PHENETIC ANALYSES OF THE BAT SUBFAMILY STENODERMATINAE (CHIROPTERA: PHYLLOSTOMIDAE)

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ABSTRACT.—The 64 species of stenodermatine bats were analyzed phenetically under the common-part-removed transformation of Wood (1983). Two clustering techniques, two ordination techniques, and a minimum-spanning tree were employed to assess patterns of overall similarity among species. Phenetic relationships within and among genera were discussed, and these relationships were compared to the phylogenetic classification proposed by Owen (1987*a*). Most of the 17 recognized genera were shown to be phenetically distinct. Of the two that were not, one (*Chiroderma*) was shown by Owen (1987*a*) to be well defined and supported phylogenetically, whereas the other (*Vampyressa*) may be polyphyletic. Phenetic relationships among stenodermatine bats generally do not reflect hypothesized phylogenetic relationships, particularly at higher taxonomic levels, indicating a considerable degree of parallel or convergent evolution within the subfamily.

For a number of reasons, study of the systematics of bats has not progressed as rapidly as that of some other mammalian groups. Major forces in chiropteran evolution have been those associated with flight and feeding (Findley and Wilson, 1982), and taxonomists have not been in agreement on how best to evaluate morphologic characters in systematic analyses. Investigators generally agree that many characters and techniques traditionally used in mammalian systematics are, at best, insufficient for use with bats, but only a few intensive quantitative examinations have been undertaken (Findley, 1972; Freeman, 1981; Owen, 1987*a*; Smith, 1972).

Stenodermatinae is the most species-rich subfamily within the Phyllostomidae, yet in several aspects it is the most homogeneous of the larger subfamilies. Unlike the phyllostomines, for example, all stenodermatines are dependent on one general food type; each species is primarily or entirely frugivorous (Wilson, 1973). As now constituted, the subfamily, consisting of 17 genera (Owen, 1987*a*) and about 64 species (Honacki et al., 1982; Jones and Carter, 1976), includes four genera that contain together over half the species; in addition, nine genera are monotypic. The studies of Baker (1973), de la Torre (1961), Gardner (1977), and Owen (1987*a*) are the only ones to evaluate all stenodermatine genera, and only those of Baker (1973) and Owen (1987*a*) suggested that some nominal genera in the subfamily might not be natural assemblages. Following the phylogenetic assessment of this group by Owen (1987*a*), it is of interest to evaluate phenetic relationships within and among the stenodermatine genera. I have undertaken such a study to determine whether the genera, as currently defined, constitute phenetically distinct groups, and additionally to evaluate morphometric trends within the several stenodermatine clades.

MATERIALS AND METHODS

Species, specimens, and measurements.—The 64 species evaluated in this study include all currently recognized species of stenodermatine bats except *Artibeus lituratus*. My specimens examined of *A. "lituratus"* were reidentified as *A. intermedius* following Davis (1984). I follow Owen (1987*a*) in generic nomenclature. My goal was to examine at least 10 adult specimens (five male, five female) of each species. In a few instances, 10 specimens were not available, and in several I measured more than 10. Appendix I of Owen (1987*a*) lists the specimens examined. Most specimens were complete and intact, with no missing characters. Table 1 herein lists characters measured on each specimen, and Appendix A2 of Owen (1987*b*) contains the raw data from each specimen.

Data transformation procedure.—All values were transformed to their natural logarithms. As biological size relationships typically are allometric, the log transformation results in a higher degree of linearity of the size component of the data. The log transformation has the additional function of legitimizing linear statistics on the data (Humphries et al., 1981), and of approximating independence from the relative mag-

TABLE 1.—*Character loadings and percent variance for the first three principal components from principal component analysis. Loadings given for first (all species) and second (42 "typical" species) analyses. Characters described in Owen (1987a: Appendix III).*

Character	All species			42 "typical" species		
	I	II	III	I	II	III
Males						
Length of skull	0.482	−0.050	0.403	0.529	−0.497	0.026
Condylobasal length	0.619	−0.403	0.182	0.213	−0.163	−0.345
Rostral length	0.703	−0.497	−0.015	−0.402	0.239	0.255
Lacrimal width	−0.684	−0.253	−0.154	0.691	0.306	−0.059
Postorbital width	−0.749	−0.183	−0.257	0.671	0.617	−0.071
Zygomatic width	−0.234	0.110	−0.315	0.234	−0.616	−0.368
Mastoid width	−0.887	0.090	0.084	0.724	−0.277	0.353
Width of braincase	−0.902	0.067	−0.124	0.917	0.128	−0.038
Height of braincase	−0.913	0.134	−0.086	0.890	0.248	0.110
Length of braincase	−0.687	0.200	0.016	0.777	0.299	−0.149
Palatal length	0.804	−0.339	−0.335	−0.654	−0.128	−0.347
Length of maxillary toothrow	0.910	0.293	−0.093	−0.863	0.376	0.083
Length of molariform toothrow	0.796	0.492	−0.051	−0.774	0.359	0.234
Width of palate at canines	−0.548	−0.147	−0.591	0.639	0.450	0.263
Width of palate at second molar	−0.174	0.304	−0.594	−0.171	0.769	−0.314
Length of mandibular fossa	−0.077	−0.865	−0.058	−0.391	0.169	−0.540
Width of mandibular fossa	−0.238	−0.053	0.550	0.103	0.057	−0.048
Length of upper second molar	0.633	0.681	−0.022	−0.646	0.395	−0.284
Width of upper second molar	0.210	0.809	0.107	0.630	−0.354	0.015
Height of upper canine	0.157	−0.205	−0.599	−0.256	0.035	0.839
Dentary length	0.893	−0.319	−0.004	−0.774	−0.254	−0.016
Condylocanine length	0.920	−0.301	−0.005	−0.842	−0.272	0.001
Length from condyle to first molar	0.714	−0.582	0.125	−0.727	−0.123	0.129
Length of mandibular toothrow	0.921	0.184	−0.172	−0.881	0.207	0.051
Mandibular foramen to dentary anterior	0.916	−0.292	−0.083	−0.848	−0.053	0.159
Condylomolar length	−0.088	−0.909	−0.064	0.373	0.222	−0.132
Temporal moment-arm length	−0.269	−0.738	0.415	0.253	−0.318	0.395
Masseter moment-arm length	0.056	−0.811	0.253	−0.124	−0.715	−0.379
Coronoid height	−0.138	0.034	0.762	−0.141	−0.856	0.248
Length of angular process	−0.697	−0.306	0.102	−0.149	−0.077	−0.358
Dentary thickness	−0.632	−0.318	0.113	0.131	−0.441	0.162
Length of lower canine	0.073	−0.095	−0.482	−0.148	0.036	0.793
Length of condyle	−0.258	0.581	0.588	−0.124	−0.105	−0.281
Females						
Length of skull	0.068	0.453	0.552	0.646	−0.430	0.008
Condylobasal length	0.417	−0.013	0.485	0.439	−0.254	−0.425
Rostral length	0.664	−0.291	0.150	−0.554	−0.025	0.087
Lacrimal width	−0.786	−0.038	−0.128	0.686	0.266	−0.058
Postorbital width	−0.840	−0.059	−0.262	0.702	0.554	−0.125
Zygomatic width	−0.657	0.560	0.233	0.344	−0.657	−0.420
Mastoid width	−0.900	0.240	0.122	0.799	−0.225	0.228
Width of braincase	−0.911	0.122	−0.077	0.908	0.087	−0.069
Height of braincase	−0.918	0.160	−0.078	0.917	0.217	0.091
Length of braincase	−0.726	0.251	−0.005	0.802	0.350	−0.138
Palatal length	0.816	−0.276	−0.324	−0.614	−0.118	−0.531
Length of maxillary toothrow	0.794	0.531	−0.001	−0.851	0.345	0.008
Length of molariform toothrow	0.631	0.688	0.062	−0.747	0.364	0.161
Width of palate at canines	−0.629	−0.049	−0.544	0.581	0.392	0.299
Width of palate at second molar	−0.241	0.429	−0.521	−0.189	0.717	−0.339
Length of mandibular fossa	−0.154	−0.830	−0.084	−0.232	0.038	−0.592
Width of mandibular fossa	−0.416	0.284	0.632	−0.073	−0.138	−0.023
Length of upper second molar	0.460	0.809	0.010	−0.576	0.462	−0.319
Width of upper second molar	0.004	0.884	0.142	0.581	−0.219	−0.064
Height of upper canine	0.044	0.266	−0.452	−0.250	−0.122	0.703
Dentary length	0.908	0.003	0.216	−0.768	−0.254	−0.110
Condylocanine length	0.937	0.022	0.212	−0.833	−0.301	−0.115
Length from condyle to first molar	0.709	−0.409	0.331	−0.721	−0.181	0.019
Length of mandibular toothrow	0.841	0.420	−0.069	−0.870	0.267	−0.047
Mandibular foramen to dentary anterior	0.923	−0.020	−0.002	−0.835	0.005	0.157
Condylomolar length	−0.252	−0.867	0.070	0.515	0.164	−0.308
Temporal moment-arm length	−0.465	−0.475	0.591	0.271	−0.478	0.278
Masseter moment-arm length	−0.017	−0.689	0.377	−0.021	−0.664	−0.358
Coronoid height	−0.241	0.169	0.773	−0.064	−0.875	0.180
Length of angular process	−0.721	−0.223	0.260	0.024	−0.170	−0.403
Dentary thickness	−0.707	−0.044	0.195	0.253	−0.432	−0.058
Length of lower canine	−0.080	0.532	−0.304	−0.246	0.029	0.819
Length of condyle	−0.356	0.573	0.606	−0.265	−0.267	−0.224
Percent variance	39.63	19.45	11.05	34.38	13.87	9.71

