (s/sk), 19957 (s/sk), 19958 (sk), 19959–61 (sb), 23277 (s/sk), 23281 (s/sk), 24639–42 (s/sk), 25797 (s/sk), 29081 (s/sk), 30260 (s/sk), 31617–18 (s/sk), 31628 (s), 31629 (s/sb), 34548–52 (s/sk), 36083 (s/sb), 38390 (sb), 38872 (sk), 40787 (s/sk), 43684–85 (s/sk), 43686 (s/sb), 47108 (s/sk), 47799 (s/sk), 58795 (s/sk), 60277 (s/sk).

Euderma maculatum (2, 5)—United States: MSB 23378 (s/sk), 24999 (s/sk), 32081–82 (al), 34284 (al), 37724 (s/sb), TTU 10447 (s/sb).

Idionycteris phyllotis (3, 8)—United States: TTU 6071 (s/sk), 6072 (s/sb), 33870 (s/sk), 35770 (s/sk), MSB 11080–82 (s/sk), 11084 (s/sk), 11635 (s/sk), 14833–34 (s/sk).

Otonycteris hemprichii (3, 4)—Jordan: MBQ 1154 (sk), 1170 (sk), 1190 (sk), 1201 (sk), 1226 (sk), the former USSR: AMNH 245380 (s/sk), TTU 38972 (s/sk).

Plecotus auritus (2, 3)—England: MCZ 13196 (s/sk). Germany: MCZ 36986–88 (s/sk), TTU 9010 (s/sk).

Plecotus austriacus (31, 10)—Tunisia: TTU 63097–63137 (s/sk).

Outgroup Taxa

Nycticeius humeralis (10, 10)—Mexico: TTU 8267 (s/sb), 8375 (s/sb), 9967 (s/sb), 9985–86 (s/sb), 10158 (s/sb). United States: TTU 7323 (s/sb), 11529 (s/sb), 11535–40 (s/sb), 11542 (s/sb), 11548 (s/sb), 11885 (s/sk), 11887–89 (s/sk).

Rhogeessa tumida (10, 10)—El Salvador: TTU 13323–32 (s/sb), 13334–36 (s/sb), 13341–42 (s/sb), 13344 (s/sb). Mexico: TTU 9979–81 (s/sb), 9983 (s/sb).

Eptesicus fuscus (10, 10)—United States: TTU 11878 (s/sk), 16114–16 (s/sk), 16691–94 (s/sk), 23018 (s/sk), 32494–97 (s/sk), 35956 (s/sk), 42642 (s/sk), 42643–47 (s/sb).

Myotis ciliolabrum (10, 10)—United States: TTU 6752 (s/sb), 7628 (s/sb), 8404–05 (s/sb), 8407–08 (s/sb), 9149 (s/sb), 9151 (s/sb), 9166 (s/sb), 9167 (s/sk), 9169 (s/sb), 9171 (s/sb), 17445 (s), 19941 (s/sk), 25695 (s/sk), 36943 (s/sk), 37221 (s/sk), 58708 (s/sk), 58055–56 (s/sk).

Myotis lucifugus (10, 10)—United States: TTU 60435 (s/sk), 60462–63 (s/sk), 60466–68 (s/sk), 60469 (s/sb), 60470 (s/sk), 60471 (s/sb), 60472–79 (s/sk), 60480 (s/sb), 60481–82 (s/sk).

Miniopterus schreibersi (10, 10)—Greece: TTU 41307 (s/sk). Croatia: TTU 49811–20 (s/sk), 49822 (s/sk), 49825 (s/sk). Zambia: TTU 18336–42 (s/sk).

APPENDIX II
List of Characters and Coding

Sources for each morphological character description are abbreviated as follows: FT—Frost and Timm (1992); TD—Tumlison and Douglas (1992); BKO—present study. Karyological characters were derived from the literature (Baker et al., 1985; Bickham, 1979; Leniec et al., 1987; Ono and Obara, 1994; Stock, 1983; Volleth, 1989; Volleth and Heller, 1994*b*; Zima et al., 1992), following a revised scheme of chromosomal complements proposed by Volleth and Heller (1994*a*). Where appropriate, the character number follows the abbreviations in accordance with the original publication. "0" is the plesiomorphic condition, unless otherwise stated.

Cranium

1. Greatest cranial depth location: (0) posterior of cranium; (1) anterior of cranium (TD-5).

2. Greatest braincase breadth location (point of widest inflation): (0) middle of braincase; (1) anterior of braincase (TD-6).

