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# GENIC STUDIES OF LASIURUS (CHIROPTERA: VESPERTILIONIDAE)

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Bats of the genus *Lasiurus* present a number of interesting systematic problems that are difficult to resolve by traditional techniques. Members of the genus share a suite of derived morphological (Hall and Jones, 1961; Handley, 1960) and karyotypic (Bickham 1979, 1988) characteristics. However, until 1960 (Handley, 1960), members were placed in two genera—*Lasiurus* and *Dasypterus*—based primarily upon the presence or absence of the small, first upper premolar. Handley (1960) analyzed the differences and similarities among these two genera and concluded they were not distinct even at a subgeneric level. One goal of this study was to provide an estimate of genetic differentiation among the more divergent taxa in *Lasiurus*.

Additionally, a number of species-level taxonomic problems exist within the genus. *Lasiurus borealis* and *L. seminolus* are broadly sympatric in the eastern United States. They are morphologically similar, both externally and cranially, to the extent that they properly may be described as sibling species. Some workers, in fact, have suggested that these two taxa may represent only color phases of a single species.

The zoogeographic affinities of bats of the Antillean Islands were reviewed by Baker and Genoways (1978) and several problem species groups were noted. One of the taxa that needed more study included the several populations recognized by Varona (1974) as *Lasiurus borealis*. Representatives of this group of bats

are found on all Greater Antillean Islands and populations from each island have, at some time in the past, been accorded specific distinction. Varona (1974), without providing any supporting data, reduced all red bats from the Antillean Islands to subspecies of *L. borealis.*

A chromosomal difference exists between two currently recognized subspecies of *Lasiurus ega* that may signal these two taxa as specifically distinct (Baker and Patton, 1967; Baker *et al.*, 1971). The X-chromosome of *L. e. xanthinus* from western México is submetacentric and resembles that of most vespertilionid bats, whereas in *L. e. panamensis* from southern Texas and eastern and southern México the X is acrocentric or subtelocentric, having undergone a pericentric inversion (Bickham, 1979, 1988).

This study examines the genic relationships of *Lasiurus borealis* (including specimens from Jamaica, Venezuela, Baja California, and the eastern United States), *L. seminolus, L. cinereus, L. ega* (including specimens from Suriname, Venezuela, Central America, and México), and *L. intermedius.* The choice of taxa was designed to give the kind of data necessary to examine the problems outlined above. Also, representatives of other vespertilionid genera were examined to provide outgroups for cladistic analysis (Hennig, 1966) in an attempt to better document the evolutionary relationships of the taxa of *Lasiurus* studied.

## Methods and Materials

Methods for tissue preparations, starch gel electrophoresis, and enzyme designations were similar to those of Selander *et al.* (1971) except for creatine kinase (CK) and peptidase (PEPT), which were described by Avise *et al.* (1980). PEPT-1 represents the most cathodally-migrating peptidase using the substrate L-leucyl-L-alanine; PEPT-2 and -3 represent the two most anodal zones of activity using the substrate leucyl-glycyl-glycine. Twenty-two presumptive loci, consisting of enzymatic and nonenzymatic proteins, were assayed (Table 1) as follows: CK-1, CK-2, CK-3, alpha-glycerophosphate dehydrogenase ($\alpha$-GPD), glucose-6-phosphate isomerase (GPI), amino asparate transaminase-1, 2 (AAT-1, AAT-2) superoxide dismutase-1, 2 (SOD-1, SOD-2), isocitrate dehydrogenase-1, 2 (ICD-1, ICD-2), lactate dehydrogenase-1, 2 (LDH-1, LDH-2), malate dehydrogenase-1, 2 (MDH-1, MDH-2), mannosephosphate isomerase (MPI), PEPT-1, PEPT-2, PEPT-3, phosphoglucomutase-1, 2 (PGM-1, PGM-2), 6-phosphogluconate dehydrogenase (6-PGD).