nitude of original variables (Pimentel, 1979). By this latter attribute, the log transformation functions much as standardization of characters (Schnell, 1970*a*, 1970*b*). I, therefore, did not standardize characters in any analysis.

Because sexual dimorphism is known for a number of stenodermatine species, the number of characters was doubled by using the male and female mean values of each character as separate characters. Although this results in largely redundant variation, the nonredundant portion of the variation (i.e., the nonuniform sexual dimorphism) may have systematic usefulness (Schnell et al., 1978).

Wood (1983) described a common-part-removed transformation for phenetic analysis of continuous data that involves regression of the vector of character values from each study species on the analogous vector(s) for one or more closely related species. For my analysis, the vector of character values for each species was regressed on that for *Carollia brevicauda*. This species is a member of the Carolliinae, the sister subfamily to Stenodermatinae (Honeycutt, 1981; Honeycutt and Sarich, 1987; Hood and Smith, 1982). Thus, this regression results in a common-part vector containing the portion of the stenodermatine variation predicted by the analogous character-state values from this close relative. The values of the residuals for each stenodermatine species are uncorrelated with the regression-predicted values. For each species, the vector of residual values was retained. These vectors were combined as the transformed data matrix (Wood, 1983), the basis for all analyses described later.

Phenetic procedures.—I used two clustering and two ordination methods to evaluate phenetic variation. Computer programs were from the Numerical Taxonomy System of Multivariate Statistical Programs (Rohlf et al., 1979). The unweighted pair-group method using arithmetic averages (Sneath and Sokal, 1973) was performed on the matrix of average taxonomic distances computed from the transformed data matrix. Linear adaptive hierarchical clustering (Rohlf, 1970) was applied to assess the possibility of taxon clusters that are elongate or non-hyperspheroidal in the multidimensional character space of the transformed data matrix. It is impractical in the latter analysis to use large numbers of characters (G. D. Schnell et al., in litt.). Therefore, a matrix of Pearson's product-moment correlations between characters was calculated, and this correlation matrix was subjected to principal component analysis. Linear adaptive hierarchical clustering then was performed on the species projections for those components with eigenvalues greater than 1.0 (nine components for the complete data set, 11 for the "reduced" data set). A value of 1.0 was used in these analyses for W, the variance of the artificial variance-covariance matrix (Rohlf, 1970; G. D. Schnell et al., in litt.).

Ordination methods were employed to reduce the multidimensional character space to three dimensions, in which the species relationships could be summarized diagramatically. Nonmetric multidimensional scaling based on average taxonomic distances (Pimentel, 1979; Sneath and Sokal, 1973) was calculated from the transformed data matrix. In this procedure, axes are computed so that the intertaxon distances in the reduced space bear as nearly a monotonal relationship to the intertaxon distances in the original matrix as possible. An advantage of multidimensional scaling over most other ordination methods is that distortion of intertaxon relationships is not concentrated among closely related taxa; rather, the method provides balance between large intercluster distances and smaller within-cluster distances (Rohlf, 1972). Beginning with the one-dimensional case, each solution was used as an initial matrix for the next higher-dimensional solution. The three-dimensional configuration then was used to evaluate visually the associations of species.

Principal component analysis was performed on the character correlation matrix (Pimentel, 1979; Sneath and Sokal, 1973). Rather than minimizing stress (as with multidimensional scaling), principal component analysis is designed to explain the maximum percentage of the matrix variation with a given number of orthogonal components, or axes. An advantage is that the components are interpretable in terms of individual character loadings. For both the multidimensional scaling and principal component analysis results, projections of the operational taxonomic units onto the three extracted components were plotted. A minimum-spanning tree (Sneath and Sokal, 1973), computed from the average taxonomic-distance matrix, was superimposed onto these three-dimensional diagrams to further elucidate relations among species.

In both clustering and ordination analyses of the 64 stenodermatine taxa, a disproportionate amount of the variation is associated with the genus *Sturnira* and with species of the eight "short-faced" genera (i.e., *Ardops*, *Ariteus*, *Phyllops*, *Stenoderma*, *Pygoderma*, *Ametrida*, *Sphaeronycteris*, and *Centurio*). All analyses, therefore, were rerun on the data with these two groups of bats omitted. This second set of analyses, conducted on the "reduced" data set of 42 species, allowed greater differentiation among the more typical stenodermatine forms.

Results

The common-part-removed transformation resulted in removal of from 86.2% (*Centurio senex*) to 98.7% (*Sturnira bogotensis*) of the total variation from each species's character vector (Owen,

1987*a*:37, table 4). Thus, phenetic analyses were performed on the remaining 1.3–13.8% of the variance that describes the morphometric differences among stenodermatine species. These values are comparable to those found by Wood (1983) in three data sets on birds.

Analyses of all species.—The phenogram from the average taxonomic distance matrix (Fig. 1) indicates phenetic distinctness for each of the polytypic genera *Sturnira*, *Uroderma*, *Dermanura*, *Vampyrops*, and *Phyllops*. *Artibeus* is distinct except for the inclusion of *Vampyrodes*. The mainland short-faced bats (*Pygoderma*, *Centurio*, *Sphaeronycteris*, and *Ametrida*) and the Antillean short-faced bats (*Phyllops*, *Ardops*, *Ariteus*, and *Stenoderma*), each comprise a distinct group, and together form a cluster separate from the other stenodermatines. *Vampyressa* and *Chiroderma* are each shown as phenetically nondistinct genera; that is, members of both are dispersed throughout the portion of the phenogram containing the "typical" stenodermatine bats. Based on all clustering results, typical stenodermatines are considered herein to be those not of the short-faced group or of the genus *Sturnira*.

Adaptive clustering results show *Pygoderma* to be outside the cluster of all other stenodermatines (Fig. 2). This phenogram also shows a separation of the other seven short-faced genera from the remainder of the subfamily. Within the remainder, as with results of the unweighted pair-group analysis, the next division is between the genus *Sturnira* and the typical stenodermatine bats. Within the typical species, only one polytypic genus (*Uroderma*) is shown as distinct. The cluster including most of the *Artibeus* species contains *Vampyrodes caraccioli*, but not *A. intermedius*. The *Vampyrops* cluster also includes both *Uroderma* species, two *Chiroderma* species, and *Vampyressa nymphaea*. As in the unweighted-pair-group phenogram, *Vampyressa macconnelli* and *Ectophylla alba* are shown as most similar to each other.

