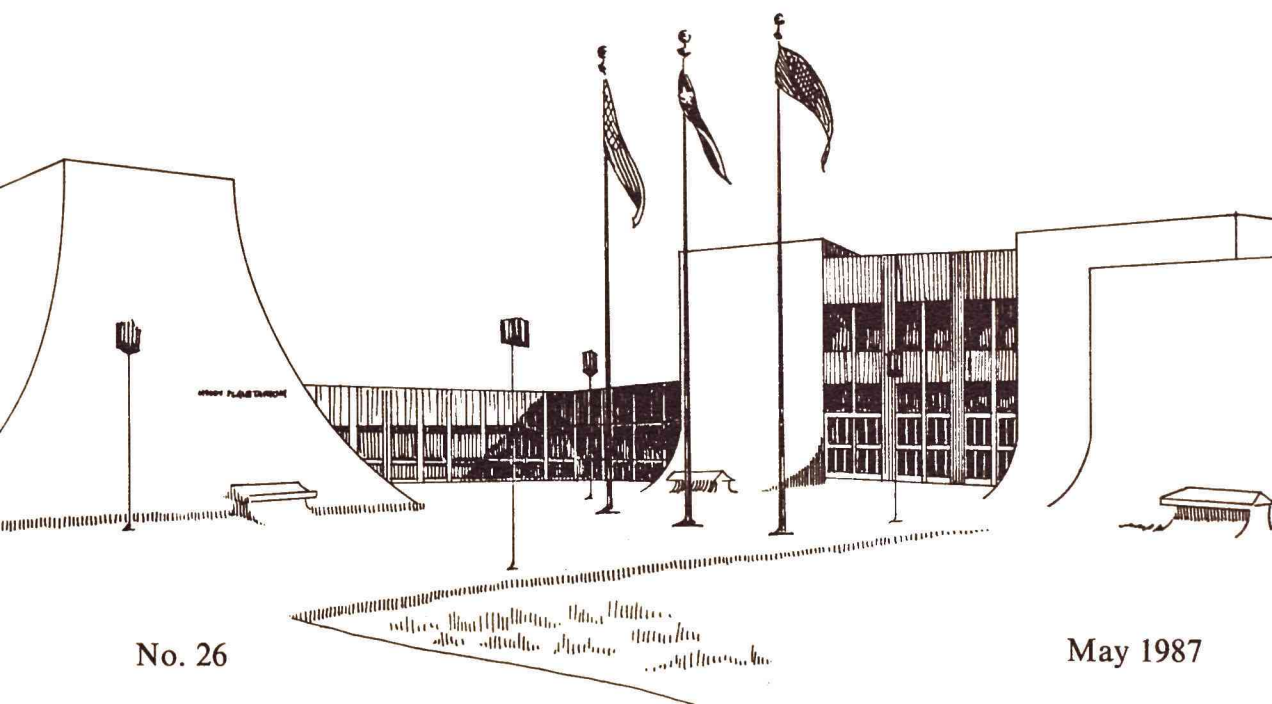# SPECIAL PUBLICATIONS
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Robert D. Owen

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Understanding of the systematic relationships of bats has not progressed as rapidly as for many other mammalian groups. Investigators generally agree that many characters and techniques traditionally used in mammalian systematics are at best insufficient for use with bats, but few studies have been undertaken that have included an intensive quantitative examination of a chiropteran group. Exceptions are Findley's (1972) analysis of phenetic relationships among bats of the genus *Myotis*, Smith's (1972) systematic analysis of the family Mormoopidae, and Freeman's (1981) study of the family Molossidae.

Several investigators, including Dobson (1875), Winge (1892), Smith (1976, 1977, 1980), Van Valen (1979), Novacek (1980), Arnold *et al.* (1982), and Hood and Smith (1982), have evaluated phylogenetic relationships among bats from the generic to the ordinal level. Concerning the family Phyllostomidae, other workers have attempted to determine relationships at the subfamilial and lower levels. These studies have involved a variety of approaches, including immunology (Forman *et al.*, 1968; Gerber and Leone, 1971), karyology (Baker, 1967, 1973; Forman *et al.*, 1968; Davis and Baker, 1974; Greenbaum *et al.*, 1975; Gardner, 1977; Baker *et al.*, 1979; Johnson, 1979; Haiduk and Baker, 1982), electrophoresis (Straney *et al.*, 1979; Koop and Baker, 1983), soft-tissue morphology (McDaniel, 1976; Griffiths, 1982; Tandler *et al.*, 1986), classical morphologic assessment—including dentition (Miller, 1907; Andersen, 1908; Sanborn, 1955; Davis, 1958; Peterson, 1968), and morphometrics (Forman *et al.*, 1968; Davis and Baker, 1974).