TABLE 1.—*Relative mobility of alleles for loci determined polymorphic within the genus* Lasiurus. *Where samples were polymorphic frequency of each allele is given in parenthesis. Monomorphic loci for* Lasiurus *were LDH-1,2; AAT-1,2; MDH-1,2 CK-2,3; SOD-1; PEPT-3.*

| Locus | (1) *blossevillii* | (2) *blossevillii* | (3) *borealis* | (4) *degelidus* | (5) *seminolus* | (6) *cinereus* | (7) *xanthinus* | (8) *ega* (Mx) | (9) *ega* (SA) | (10) *intermedius* | (11) *P. subflavus* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ICD-1 | 105 | 105 | 100 | 120 | 120 | Null | 145(.25)<br>140(.68)<br>120(.07) | 120 | 130(.08)<br>120(.92) | 130 | 150 |
| ICD-2 | −100 | −100 | −100 | −90 | −90 | −90 | −90 | −90 | −90 | −90 | −60 |
| 6PGD | 100 | 100(.64)<br>90(.36) | 100(.79)<br>90(.21) | 50(.50)<br>30(.50) | 80 | 100 | 110(.06)<br>90(.94) | 110(.75)<br>90(.25) | 110(.16)<br>90(.84) | 110(.33)<br>90(.67) | 140 |
| α-GPD | 40 | 100(.67)<br>80(.33) | 100 | 100 | 100 | 105 | 103(.10)<br>60(.90) | 60 | 60 | 103 | 120 |
| GPI | 50 | 50 | 100 | 100 | 100 | 48 | 45 | 125 | 125 | 125 | 130 |
| MPI | 110 | 110 | 100 | 110 | 100 | 100 | 140 | 100 | 100 | 100 | 80 |
| PGM-1 | 100 | 100 | 100 | 90 | 90 | 95(.75)<br>90(.25) | 92(.15)<br>90(.85) | 105(.16)<br>92(.68)<br>80(.16) | 92 | 85 | 140 |
| PGM-2 | 100 | 100 | 100 | 100 | 100 | 80 | 75 | 100 | 100 | 100 | 125 |
| CK-1 | 100 | — | 100 | 100 | 100 | — | — | — | 130 | 130 | — |
| SOD-2 | 100 | 100 | 100(.86)<br>−300(.14) | 200 | 200 | Null | 250 | 200 | 200 | 200 | 150 |
| PEPT-1 | 100 | 100 | 100 | 100 | 100 | 80 | 80 | 80 | 80 | 80 | 210 |
| PEPT-2 | 100 | 100 | 100 | 100 | 105(.25)<br>100(.75) | 100 | 95 | 100(.33)<br>95(.67) | 100(.25)<br>95(.75) | 100(.17)<br>95(.83) | 100 |

Electromorph (allele) frequencies of 21 loci (CK-1 was excluded) were calculated from banding patterns. Nei's Identity (*I*) and Distance (*D*) matrices (Nei, 1972) were generated using modifications suggested by Hillis (1984). Cladistic analysis (Buth, 1984; Derr *et al.*, 1987; Patton *et al.*, 1981) was performed by hand using discrete character-state coding in which the locus was considered the character and the allelic composition of the locus was the character state. Additionally, side-by-side comparisons of alleles in *Lasiurus* were run with samples from *Myotis velifer, M. thysanodes, M. yumanensis, M. nigricans, M. dominicensis, Pipistrellus subflavus, Nycticeius humeralis,* and *Eptesicus fuscus*. Except as related to genic evolution in the genus *Lasiurus* (identification of unique alleles and the primitive and derived conditions for outgroup comparison), the details of the electrophoretic data from the other genera of vespertilionids are beyond the scope of this report.

## Results

Twenty-two electrophoretic loci were assayed. Loci found to be monomorphic for all *Lasiurus* examined, were as follows: LDH-1, -2; AAT-1, -2; MDH-1, -2; CK-2, -3; PEPT-3; SOD-1. Of these 10, three (AAT-1, CK-2, and SOD-1) distinguish *Lasiurus* from samples of the other four genera of Vespertilioninae examined. Electrophoretic data for the 12 polymorphic loci from the 10 samples are summarized in Table 1. None of the loci that was found to be polymorphic in *Lasiurus* shared an allele with other species of Vespertilioninae except PEPT-2 of *Pipistrellus*. Pairwise comparisons for Nei's Identity (*I*) and Distance (*D*) for the 10 samples are given in Table 2. The electrophoretic data are summarized phenetically (Fig. 1) by use of the unweighted pair-group method of analysis (UPGMA—Sneath and Sokal, 1973) and cladistical analysis (Fig. 2) by the methods of Hennig (1966), Patton *et al.* (1981), and Buth (1984).