In both ordination results (Fig. 3), component I separates the short-faced bats from all others, and component II separates *Sturnira* from the typical stenodermatines. In the principal component analysis, component III contrasts the mainland short-faced bats from the Antillean ones, and *Phyllops* from the other three Antillean genera. Of the 66 characters, 27 have high loadings (absolute value ≥ 0.7) on component I (16 positive, 11 negative; Table 1). Thus, nearly half of the characters serve to distinguish the short-faced bats from other stenodermatines. Nine characters load heavily on component II, separating *Sturnira* from the typical stenodermatines. *Sturnira* species have higher values than the other genera on width of second upper molar in males and females, and length of second upper molar in females. Conversely, *Sturnira* species have lower values on six other characters: length of mandibular fossa in males and females, condyle-to-molar distance in males and females, length of temporal moment arm in males, and length of masseter moment arm in males. Two characters, height of coronoid process in males and females, load heavily on component III (both positively), which distinguishes among short-faced bats. The four mainland genera (*Ametrida*, *Sphaeronycteris*, *Pygoderma*, and *Centurio*) have relatively long coronoid processes, with the Antillean genus *Phyllops* intermediate, and the other three genera (*Stenoderma*, *Ariteus*, and *Ardops*) having short processes. Although these two characters are useful in separating these groups of short-faced bats, other characters contribute more in determining their overall resemblances, as indicated by the multidimensional scaling results, in which the previously described groupings are not evident.

Results of all clustering and ordination procedures are in agreement concerning the distinctness of four (or possibly five) major stenodermatine groups. These are *Sturnira*, the Antillean short-

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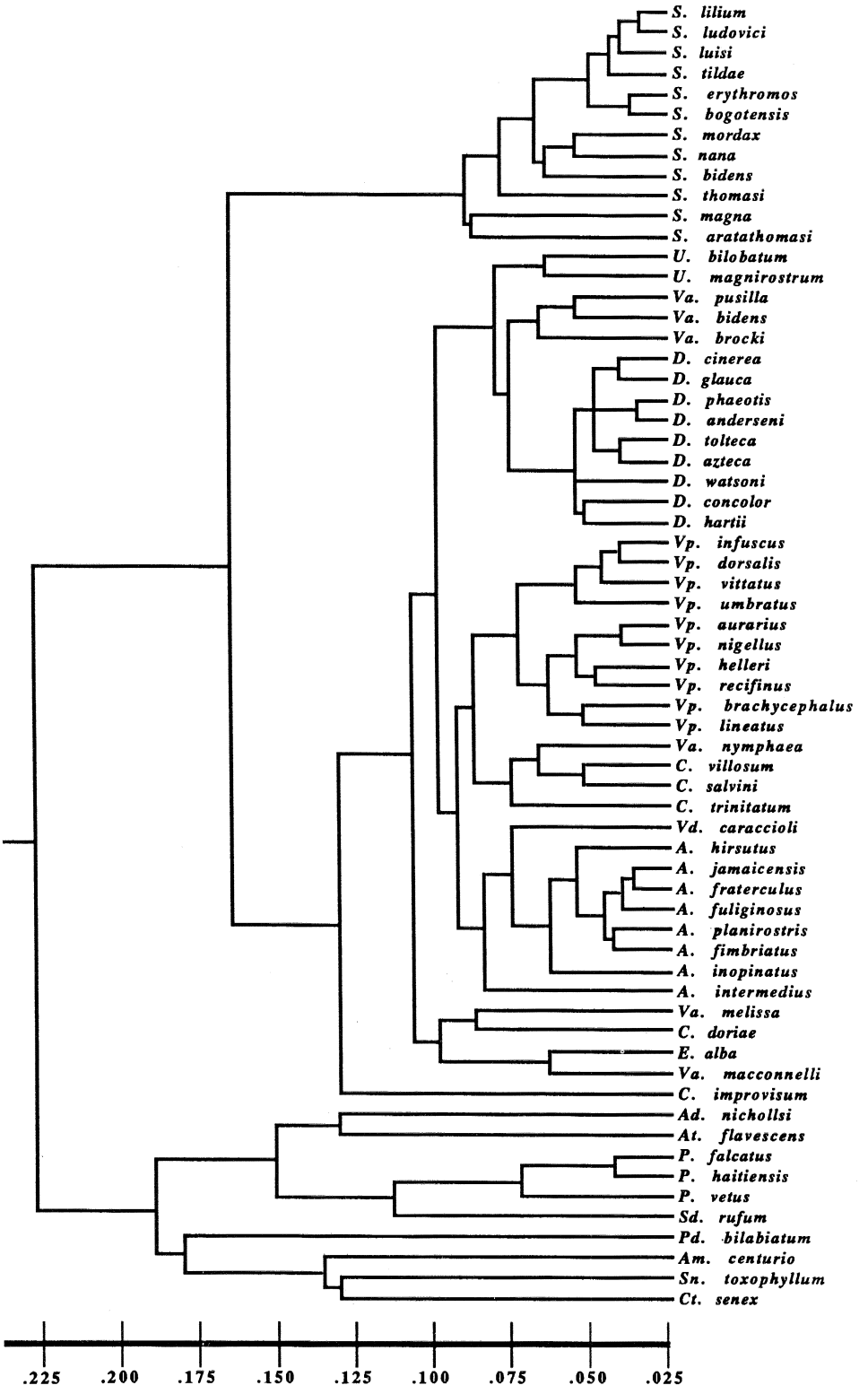
FIG. 1.—Phenogram (unweighted pair-group method using arithmetic averages) for average taxonomic distances calculated from transformed data matrix, with all stenodermatine species included. Cophenetic correlation coefficient is 0.923. Relationships are unchanged among "typical" stenodermatines when *Sturnira* (top cluster) and the short-faced species (bottom cluster) are excluded from analysis. Cophenetic correlation coefficient for phenogram containing only "typical" species is 0.730. Generic abbreviations are: A, *Artibeus*; Ad, *Ardops*; Am, *Ametrida*; At, *Ariteus*; C, *Chiroderma*; Ct, *Centurio*; D, *Dermanura*; E, *Ectophylla*; P, *Phyllops*; Pd, *Pygoderma*; S, *Sturnira*; Sd, *Stenoderma*; Sp, *Sphaeronycteris*; U, *Uroderma*; Va, *Vampyressa*; Vd, *Vampyrodes*; Vp, *Vampyrops*.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S. magna
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U. bilobatum
U. magnirostrum
Va. pusilla
Va. bidens
Va. brocki
D. cinerea
D. glauca
D. phaeotis
D. anderseni
D. tolteca
D. azteca
D. watsoni
D. concolor
D. hartii
Vp. infuscus
Vp. dorsalis
Vp. vittatus
Vp. umbratus
Vp. aurarius
Vp. nigellus
Vp. helleri
Vp. recifinus
Vp. brachycephalus
Vp. lineatus
Va. nymphaea
C. villosum
C. salvini
C. trinitatum
Vd. caraccioli
A. hirsutus
A. jamaicensis
A. fraterculus
A. fuliginosus
A. planirostris
A. fimbriatus
A. inopinatus
A. intermedius
Va. melissa
C. doriae
E. alba
Va. macconnelli
C. improvisum
Ad. nichollsi
At. flavescens
P. falcatus
P. haitiensis
P. vetus
Sd. rufum
Pd. bilabiatum
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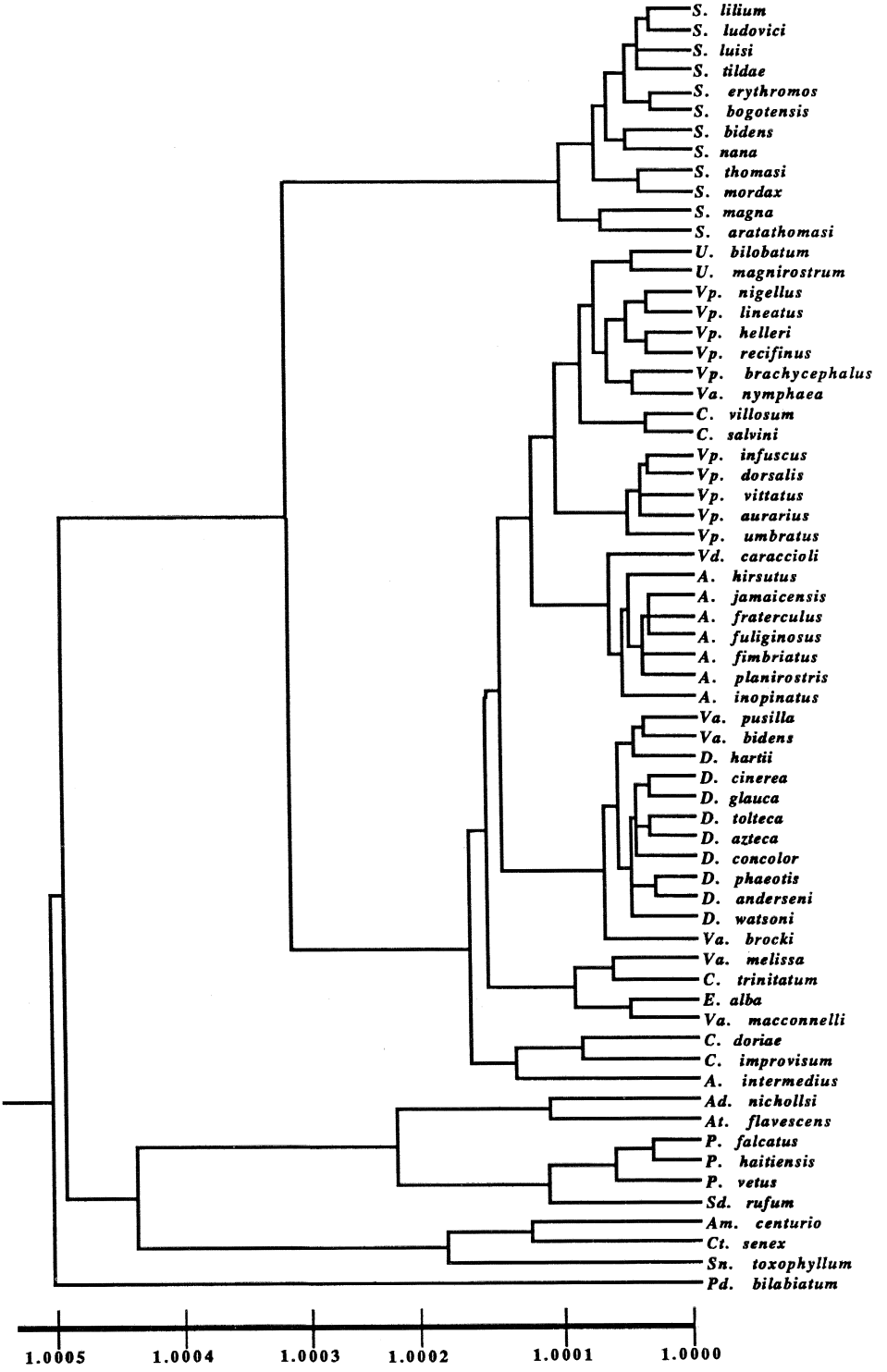
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S. magna
S. aratathomasi
U. bilobatum
U. magnirostrum
Vp. nigellus
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A. fimbriatus
A. planirostris
A. inopinatus
Va. pusilla
Va. bidens
D. hartii
D. cinerea
D. glauca
D. tolteca
D. azteca
D. concolor
D. phaeotis
D. anderseni
D. watsoni
Va. brocki
Va. melissa
C. trinitatum
E. alba
Va. macconnelli
C. doriae
C. improvisum
A. intermedius
Ad. nichollsi
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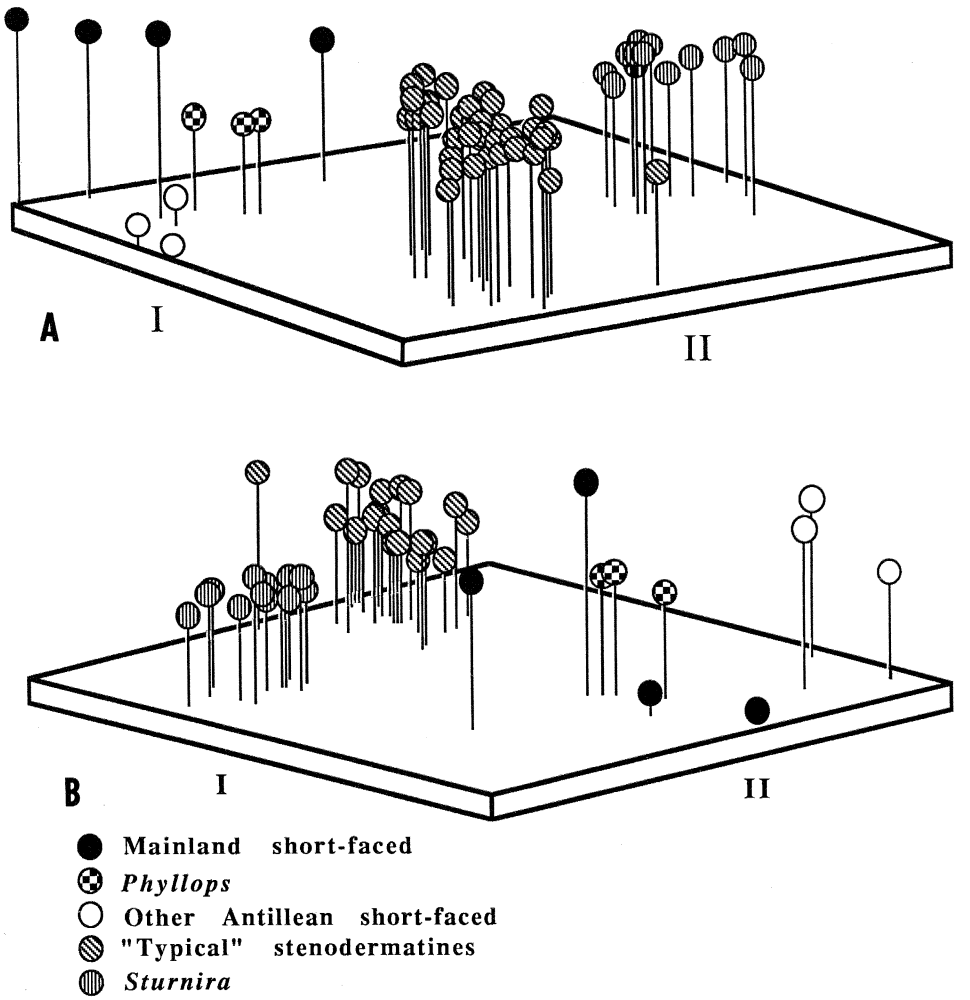