3. Braincase shape, dorsal view (anterior-posterior transition): (0) squarish, more broad posteriorly; (1) rounded, narrowing posteriorly (BKO).

4. Braincase: (0) relatively shallow, dorsal surface of skull relatively flat; (1) relatively

deep, doming prevents skull from lying flat while on dorsal surface (FT-2).

5. Sagittal crest: (0) well defined; (1) reduced to a hump; (2) absent (TD-18). We follow Tumlison and Douglas (1992) with their "present" and "absent" conditions, but we also introduced an additional intermediate state (state 1 here). The linear character transformation was hypothesized to be (0 → 1 → 2). This character is informative only under an assumption of additivity.

6. Rostrum: (0) flattened, with median concavity; (1) flattened, with slight concavity; (2) arched without median concavity (FT-1). Frost and Timm (1992) considered *Plecotus* as representing state 1 and *Corynorhinus* representing state 2; however, we concur with Handley (1959) that *Plecotus* is more representative of state 2 and *Corynorhinus* of state 1. The linear character transformation is hypothesized to be (0 → 1 → 2).

7. Premaxilla shape, lateral view: (0) truncated, rectangular; (1) sloping, triangular (TD-26). Tumlison and Douglas (1992) suggest opposite character state polarization. This character is correlated to the angle of the upper incisors, where in state 0 the incisors project ventrally and in state 1 they project somewhat anteriorly.

8. Preorbital-supraorbital region: (0) smoothly rounded or faintly ridged; (1) sharply ridged (FT-3; TD-11).

9. Temporal ridges: (0) confluent medially, interorbitally (or nearly so); (1) not confluent medially, with distinct muscle scars (FT-4).

10. Fragility of zygomatic arch: (0) relatively thin and fragile; (1) relatively thick and strong (FT-5).

11. Zygomatic arch: (0) postorbital expansion absent; (1) expansion on middle third of arch; (2) expansion on posterior third of arch (FT-6; TD-13). We follow Tumlison and Douglas (1992) with the three character states. Frost and Timm (1992) combined states 0 and 1 into a single state. The linear character transformation is hypothesized to be (0 → 1 → 2).

12. Zygomatic arch shape, lateral view: (0) straight, nearly level with toothrow; (1) bowed dorsally (BKO).

13. Auditory bullae shape, lateral view: (0) roughly circular in outline, slightly enlarged; (1) enlarged, slightly elongate; (2) enlarged and elliptical (FT-7; TD-15). We follow Frost and Timm (1992) with the three states. Tumlison and Douglas (1992) consolidated states 0 and 1 into the single "round" condition. The linear character transformation is hypothesized to be (0 → 1 → 2).

14. Anterior border shape of auditory bullae: (0) pointed; (1) rounded (TD-4).

15. Medial aspect of auditory bullae: (0) smooth; (1) emarginated (TD-14). Contrary to Tumlison and Douglas (1992), we found that *Idionycteris* and *Corynorhinus* exhibited emarginated bullae.

16. Hamulus position on pterygoids: (0) curves medially, with bulge on inner edge; (1) straight and parallel with longitudinal axis of skull (TD-1).

17. Lateral borders of pterygoids to longitudinal axis of skull: (0) angled medially; (1) vertical (TD-2).

18. Pterygoids: (0) shelf-like process on lateral wall absent; (1) process present (TD-17).

19. Posterior parapterygoid foramen: (0) behind or even with posterior extent of hamulus of pterygoid; (1) anterior to hamulus (TD-27).

20. Shape of anterior nasal opening, dorsal view: (0) round; (1) bell-shaped; (2) trapezoid (BKO). The linear character transformation is hypothesized to be (0 ← 1 → 2).

21. Posterior extension of anterior naris: (0) vomer septum not exposed; (1) positioned so far back as to expose vomer septum (FT-15).

22. Anterior palate: (0) ventral emargination of nasal opening extends to canines; (1) emargination extends past canines (TD-22).

23. Medial roof of pharynx (presphenoid and basisphenoid): (0) flat; (1) convex (BKO).

24. Basial pits in basioccipital: (0) absent; (1) present (FT-17; TD-16). Tumlison and Douglas (1992) suggest state 1 to be ancestral.

25. Position of infraorbital foramen: (0) perpendicular to the junction between P4–M1; (1) perpendicular to middle of M1 (BKO).