## Discussion

Two aspects of our biochemical data support Handley's (1960) conclusion that yellow bats and red bats are congeneric. First, representatives from the two formerly recognized genera, *Dasypterus* and *Lasiurus*, are not more divergent from each other than *L. borealis* is from *L. cinereus* (species that were considered congeneric in the older classification). Second, the magnitude of biochemical divergence that distinguishes the three lineages in

TABLE 2.—*Genetic distances (upper right) computed using the modification of Hillis (1984) of the formulae. Genetic identities (Nei, 1982) lower left, for data given in Table 1 and text.*

| | blo (1) | blo (2) | bor (3) | deg (4) | sem (5) | cin (6) | xan (7) | ega (8) | ega (9) | int (10) | sub (11) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *L. blossevillii* (Ven) | | .055 | .222 | .405 | .484 | .560 | .742 | .607 | .618 | .629 | 1.10 |
| 2. *L. blossevillii* (NA) | .946 | | .168 | .343 | .417 | .540 | .694 | .694 | .577 | .590 | 1.10 |
| 3. *L. borealis* | .801 | .845 | | .337 | .275 | .482 | .738 | .518 | .515 | .526 | 1.10 |
| 4. *L. degelidus* | .667 | .709 | .714 | | .103 | .530 | .550 | .347 | .383 | .464 | 1.10 |
| 5. *L. seminolus* | .617 | .695 | .760 | .902 | | .456 | .550 | .330 | .321 | .398 | 1.11 |
| 6. *L. cinereus* | .571 | .565 | .617 | .589 | .634 | | .533 | .446 | .756 | .469 | 1.10 |
| 7. *L. xanthinus* | .476 | .500 | .478 | .577 | .577 | .587 | | .366 | .323 | .405 | 1.25 |
| 8. *L. ega* (Mex) | .545 | .551 | .596 | .688 | .736 | .640 | .694 | | .028 | .123 | 1.18 |
| 9. *L. ega* (SA) | .539 | .562 | .597 | .682 | .725 | .634 | .724 | .973 | | .152 | 1.20 |
| 10. *L. intermedius* | .533 | .554 | .591 | .629 | .672 | .629 | .667 | .841 | .859 | | 1.22 |
| 11. *P. subflavus* | .333 | .333 | .333 | .333 | .331 | .333 | .286 | .307 | .301 | .295 | |