FIG. 3.—(A) Projections of all stenodermatine species onto first three principal components from transformed-data matrix. Component III indicated by height. Components account for 39.6, 19.4, and 11.0% of total variance, respectively. Matrix correlation is 0.968. (B) Projections of all species onto axes for three-dimensional nonmetric-multidimensional-scaling solution based on transformed-data matrix. Axis III is indicated by height. Apparent smaller number of "typical" stenodermatines is related to "hidden" taxa in graphical output from computer analyses. Stress value is 0.11. Matrix correlation is 0.986.

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FIG. 2.—Phenogram (adaptive hierarchical clustering scheme) with all stenodermatine species included. Clustering based on species projections for first nine principal components (90.4% of total variance) from transformed data matrix. Cophenetic correlation coefficient is 0.919. Generic abbreviations are: A, *Artibeus*; Ad, *Ardops*; Am, *Ametrida*; At, *Ariteus*; C, *Chiroderma*; Ct, *Centurio*; D, *Dermanura*; E, *Ectophylla*; P, *Phyllops*; Pd, *Pygoderma*; S, *Sturnira*; Sd, *Stenoderma*; Sp, *Sphaeronycteris*; U, *Uroderma*; Va, *Vampyressa*; Vd, *Vampyrodes*; Vp, *Vampyrops*.