26. Infraorbital plate: (0) ridge absent, forming smooth hump, or simple ridge without a process; (1) ridge twisted, forming a process dorsoposterior to infraorbital foramen (TD-24). We concur with Tumlison and Douglas (1992) for states 0 and 1, although we add the "ridge absent" term to state 0.

27. Secondary cusp on I1: (0) present, separated by a notch; (1) present as a ridge or shoulder; (2) absent (BKO). *Corynorhinus townsendii* exhibits all three states. The linear character

transformation is hypothesized to be (0 → 1 → 2).

28. Posterolingual part of upper last premolar (P4): (0) not reduced; (1) reduced (FT-9 in part; BKO). This and the subsequent character (No. 29) were combined into a single character by Frost and Timm (1992). However, we found that *Euderma* could not be placed into a single state when these two characters are joined.

29. Upper last premolar (P4): (0) wider than long; (1) approximately equal to or longer than wide (FT-9 in part; TD-28). We concur with Tumlison and Douglas (1992).

30. Metacone of upper third molar (M3): (0) present; (1) greatly reduced or absent (FT-10). We follow Frost and Timm (1992) for these states, but we also add the condition of "greatly reduced" to state 1.

Mandible

31. Angle of dentary, lateral view: (0) curved; (1) straight (TD-9).

32. Coronoid process shape, lateral view: (0) smoothly rounded or pointed; (1) projection posteriorly, forming a squarish coronoid process (TD-8). We alter state 1 ("with hook-like process") of Tumlison and Douglas (1992) as indicated. In our opinion, this better describes the shape of the entire coronoid process in lateral view, and places *Idionycteris* into the state 1 condition.

33. Bone connection from coronoid to condyle on lateral side of dentary: (0) straight; (1) slightly to moderately decurved; (2) strongly decurved (TD-12). The linear character transformation is hypothesized to be (0 → 1 → 2).

34. Angular process, dorsal view: (0) prominent tubercle on anterolateral surface present; (1) tubercle on anterolateral surface absent (TD-10). Tumlison and Douglas (1992) suggest state 1 to be ancestral. Because of intraspecific variation, we added "lateral" in describing the presence of the tubercle. This addition places *Plecotus* into a different state when compared with Tumlison and Douglas (1992).

35. Anterointernal cusp of lower canine (c1): (0) relatively large, 55–66% the height of primary cusp; (1) small, greatly exceeded by primary cusp; (2) cusp absent (FT-11). We follow Frost and Timm (1992) for states 0 and 1, although we add state 2 for *Otonycteris*. Based on the outgroup comparison, the linear character transformation should be (0 ← 1 → 2; but see Frost and Timm, 1992).

36. Last lower premolar (p4): (0) double-rooted; (1) single-rooted (FT-14; TD-20). We follow Handley (1959) and Tumlison and Douglas (1992) in that *Corynorhinus* has the "single-rooted" state of this character, contrasting the "double-rooted" condition for *Corynorhinus* indicated by Frost and Timm (1992).

37. Paraconid of lower p4: (0) cusp-like in appearance, projecting anteriolingually; (1) reduced into cingulum (BKO).

External

38. Second phalanx of third digit: (0) less than or equal in length to the first; (1) much longer than the first (FT-19; TD-31). We concur with Tumlison and Douglas (1992), including *Barbastella* under state 1, contrary to Frost and Timm (1992) who indicated that *Barbastella* exhibited state 0.

39. Muzzle glands: (0) absent or slightly visible; (1) present, but not greatly enlarged; (2) greatly enlarged (FT-21). The linear character transformation should be (0 → 1 → 2) as taken from outgroup comparison.

40. Size of auricles: (0) small; (1) extremely enlarged (FT-22; TD-30). Our outgroup analysis suggests that the small ear is ancestral (but see discussion in Qumsiyeh and Bickham, 1993).

41. Auricles: (0) unjoined at midline; (1) joined at midline (BKO).

42. Tragus: (0) narrow, blade-like, no prominent constriction near the base; (1) more paddle-like, a prominent constriction near the base (FT-23). We do not use the "intermediate" condition (state 1 of Frost and Timm, 1992). The emphasis is towards the "prominent constriction" near the base of the tragus.

43. Anterior basal lobe of auricle: (0) complete; (1) reduced to absent (BKO).

44. Accessory anterior basal lobe of auricle: (0) absent; (1) present (FT-24).

45. Transverse ribs of auricle: (0) reaching posterior border uninterrupted by vertical rib; (1) interrupted by vertical rib near posterior border (FT-25). We follow Handley (1959) and Frost and Timm (1992) for the condition of the transverse ribs. Outgroup taxa not having transverse ribs on the auricle were coded as having state 0.