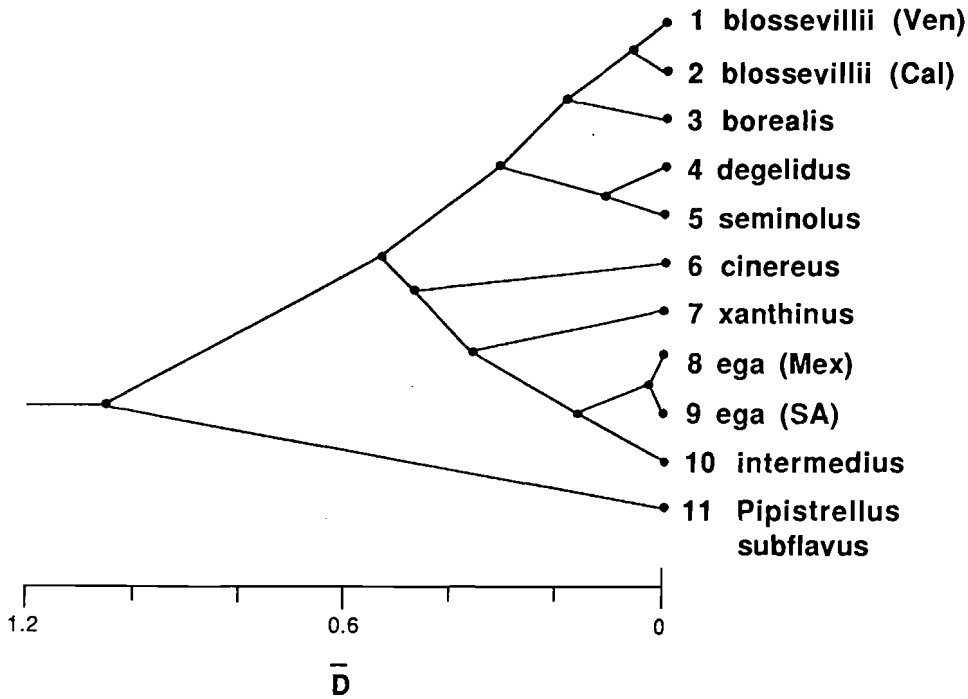


FIG. 1.—Phenogram generated from the electrophoretic data using average Nei's distance values ($\bar{D}$) and a UPGMA clustering analysis.

the genus *Lasiurus* is well within the range of divergence that characterizes comparisons of congeneric species of bats as well as other mammals (Arnold *et al.*, 1982, 1983; Avise, 1974; Baker *et al.*, 1981, 1985; Honeycutt *et al.*, 1981; Koop and Baker, 1983; Straney *et al.*, 1979). If only biochemical data were used as a basis for a systematic arrangement, the best alternative (because of the low level of genic differences that distinguish the three groups) would be to recognize a single genus with no subgenera (Fig. 1) and the second best arrangement would be to recognize three subgenera—1) *Lasiurus*, containing the red bats (distinguished by three shared fixed differences), 2) *Dasypterus*, including the yellow bats (distinguished by six shared fixed differences), and 3) a third subgenus containing the hoary bats (distinguished by six shared fixed differences). Essentially, our biochemical data are in agreement with Hall and Jones (1961), who proposed the early phylogeny of *Lasiurus* as consisting of three primary lineages.

### *Species-level Problems*

*Red bats.*—As only PEPT-$2^{100}$ was shared among *Lasiurus* and other vespertilionine genera examined, it was rarely possible to determine which of the electromorphs was primitive or derived in

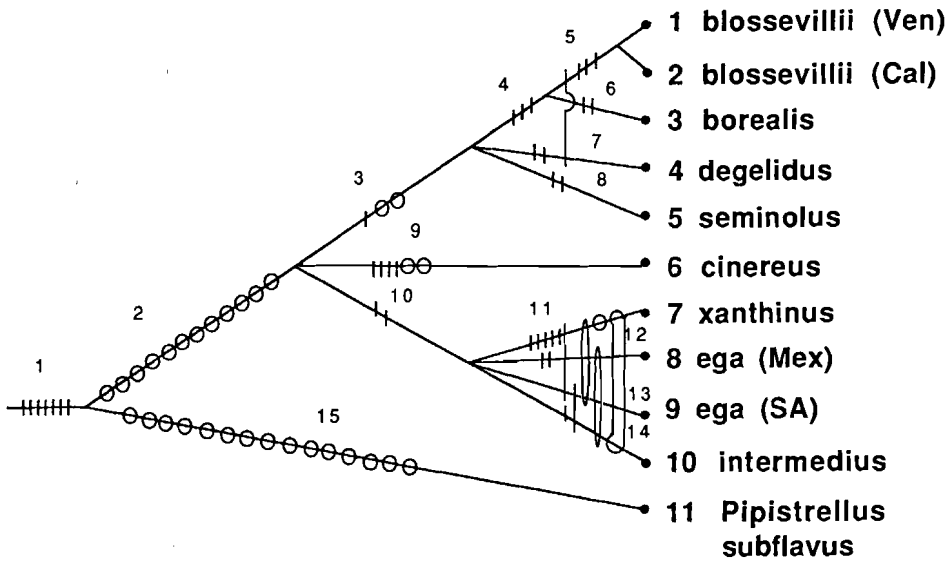


FIG. 2.—Phylogenetic tree generated by qualitative analysis of characters given in Table 3 and text using the method of Hennig (1966) and Patton *et al.* (1980). See Table 3 for definition of character states.