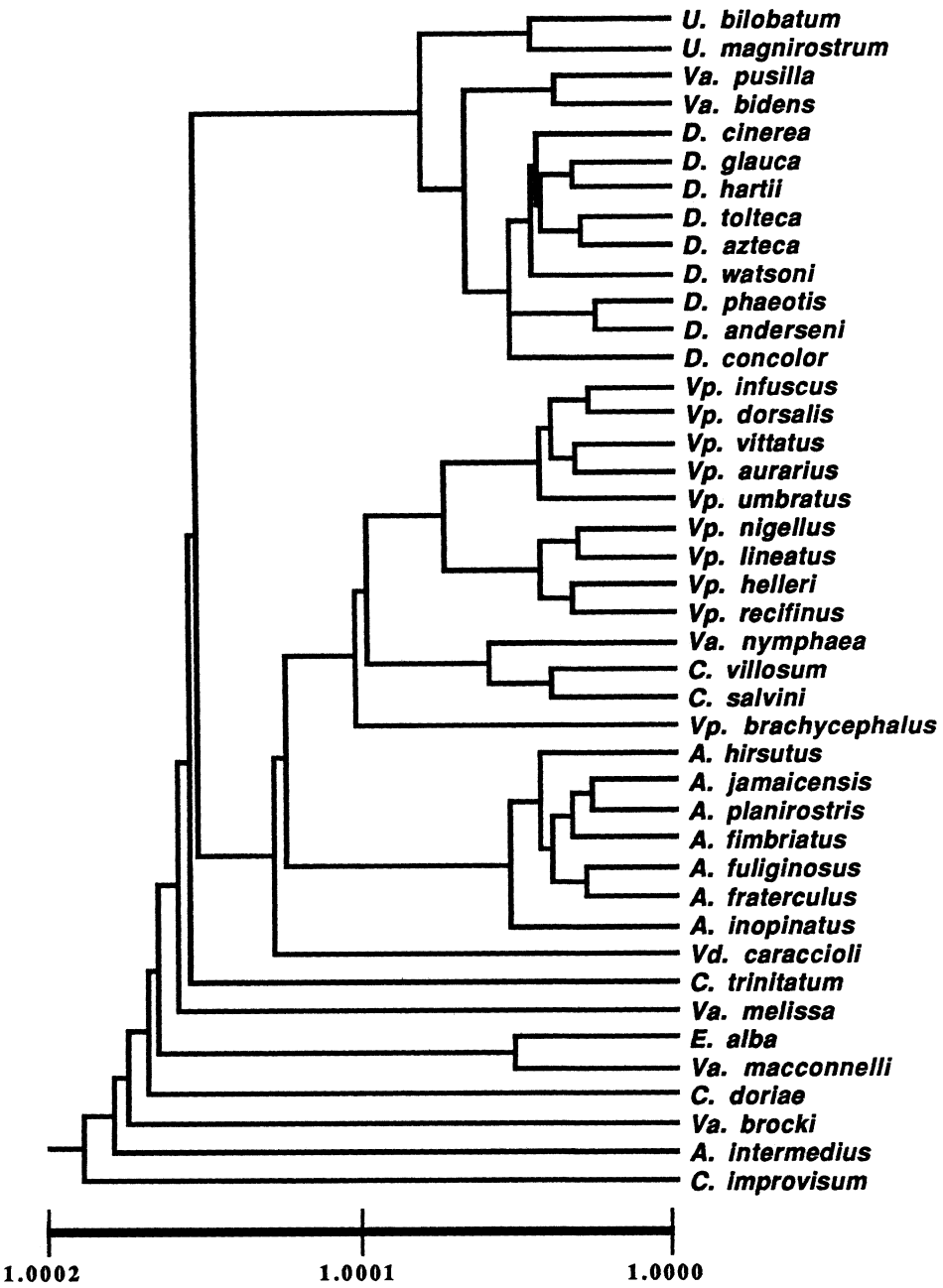

FIG. 4.—Phenogram (adaptive hierarchical-clustering scheme), with 42 "typical" stenodermatine species included. Clustering based on species projections for first 11 principal components (89.8% of total variance) from transformed-data matrix. Cophenetic correlation coefficient is 0.740. Generic abbreviations are: A, *Artibeus*; Ad, *Ardops*; Am, *Ametrida*; At, *Ariteus*; C, *Chiroderma*; Ct, *Centurio*; D, *Dermanura*; E, *Ectophylla*; P, *Phyllops*; Pd, *Pygoderma*; S, *Sturnira*; Sd, *Stenoderma*; Sp, *Sphaeronycteris*; U, *Uroderma*; Va, *Vampyressa*; Vd, *Vampyrodes*; Vp, *Vampyrops*.

TABLE 2.—*Cophenetic correlation coefficients, matrix correlations, and correlations among cophenetic and correlation matrices resulting from all clustering and ordination procedures. Matrix correlations from ordination methods are analogous to cophenetic correlations for clustering procedures, being computed as a measure of the agreement between species-similarity values from the three-dimensional projections and those from the transformed-distance matrix. Values in upper right half from analyses with all 64 species; those in lower left from analyses with* Sturnira *and short-faced bats deleted (42 species included).*

	r	Unweighted pair-group method using arithmetic averages	Adaptive hierarchical clustering scheme	Nonmetric multi-dimensional scaling	Principal component analysis
r		0.923	0.919	0.986	0.968
Unweighted pair-group method using arithmetic averages	0.730		0.990	0.915	0.900
Adaptive hierarchical clustering scheme	0.740	0.872		0.913	0.894
Nonmetric multidimensional scaling	0.972	0.703	0.718		0.965
Principal component analysis	0.936	0.673	0.663	0.956	

faced bats, the mainland short-faced bats (possibly excluding *Pygoderma*), and the typical stenodermatines (Figs. 1, 2, 3). In all of the results, variation among typical stenodermatines is slight relative to that caused by *Sturnira* and the short-faced genera; thus, little differentiation among typical species is possible in joint analysis with these two groups. Additionally, it is inappropriate to assume that trends in variation caused primarily by these atypical genera also would be those that contribute most in defining phenetic relationships among the typical stenodermatines. Therefore, as mentioned earlier, the analyses also were performed on a reduced data set containing only the 42 typical stenodermatine species (genera *Uroderma, Dermanura, Vampyrops, Artibeus, Chiroderma, Vampyressa, Ectophylla,* and *Vampyrodes*).

Analyses of "typical" species.—Within the group of typical species, clusters are not particularly well defined, as indicated by the relatively low cophenetic correlation coefficients for the phenograms (Table 2). The phenetic relationships expressed by the unweighted-pair-group phenogram are unchanged from the analysis of all species (Fig. 1).

The adaptive clustering results from the reduced set (Fig. 4) indicate somewhat greater generic coherence than those for the overall analysis. This suggests that, although these species may form elongate clusters in multivariate space, the nonparallel orientation of the species groups may preclude inclusion of smaller clusters into larger ones intact. The problem of nonparallel elongation may be of special concern in such data transformed so that a primary linear component of the variation is removed.

The clustering pattern from the adaptive clustering analysis of the reduced data set (Fig. 4) is similar to that in the unweighted-pair-group phenogram (Fig. 1, Table 2). In the former phenogram from the reduced data set (Fig. 4), *Uroderma* and *Dermanura* are distinct groups. The cluster including all *Vampyrops* also contains *Vampyressa nymphaea, Chiroderma villosum,* and *C. salvini. Artibeus intermedius* is some distance from the cluster containing all the other *Artibeus. Vampyressa macconnelli* is associated with *Ectophylla alba.*

As expected, the two ordination results from the reduced data set (Figs. 5 and 6) showed much higher matrix correlation values than those from the clustering methods (Table 2). The two ordination results also were in close agreement with each other (Table 2). In the principal component analysis, 23 characters load heavily on component I; nine of these are positive (Table 1). Generally, this component contrasts *Dermanura* species at the negative end, with *Uroderma, Artibeus,* and *Ectophylla* intermediate, and most *Vampyrops* and *Chiroderma* at the positive end (Fig. 5). The second component shows positive loadings for width of palate at the molars in males and females, and negative loadings for length of masseter moment arm in males, and height of coronoid process in males and females. Specimens of *Artibeus* and some *Chiroderma* exhibit relatively wider palates and reduced mandibular processes than other typical stenoder-