Chromosomes

46. Chromosome arms 7 and 19: (0) unfused; (1) fused.

47. Chromosome arms 8 and 18: (0) unfused; (1) fused.

48. Chromosome arms 8 and 21: (0) unfused; (1) fused.

49. Chromosome arms 9 and 12: (0) unfused; (1) fused.

50. Chromosome arms 9 and 13: (0) unfused; (1) fused.

51. Chromosome arms 10 and 12: (0) unfused; (1) fused.

52. Chromosome arms 10 and 15: (0) unfused; (1) fused.

53. Chromosome arms 13 and 18: (0) unfused; (1) fused.

54. Chromosome arms 15 and 21: (0) unfused; (1) fused.

55. Chromosome arms 19 and 22: (0) unfused; (1) fused.

56. Chromosome arms 20 and 23: (0) unfused; (1) fused.

The following 15 characters from the studies by Frost and Timm (1992), Tumlison and Douglas (1992), and Volleth and Heller (1994*a*) were not used:

1. TD-18, modified: sagittal crest being coded as well defined (state 0), reduced to a hump (state 1), or absent (state 2). The linear character transformation was hypothesized to be (0 → 1 → 2). The states 1 and 2 were present only in *I. phyllotis* and *E. maculatum,* respectively. This character has been excluded only from the analyses utilizing the assumption of lack of additivity; it is retained in analyses where additivity is assumed.

2. TD-23: infraorbital foramen relatively small and round (state 0) or large and oval (state 1). Eliminated because of an equivocal state at the outgroup node.

3. TD-7: spine at anterior tip of nasals absent (state 0) or present (state 1). Autapomorphy of *I. phyllotis.*

4. FT-16: the median postpalatal process being coded as a weak single spine (state 0), a prominent single spine (state 1), a bifid prominence (state 2), or absent (state 3). Frost and Timm (1992) could not order this character. More importantly, there is considerable variability expressed in this character, even within species (R. Tumlison, in litt.; our observations).

5. TD-19: pterygoid hamulus in lateral view extending as a process (state 0) or broadly connected to pterygoid (state 1). Autapomorphy of *I. phyllotis.*

6. FT-8: upper incisors I2 and I1 are subequal (state 0), I1 is much longer than I2 (state 1), or I2 is missing (state 2). We followed Frost and Timm (1992) for states 0 and 1, although we added state 2 (I2 missing) for *Otonycteris.* Equivocal state found at outgroup node.

7. TD-25: upper canine (C1) longer than P4 (state 0) or shorter than P4 (state 1). Autapomorphy of *E. maculatum.*

8. TD-3: upper premolar P3 in line with toothrow (state 0), offset from toothrow (state 1), or absent (state 2); we introduce state 2 (P3 absent) for *Otonycteris.* Equivocal state found at outgroup node.

9. FT-13: lower premolar p3 present (state 0) or absent (state 1). Equivocal state found at outgroup node.

10. FT-12: the cross-sectional outline of the lower third premolar (p3) being coded as undistorted (state 0), distorted (state 1), or as unknown (?) when lacking the lower p3. We found that "distorted" is too subjective, finding no clear distinction for the distortion for any species. Also, since *Barbastella, Euderma,* and *Otonycteris* lack the p3, we consider that this increases the ambiguity of the character states.

11. FT-18: manubrium as wide or wider than long (state 0) or distinctly longer than wide (state 1). Because we did not have sufficient post-cranial skeletal preparations available to us for all species, and because we elected to confirm all characters and states by examination, we were unable to include post-cranial skeletal characters.

12. FT-20: nostril unspecialized (state 0) or with a large posterior elongation with conspicuous shallow basin posteriad, separated by a septum (state 1). Equivocal state found at outgroup node.

13. FT-21: the length-width relationship of the external narial vacuities in dorsal view being coded as wider than long (state 0) or longer than wide (state 1). We found too much variation in scoring each of the two states at the specific level.

14. TD-32: the posterior basal lobe of auricle not attached (state 0) or attached to base of tragus (state 1). Autapomorphy of *E. maculatum.*

15. Chromosome arms 11 and 14 unfused (state 0) or fused (state 1). Synapomorphy of the entire tribe (Volleth and Heller, 1994*a*).