*Lasiurus*. Therefore, the functional outgroups for the red bats (*L. borealis, L. seminolus,* and the Jamaican *Lasiurus*) were restricted to the yellow bats (*L. ega* and *L. intermedius*) and *L. cinereus,* and for the yellow bats, the red bats and hoary bat served as the outgroups. Nonetheless, our data reveal patterns that have systematic implications.

Within *L. borealis* (as currently recognized), there is a significant genic demarcation between our samples from the eastern United States (Texas, South Carolina, and Georgia) and those from New Mexico, México, and South America. Eastern United States samples are separated from the New Mexican, Mexican, and Venezuelan samples by identity values at the 0.80 and 0.85 levels. Although the New Mexican, Mexican, and Venezuelan samples are separated by much greater geographic distance, their similarity values are much higher (0.95). Differences in ICD-1, GPI, and MPI are fixed between the populations in our samples. Cryptic species of other mammalian groups have similarity values in the range found in our comparison of South American-Mexican-New Mexican samples with those from the eastern United States (Avise, 1974).

Schmidly and Hendricks (1984) have demonstrated morphometric differences between eastern and western populations of *L. borealis*. Their samples from eastern Texas, representing *L. b. borealis,* were significantly larger in five of six cranial measure-

TABLE 3.—*Electromorphs defining root and branches of phylogenetic tree represented by Fig. 2 as defined by Hennig (1966) and modified by Patton,* et al. *(1981). Characters representing assumed apomorphs (phenetically placed characters) are enclosed in brackets. Characters that must be strictly interpreted (in a cladistic sense) as ambiguous are italicized.*

| | |
|---|---|
| 1. | LDH-$1^{100}$, LDH-$2^{-100}$, MDH-$1^{100}$, MDH-$2^{-100}$, AAT-$2^{-100}$, CK-$3^{100}$, PEPT-$2^{100}$ |
| 2. | [ICD-$1^{120}$, ICD-$2^{-90}$, 6PGD$^{100}$, AAT-$1^{100}$, CK-$2^{100}$, MPI$^{100}$, PGM-$1^{90}$, PGM-$2^{100}$, SOD-$1^{100}$, SOD-$2^{200}$, PEPT-$2^{100}$, PEPT-$1^{80}$] |
| 3. | $\alpha$GPD$^{100}$, [GPI$^{100}$, PEPT-$1^{100}$] |
| 4. | ICD-$2^{-100}$, PGM-$1^{100}$, SOD-$2^{100}$ |
| 5. | ICD-$1^{105}$, $\alpha$GPD$^{80}$, GPI$^{50}$, *MPI*$^{110}$ |
| 6. | ICD-$1^{100}$, SOD-$2^{-300}$ |
| 7. | 6PGD$^{50}$, 6PGD$^{30}$, *MPI*$^{110}$ |
| 8. | 6PGD$^{80}$, PEPT-$2^{105}$ |
| 9. | ICD-$1^{null}$, PGM-$1^{95}$, PGM-$2^{80}$, SOD-$2^{null}$, [$\alpha$GPD$^{105}$, GPI$^{48}$] |
| 10. | 6PGD$^{110}$, PEPT-$2^{95}$ |
| 11. | ICD-$1^{145}$, ICD-$1^{140}$, MPI$^{140}$, PGM-$2^{75}$, SOD-$2^{250}$, *PGM-1*$^{92}$, [*GPI*$^{45}$, *$\alpha$GPD*$^{103}$, *$\alpha$GPD*$^{60}$] |
| 12. | PGM-$1^{105}$, PGM-$1^{80}$, *PGM-1*$^{92}$, [*GPI*$^{125}$, *$\alpha$GPD*$^{60}$] |
| 13. | *ICD-1*$^{130}$, *PGM-1*$^{92}$, [*GPI*$^{125}$, *$\alpha$GPD*$^{60}$] |
| 14. | PGM-$1^{85}$, *ICD-1*$^{130}$, [*GPI*$^{125}$, *$\alpha$GPD*$^{103}$] |
| 15. | [ICD-$1^{150}$, ICD-$2^{-60}$, 6PGD$^{150}$, $\alpha$GPD$^{120}$, AAT-$1^{120}$, GPI$^{130}$, MPI$^{80}$, PGM-$1^{140}$, PGM-$2^{175}$, SOD-$1^{175}$, SOD-$2^{150}$, PEPT-$2^{105}$, PEPT-$1^{210}$] |

ments of males and all six measurements of females than three samples of *L. b. teliotis,* including two from Tamaulipas in northeastern México. The western populations also differ from those to the east in pelage characteristics, including rusty-red rather than brownish dorsal coloration, noticeably fewer frosted dorsal hairs, and the posterior margin of the uropatagium is bare or only sparsely haired rather than well furred to the posterior margin (Bogan and Williams, 1970).