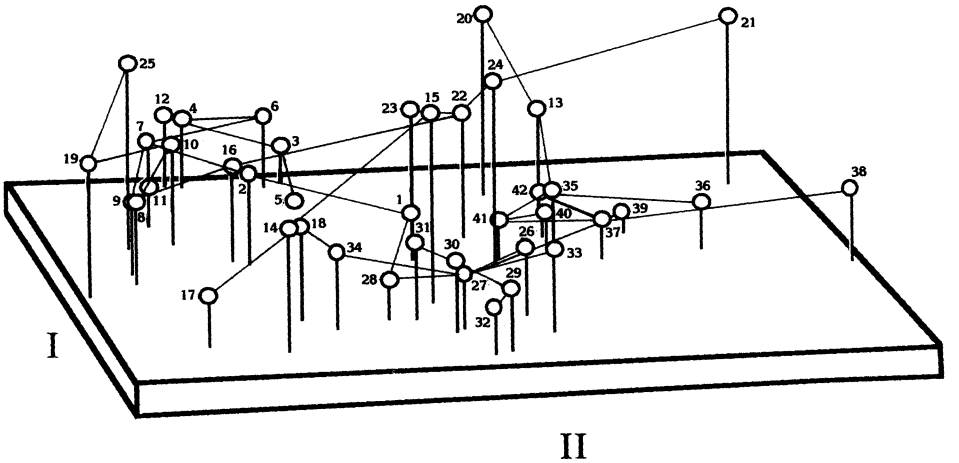

FIG. 5.—Projections of 42 "typical" stenodermatine species onto first three principal components from transformed-data matrix. Component III indicated by height. Components account for 34.4, 13.9, and 9.7% of total variance, respectively. Matrix correlation is 0.936. Species are: 1, *Uroderma bilobatum*; 2, *U. magnirostrum*; 3, *Vampyrops infuscus*; 4, *V. vittatus*; 5, *V. umbratus*; 6, *V. aurarius*; 7, *V. nigellus*; 8, *V. brachycephalus*; 9, *V. helleri*; 10, *V. lineatus*; 11, *V. recifinus*; 12, *V. dorsalis*; 13, *Vampyrodes caraccioli*; 14, *Vampyressa pusilla*; 15, *V. melissa*; 16, *V. nymphaea*; 17, *V. brocki*; 18, *V. bidens*; 19, *V. macconnelli*; 20, *Chiroderma doriae*; 21, *C. improvisum*; 22, *C. villosum*; 23, *C. salvini*; 24, *C. trinitatum*; 25, *Ectophylla alba*; 26, *Dermanura cinerea*; 27, *D. glauca*; 28, *D. watsoni*; 29, *D. phaeotis*; 30, *D. tolteca*; 31, *D. azteca*; 32, *D. anderseni*; 33, *D. concolor*; 34, *D. hartii*; 35, *Artibeus hirsutus*; 36, *A. inopinatus*; 37, *A. jamaicensis*; 38, *A. intermedius*; 39, *A. planirostris*; 40, *A. fuliginosus*; 41, *A. fraterculus*; 42, *C. fimbriatus*.

matines. The third component shows high positive loadings for upper and lower canine length in males and females. *Dermanura*, most *Artibeus*, and a few species of *Vampyrops* and *Vampyressa* have relatively shorter canine teeth.

The minimum-spanning tree superimposed on the three-dimensional diagrams (Figs. 5 and 6) confirms that the genera *Vampyressa* and *Chiroderma* do not occupy exclusive portions of the morphospace (i.e., the species of each of these genera are not mutually close neighbors). *Vampyressa pusilla*, *V. melissa*, *V. brocki*, and *V. bidens* phenetically are nearest *Dermanura*;

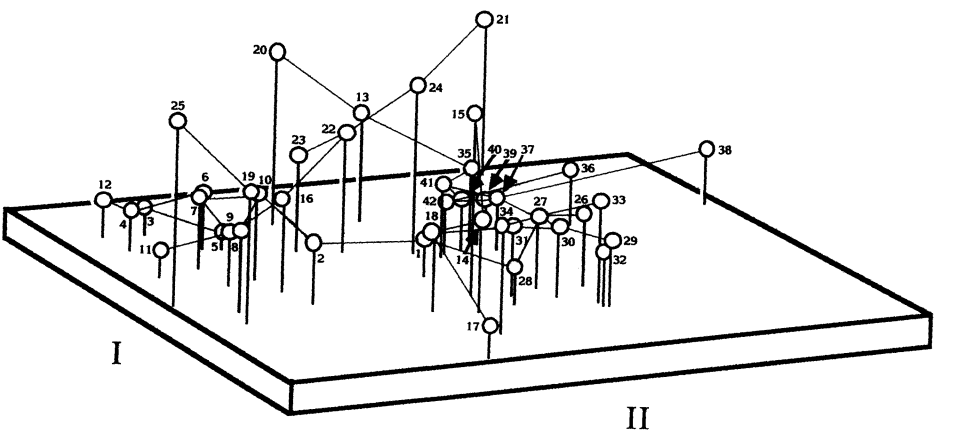

FIG. 6.—Projections of taxa onto axes of three-dimensional nonmetric-multidimensional-scaling solution, with 42 "typical" stenodermatine species included. Axis III indicated by height. Stress value is 0.20. Matrix correlation is 0.972. Species numbered as in Fig. 5.

V. nymphaea is between *Vampyrops* and four of the five *Chiroderma*; and *V. macconnelli* (with *Ectophylla alba*) is closest to *Vampyrops*. *Chiroderma improvisum*, *C. villosum*, *C. salvini*, and *C. trinitatum* (with *Vampyressa nymphaea*) are allied with *Vampyrops*; *C. doriae* (with *Vampyrodes caraccioli*) is closest to *Artibeus*. *Artibeus*, *Dermanura*, *Uroderma*, and *Vampyrops* are each distinct on the minimum-spanning tree; that is, each member of the genus is connected to all others without the connected group including a nonmember of the genus.

Discussion

Phenetic methodologies.—The two clustering methods show results that contrast somewhat, although their cophenetic correlation coefficients are essentially equal both for the complete and the reduced data sets (Table 2). One point of difference is in the effect of eliminating the "atypical" species from the analysis. In the unweighted-pair-group analyses (Fig. 1), the relationships remain unchanged among the typical stenodermatines. In the adaptive clustering analyses (Figs. 1, 4), a number of differences are evident between the two phenograms. Without the atypical forms to "predirect" the dominant axes of some of these internal clusters, the adaptive clustering analysis of the reduced data set is considerably more like the unweighted-pair-group result. Thus, although the adaptive clustering procedure may be better able to cluster members of non-hyperspheroidal groups than the unweighted pair-group method in some circumstances, problems may arise if either the subgroup centroids are arranged in a substantially nonuniform pattern in the hyperspace, or the dominant axis of one or more of the subgroups is curvilinear in the hyperspace.

Between the two ordination methods, the multidimensional-scaling result has a marginally higher matrix-correlation value than the principal component result, for both the complete and reduced data sets (Table 2). This indicates that the three-dimensional relationships shown in Fig. 6 should represent the original phenetic-distance matrix slightly better than those of Fig. 5. The relationships among phenetically close species should be portrayed more accurately by the multidimensional scaling results. Evaluation of overall morphometric trends among genera, however, must be made from results of principal component analyses for which the axes may be interpreted in terms of individual character loadings.

Phenetic relationships within and among genera.—The least typical group among the stenodermatines is that of the eight genera of short-faced bats (*Ardops*, *Ariteus*, *Phyllops*, and *Stenoderma* from the Antilles, and *Pygoderma*, *Ametrida*, *Sphaeronycteris*, and *Centurio* from mainland South and Central America). The two clustering analyses (Figs. 1 and 2) and two ordination analyses (Fig. 3) show the similarities of the three *Phyllops* species, with *P. vetus* (the fossil taxon) the most different of the three in the phenograms. *Phyllops* is most similar to *Stenoderma*, and this group clusters with *Ardops* and *Ariteus*, the remaining Antillean genera. Three of the four mainland short-faced genera (*Ametrida*, *Sphaeronycteris*, and *Centurio*) form a loose group in both clustering analyses, and in the unweighted-pair-group phenogram, *Pygoderma* also is included in this cluster. Although these eight genera tend to cluster together, they are not a phenetically homogenous group. Similarity levels among these genera are far below those among most others in the subfamily (Figs. 1, 2).

The other phenetically atypical group of stenodermatines is the genus *Sturnira*. *Sturnira lilium*, *S. ludovici*, *S. luisi*, and *S. tildae* are similar, as are *S. erythromos* and *S. bogotensis*, with which they cluster. The adaptive clustering tree (Fig. 2) shows *S. bidens* and *S. nana* (subgenus *Corvira*) to be most similar to each other, but the unweighted-pair-group result (Fig. 1) indicates greater similarity of *S. nana* to *S. mordax*. The two large species of *Sturnira*, *S. magna*, and *S. aratathomasi*, are relatively dissimilar to the other *Sturnira* and to each other (Figs. 1, 2).

The "typical" stenodermatines include the genera *Uroderma*, *Dermanura*, *Vampyrops*, *Artibeus*, *Chiroderma*, *Vampyressa*, *Chiroderma*, *Ectophylla*, and *Vampyrodes*. The last two are monotypic, and *Uroderma* contains only two species. In all results, *Ectophylla alba* is shown as most similar to *Vampyressa macconnelli*, with which it has at times been considered congeneric.

Vampyrodes caraccioli is depicted by the unweighted pair-group method (Fig. 1) and minimum-spanning tree (Figs. 5 and 6) as similar to *Artibeus*, but adaptive clustering (Fig. 4) does not show it as particularly similar to any other species. The two *Uroderma* species are most similar to *Dermanura* in all results. The minimum-spanning tree (Figs. 5, 6) shows *Uroderma* as linking *Dermanura* with *Vampyrops*.

Within the genus *Dermanura*, all results indicate high similarities between *D. azteca* and *D. tolteca*, and between *D. phaeotis* and *D. anderseni*. Aside from these two relationships, there is little agreement among results concerning interspecific affinities within this genus. As mentioned earlier, *Dermanura* phenetically is related most closely to *Uroderma*.

The genus *Vampyrops* contains two groups found in both phenograms (Figs. 1 and 4). *Vampyrops helleri* and *V. recifinus* are a mutually close pair, and *V. infuscus*, *V. vittatus*, *V. umbratus*, and *V. dorsalis* form a cluster (in the hierarchical-clustering tree, *V. aurarius* is included also). The genus is shown as distinct in all results except that, in the adaptive clustering phenogram, *V. brachycephalus* is separated from other *Vampyrops* by three species of other genera. The results of the same analysis show *Vampyrops* as phenetically most similar to *Artibeus* and *Vampyrodes*; in the unweighted-pair-group results it is about equally close to *Artibeus* and *Dermanura*; and the minimum-spanning tree places it closest to *Uroderma* (and connected to *Chiroderma* through *Vampyressa nymphaea*).

Artibeus is phenetically distinct except for *A. intermedius* (and presumably *A. lituratus*, not examined). This species is shown as moderately (unweighted pair-group method) or considerably (adaptive clustering analysis) different in the clustering results, although it is connected to its congeners in the minimum-spanning tree. The larger genera shown as phenetically most similar to *Artibeus* are *Vampyrops* and *Dermanura* (both by unweighted pair-group method and minimum-spanning tree).

Two recognized genera within the Stenodermatinae show little phenetic coherence. *Chiroderma* (containing five species) and *Vampyressa* (containing six) not only are fragmented in all results, but the species relationships also are inconsistent among the results. *Chiroderma improvisum*, the sole Antillean member of the genus, is shown in both clustering results as the most aberrant of all typical stenodermatine species (Figs. 1, 4); in the mininum-spanning tree, it is linked (albeit distantly) to all other *Chiroderma* except *C. doriae*. The only concordance among results is that *C. salvini* and *C. villosum* are most similar to each other.

As mentioned earlier, *Vampyressa macconnelli* always is shown as most similar to *Ectophylla alba*. All results indicate a similarity between *V. pusilla* and *V. bidens*. The unweighted pair-group method and minimum-spanning tree results also include *V. brocki* in this group. *Vampyressa nymphaea* is associated with *Chiroderma villosum*, *C. salvini*, and (in the unweighted-pair-group and minimum-spanning tree analyses) *C. trinitatum*. *Vampyressa melissa* is shown as loosely allied with *Chiroderma doriae* (unweighted pair-group method) or *V. pusilla* (minimum-spanning tree) or as a widely aberrant form with no discernible affinities (adaptive clustering analysis).

Comparison of phenetic relationships to the phylogeny of stenodermatine bats.—Based on four phylogenetic analyses of two morphological data sets, I produced a consensus cladogram (Fig. 7) that is a working hypothesis of stenodermatine relationships (Owen, 1987*a*). Because this is a consensus tree, unresolved nodes (branch points) generally reflect alternate topologies, one or more of which must be incorrect. Therefore, omission of a taxon in a clade on this tree (e.g., *Dermanura concolor* or *D. hartii* with the other *Dermanura*) generally reflects conflicting data or analytic results. Nevertheless, it should be emphasized that Fig. 7 is the synthesis of four analyses based on two independent data sets, and is the current working hypothesis concerning phylogenetic relationships among the species of Stenodermatinae. In this discussion of morphometric patterns, therefore, I will treat this figure as though it represents the true phylogeny, with the caveat that additional data or analyses may result in rearrangements within the tree. The following are comparisons of the phenetic results described herein, with the phylogenetic results of Owen (1987*a*). An extensive review of previous taxonomic work concerning Stenodermatinae

is presented in that paper, and is not repeated here. Nomenclatorial recommendations listed in the same paper also are indicated in Fig. 7 herein.

In the phylogenetic analysis, I found the eight short-faced genera to constitute a natural assemblage most closely related to *Dermanura*. Within this group, *Phyllops*, *Ardops*, and *Ariteus* are more closely related phylogenetically, and *Ametrida* and *Sphaeronycteris* also share a common ancestor. I was unable otherwise to resolve intergeneric relationships of these bats. The present study indicates phenetic distinctness not only of the eight short-faced genera as a group, but probably also between the mainland and Antillean groups. *Pygoderma* is less similar to the other mainland short-faced genera (*Centurio*, *Ametrida*, and *Sphaeronycteris*) than those bats are to each other. Within this group of 11 species, morphometric diversity appears to be as great as that within the remainder of the subfamily. It seems unlikely that this radical morphologic evolution would occur throughout this one clade entirely by chance. Given the apparent diversity of ecologic and biogeographic histories of these species, it seems unlikely also that any particular type of selective constraint would be responsible for this divergence. Rather, it is more plausible to infer that morphologic flexibility is an inherent property of this clade, and that the genetic propensity for such a characteristic may be carried as an historical attribute of the clade (Brooks and Wiley, 1986).

The genus *Sturnira* is a phenetically well-defined group whose taxonomic integrity generally is not questioned. My phylogenetic results (Owen, 1987*a*) and the present study are the first systematic evaluations of the entire genus since that of de la Torre (1961). The phylogenetic analyses did not resolve relationships among the *Sturnira* species, although I retained use of *Corvira* as a subgenus comprising the species *S.* (*C.*) *bidens* and *S.* (*C.*) *nana*. Phenetically, the genus *Sturnira* is widely divergent from the typical stenodermatines. Although these should not be construed as phylogenetic representations, Figs. 1 and 2 herein represent the only published systematic arrangements providing resolution among species of the genus *Sturnira*. These two phenograms are in agreement except on the placement of *S. mordax*. These results do not demonstrate phenetic distinctness of the subgenus *Corvira*.

Ectophylla is a monotypic genus (*E. alba*) related phylogenetically to *Uroderma* and *Artibeus* (Owen, 1987*a*). My phenetic results demonstrate consistent similarity between *Ectophylla alba* and *Vampyressa macconnelli*, and suggest that, based only on overall morphologic resemblance, it was reasonable for earlier authors (de la Torre, 1961; Starrett and Casebeer, 1968) to consider them closely related.

Uroderma, as mentioned earlier, is phylogenetically related to *Ectophylla* and *Artibeus*. Based on overall cranial similarities, though, the two species of *Uroderma* are unlike *Artibeus*, but more closely resemble *Dermanura* and some of the *Vampyressa* species.

The single species of *Vampyrodes* is related phylogenetically to *Chiroderma* and *Vampyrops* (Fig. 7). Phenetically, it is within or near *Artibeus*, with *Chiroderma doriae* also associated with it in the minimum-spanning tree results (Figs. 1, 4, 5, 6).