Based on these significant morphological and genic differences, we believe that the western and eastern populations of *L. borealis* are best considered distinct species. The specific name *L. borealis* is here restricted to eastern populations designated *L. b. borealis* by Hall (1981), but regarded by us as a monotypic species. The senior synonym for the western populations is *Vespertilio blossevillii* Lesson and Garnot, 1826 (type locality Montevideo, Uruguay). The appropriate trinomials for populations examined

in our study would be *Lasiurus blossevillii teliotis* and *Lasiurus blossevillii frantzii*. Researchers should be alert for sympatric populations or indication of hybridization between these two species in southwestern New Mexico, western Texas, and northeastern México.

*Lasiurus borealis* has a similarity level with *L. seminolus* of 0.76 (including five fixed differences—ICD-1, -2; 6 PGD; PGM-1; SOD-2), which is compatible with the conclusion that the *seminolus* and *borealis* represent distinct species, not sympatric color phases of a single species. Specimens of *Lasiurus* from Jamaica have a similarity with mainland populations of *L. borealis* of 0.71 and with *L. blossevillii* of 0.67 (Table 2), which implies that *L. degelidus* is best recognized as a species distinct from both *borealis* and *blossevillii*. However, *Lasiurus* from Jamaica have a much higher similarity level (0.90) with *L. seminolus*; therefore, another possibility would be to recognize *L. degelidus* as a race of *L. seminolus*. Cladistic analysis of the alleles (ICD-$1^{120}$, ICD-$2^{90}$, and SOD-$2^{200}$) shared by *seminolus* and *degelidus*, but which are distinct from those of *L. borealis*, failed to provide any data that document these shared alleles as derived (synapomorphies). Additionally, a cladistical analysis of the one character ($MPI^{110}$) shared by *borealis* and *degelidus*, but not present in *seminolus*, indicates that $MPI^{100}$ of *seminolus* is primitive. This means that, although there is a higher similarity value for *degelidus* and *seminolus*, cladistic characters (synapomorphies) ally *degelidus* more closely with *borealis* than with *seminolus*. However, due to the possibility of an ancestral $MPI^{100,110}$ polymorphism, it still is possible that *degelidus* arose from a *seminolus* stock rather than a *borealis* stock. Specimens of *borealis* and *seminolus* differ morphologically in that *borealis* possesses a protuberance along the anterior border of the lachrymal ridge (Hall, 1981: fig. 178). Examination of a specimen from St. Ann Parish, Jamaica (TTU 22080), and one from Department du Sud, Haiti (TTU 22804), revealed that the condition of lachrymal ridge in these specimens most closely resembles that of *L. seminolus*.

Specimens of *borealis* and *seminolus* traditionally have been distinguished on the basis of pelage color, but this character is not definitive in that the specimen from Jamaica most closely resembles *seminolus* and the one from Haiti most closely resembles *borealis*. We conclude that, in light of the above data, the best course is to recognize *L. degelidus* as a distinct species,

but future data should be evaluated in light of the possibility that *degelidus*, as well as other Antillean populations, may be subspecies of *L. seminolus*. Of course, data from Cuban, Hispaniolan, Puerto Rican, and Bahamian red bats are needed before final decisions can be made.

*Yellow bats.*—Electrophoretic data for yellow bats suggest a dichotomy within *Lasiurus ega* that, in our opinion, signals specific differences. Although specimens of *L. ega* from Venezuela and Suriname are geographically widely separated from those from Chiapas and Guerrero, similarity values are at the level (0.97) expected for conspecific populations and no fixed differences were found between the two groups. On the other hand, specimens of *L. e. xanthinus* from Baja California and Neuvo León, are fixed for four different alleles from other samples currently recognized as *L. ega* ($GPI^{45}$, $SOD\text{-}2^{250}$, $MPI^{140}$, $PGM\text{-}2^{75}$) and have a low (0.69 to 0.72) similarity to the other Mexican and South American samples.