The genus *Dermanura*, as defined by Owen (1987*a*), comprises the species *D. watsoni*, *D. glauca*, *D. tolteca*, *D. cinerea*, *D. phaeotis*, *D. azteca*, *D. anderseni*, and provisionally *D. concolor* and *D. hartii*. These bats previously were recognized under the generic name *Artibeus* (Honacki et al., 1982). My consensus tree (Fig. 7) suggested that *D. phaeotis*, *D. azteca*, and *D. anderseni* are related most closely, and that *D. watsoni* and *D. glauca* are not subspecies of *D. cinerea*. The phenetic results present somewhat varying results concerning relationships of the *Dermanura* species. They agree with the phylogeny (Fig. 7) in closely associating *D. anderseni* and *D. phaeotis* (but not *D. cinerea*), and *D. tolteca* with *D. azteca*. Concerning the generic relationships of *Dermanura*, these phenetic results do not correspond with the cladistic findings, in which I showed these bats as related most closely to the eight short-faced genera.

My consensus tree (Fig. 7) suggested a cladistic relationship among *Vampyrops vittatus*, *V. aurarius*, *V. lineatus*, and *V. umbratus*, and among *V. nigellus*, *V. helleri*, and *V. dorsalis*. The phylogenetic relationships among *Vampyrops* species are not reflected in the phenetic diagrams herein. Also, these phenetic results are in contrast with the phyletic relationships concerning

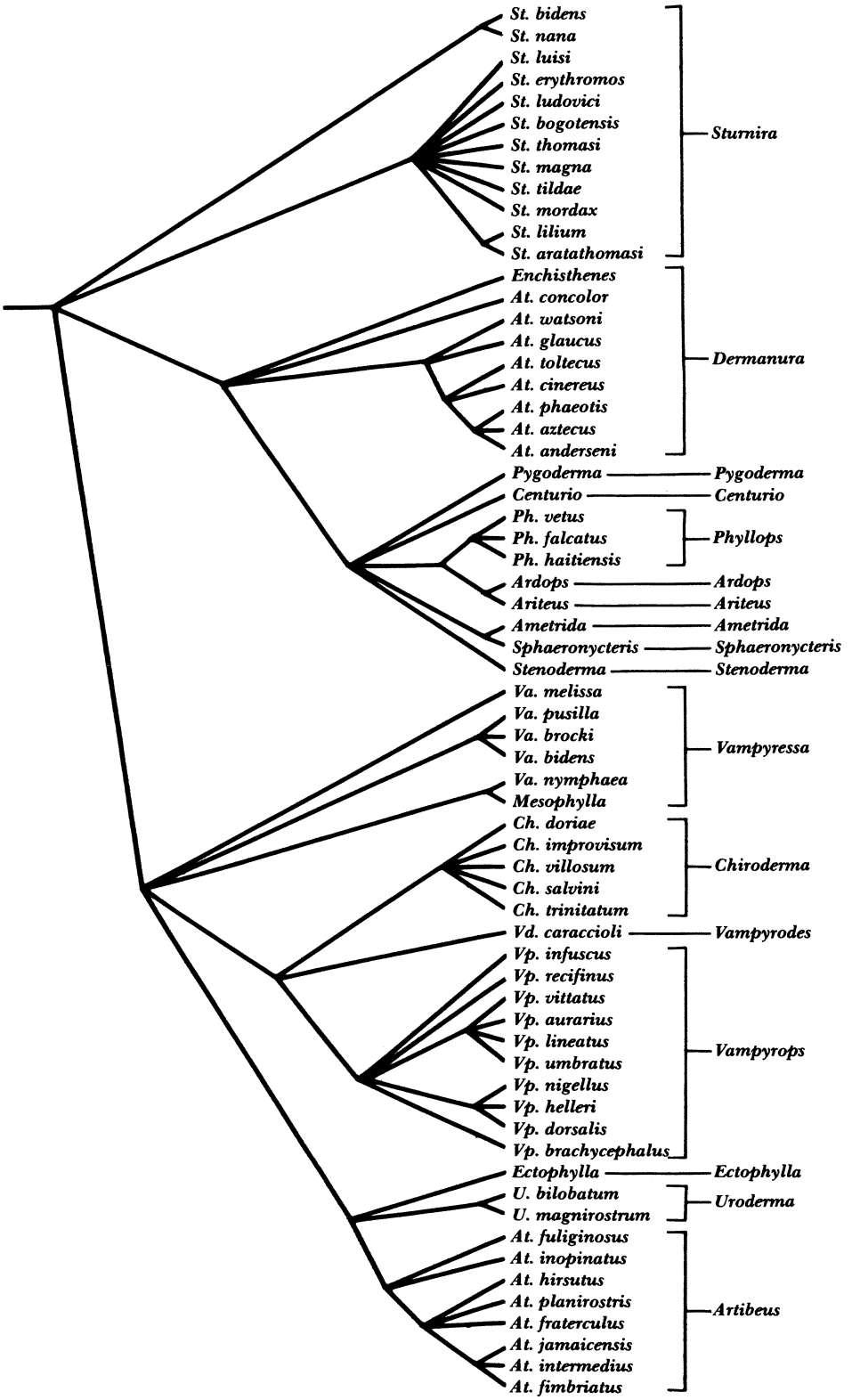

FIG. 7.—Cladogram representing consensus estimate of stenodermatine phylogeny from Owen (1987*a*). Generic names at right indicate current nomenclature based on recommendations in that paper.

generic affinities. *Vampyrops* was shown to be related phyletically to *Vampyrodes* and *Chiroderma*, whereas based on overall similarities it is more like *Artibeus*, *Dermanura*, and *Uroderma*.

The phylogenetic relationships among the species of *Artibeus* are poorly understood. Phenetically, all of the *jamaicensis*-type bats (*A. jamaicensis*, *A. planirostris*, *A. fuliginosus*, *A. fraterculus*, and *A. fimbriatus*) are closely related, with no particular pattern shared among all results. *Artibeus intermedius* is phenetically the most divergent member of the genus. *Artibeus hirsutus* and *A. inopinatus* also are phenetically dissimilar to their congeners, and to each other. Although *Artibeus* is related most closely cladistically to *Uroderma* and *Ectophylla* (Fig. 7), it is most similar phenetically to *Vampyrops* and *Dermanura*.

No genus other than *Sturnira* among the stenodermatines is as well defined as *Chiroderma*. The *Chiroderma* characteristics of missing nasal bones and spikelike upper incisors serve easily to distinguish it from all other bats. The evident distinctness of the genus notwithstanding, these five species are phenetically less homogeneous than any other genus except *Vampyressa*. A large part of the morphometric variability is contributed by *C. improvisum*, a biogeographically aberrant species known only from two specimens from the northern Lesser Antilles. Phyletically, the genus is a natural assemblage whose affinities lie with *Vampyrodes* and *Vampyrops*. Phenetically, various *Chiroderma* species are allied with several *Vampyressa* species (all analyses), *Vampyrodes* (minimum-spanning tree), and two other genera (unweighted pair-group method).

My consensus cladogram (Fig. 7) left the intrageneric relationships of *Vampyressa* partially unresolved and did not support monophyly of the genus. That cladogram suggested, however, a relationship among *V. pusilla*, *V. brocki*, and *V. bidens*, and between *V. nymphaea* and *V. macconnelli*. My phenetic results agree with the first of these two groups, and demonstrate that *V. melissa*, *V. nymphaea*, and *V. macconnelli* are widely divergent morphometrically. However, the minimum-spanning tree shows all *Vampyressa* species except *V. macconnelli* and *V. nymphaea* to be most similar to each other. *V. macconnelli* exhibits considerable similarity to *Ectophylla alba*, explaining the historical tendency for these two species to be considered congeneric (Anderson et al., 1982; de la Torre, 1961). It is clear, then, that not only is relatedness among the six *Vampyressa* species unsupportable based on shared derived characters; it also cannot be justified based on overall phenetic resemblances. It appears, rather, that the generally accepted status of the genus *Vampyressa* is based on symplesiomorphies, or shared primitive characters. Clearly, work remains to be done to determine the generic affinities of these six species.

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