Also of interest is the high level of similarity 0.84 and 0.86 between *L. intermedius* and the South American and southern Mexican specimens of *L. ega*. There is no doubt that *ega* and *intermedius* are recognizable, widely sympatric species. However, if electrophoretic data were used to indicate systematic position, we would conclude that *L. ega* (which has an acrocentric X cytotype) is more closely related to *L. intermedius* than to what currently is known as *L. e. xanthinus* (which has a biarmed X cytotype) (Fig. 1). *Lasiurus intermedius* possesses an acrocentric X chromosome that apparently has evolved by a pericentric inversion. Within vespertilionids, a submetacentric X chromosome is considered the primitive condition with the acrocentric condition having evolved independently in several genera (Baker, 1970; Bickham, 1979, 1988; McBee *et al.*, 1986).

The most parsimonious explanation of the evolution of the inverted X in two species of *Lasiurus* is to postulate a common origin for those taxa (*L. intermedius* and *L. e. panamensis*) as indicated also by electrophoretic data. However, it is also obvious that an acrocentric X has evolved at least twice (McBee *et al.*, 1986) in vespertilionids (to explain its presence in some species of *Plecotus* and in some species of *Lasiurus*), and the possibility of convergent evolution in *Lasiurus* cannot be ruled out. That congruence occurs within the electrophoretic and chromosomal data sets for the yellow bats suggests the possibility of common ancestry for the taxa of *Lasiurus* with an inverted acrocentric X

(*L. ega* and *L. intermedius* shared a common ancestry after separating from *L. xanthinus*) should remain a viable systematic hypothesis.

We believe that the appropriate interpretation of these data is to recognize *L. xanthinus* (type locality Sierra Laguna, Baja California) as a species distinct from *L. ega*. It is distinguished from *ega* by a submetacentric X-chromosome and genically by four fixed electromorphs (Table 1). Morphologically the two species are distinguished by pelage coloration, which is a brighter yellow, especially on the anterior third of the uropatagium, in most specimens of *L. xanthinus*. Comparing measurements of the two taxa from the published literature, it appears that the only measurement that may distinguish them is length of the maxillary toothrow, means for females (with extremes in parentheses) are as follows: *L. xanthinus* from Baja California, 5.7 (5.4 to 5.9) (Jones *et al.*, 1965) and Arizona, 5.9 (5.8-6.0) (Hoffmeister, 1986) as compared to *L. ega* from Texas, 5.4 (5.1 to 5.6) (Baker *et al.*, 1971) and Tamaulipas, 5.4 (5.4 to 5.5) (Schmidly and Hendricks, 1984, who originally assigned this population to *L. e. xanthinus* but we believe it is best considered as *L. e. panamensis*). Although the level of morphological distinctiveness for *xanthinus* and *ega* is not as great as is usually characteristic of currently recognized mammalian species, the degree of genic differences, which are fixed in our samples, is similar to that found in sympatric species of another vespertilionid bat, *Rhogeessa*, for which no morphological differences have been found (Baker, 1984).

Ecologically, *L. xanthinus* seems to be associated with the dry thorny vegetation of the Mexican Plateau, coastal western México including parts of Baja California, and the deserts of the southwestern United States. In the data available to us, the easternmost record of this species is from 20 mi. N Santa Anna, Nuevo León (this paper), and the southernmost record is from Oaxtepec, Morelos (Baker and Patton, 1967). We would expect potential sympatry or hybridization between *L. xanthinus* and *L. ega* along the eastern and southern edges of the Mexican Plateau. We believe that *L. e. panamensis* occupies the Gulf versant as far north as 5 mi. SE Brownsville, Texas; in southern México this taxon occupies both versants as well as most if not all of the intervening highlands.

*Hoary bats.*—Although our sample of *L. cinereus* included specimens from three states within the United States and two

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