Although the subfamily Stenodermatinae is the most species-rich group within the Phyllostomidae, it is in several aspects the most homogeneous of the larger subfamilies. Unlike the phyllostomines, for instance, the stenodermatines all are dependent on similar foods, each being primarily or entirely frugivorous (Wilson, 1973). The subfamily as now constituted, consisting of 16 or 17 nominal genera and 55 to 59 species (Jones and Carter, 1976; Honacki *et al.*, 1982), includes three genera that together contain over half of the species; in addition, seven to nine genera are considered to be monotypic, depending on the authority consulted. Although considered as a distinct group since 1855 (Miller, 1907), the subfamily Stenodermatinae has undergone several partial revisions, as have most of the genera within it. Miller (1907) recognized 19 genera within the group. Of these, *Brachyphylla* has since been placed tentatively in the Phyllonycterinae (Silva Taboada and Pine, 1969; Jones and Carter, 1976),

Vampyriscus within *Vampyressa*, and *Mesophylla* within *Ectophylla* (but see Starrett and Casebeer, 1968). Of the approximately 50 species recognized by Miller (1907), at least 17 have undergone taxonomic or nominal alteration, and a number of new species have been described.

Since the appearance of Jones and Carter's (1976) checklist, the number of known species has increased from 55 to about 65. My analyses address the interspecific relationships within the subfamily. I evaluate seven problems of current interest: (1) the interspecific and subgeneric relationships within *Sturnira*; (2) the status and relationships of the numerous described species of *Vampyrops*; (3) the relationship of *Uroderma* to other genera; (4) the phylogeny of the eight "short-faced" genera within the subfamily (that is, *Ardops, Phyllops, Ariteus, Stenoderma, Pygoderma, Ametrida, Sphaeronycteris,* and *Centurio*); (5) the relationships of species and subgenera within the relatively small genus *Vampyressa*; (6) the inclusion of *Mesophylla* within *Ectophylla*; and (7) the relationships within the genus *Artibeus*.

These questions can be addressed appropriately only by a phylogenetic analysis of the entire subfamily, because even the monophyly of a number of the genera is in question. My analyses include all known species within the subfamily, and are based upon suites of discrete-state and mensural characters. These analyses should produce robust hypotheses concerning the phylogeny of the subfamily Stenodermatinae.

Species in the Subfamily Stenodermatinae

I analyzed the relationships of 64 taxa considered to be species (Appendix 1) based on Jones and Carter (1976), and subsequent publications. For ease of discussion only, I used the generic names *Enchisthenes* and *Mesophylla* rather than including these bats in *Artibeus* and *Ectophylla*, respectively. I have followed Handley (1980) in subfamilial nomenclature.

Considerable uncertainty exists concerning affinities of the Antillean endemic genus *Brachyphylla*; I have followed Dusbabek (1968), Silva Taboada and Pine (1969), Baker and Lopez (1970), Baker *et al.* (1979), and Sites *et al.* (1981) in not including this genus in the subfamily Stenodermatinae. For a review of the taxonomic history of *Brachyphylla*, see Swanepoel and Genoways (1978).

Following Winge (1892), de la Torre (1961), Baker (1967), Gerber and Leone (1971), Gardner (1977), and Baker *et al.* (1979), I have included the enigmatic genus *Sturnira* in the subfamily. In addition to the 10 *Sturnira* species listed by Jones and Carter (1976), I have included *S. luisi* and *S. bogotensis*, both of which were recognized by Honacki *et al.* (1982).

Gardner and Carter (1972a) and Carter and Rouk (1973) considered *Vampyrops umbratus* to be conspecific with *V. dorsalis*. Handley (1976), however, recognized *V. umbratus* as distinct. Honacki *et al.* (1982) also recognized this separation, and I have treated these as two species.

One stenodermatine species (*Phyllops vetus*) is known only from fossil remains. For the sake of completeness, I have included this species in the study.

There is considerable disagreement concerning the taxonomy of the genus *Artibeus*. For many species names, it is necessary to describe exactly which populations are meant, as names have been applied in various ways by various authors. Furthermore, dispute continues over the status of names in Patten's (1971) unpublished dissertation. The three middle-sized *Artibeus* (*A. hirsutus*, *A. inopinatus*, and *A. concolor*) are well studied. Among the large *Artibeus* the systematics of the Middle American taxa also is understood relatively well, and I have used Mexican and Central American specimens to represent *A. jamaicensis*.

Artibeus lituratus was thought to be taxonomically well understood throughout its range until Davis (1984) reported a zone of overlap between two size classes of *A. lituratus* in Honduras. Consequently, he raised *intermedius* (the northern and Gulf Coast taxon) to specific status. My specimens of *A. "lituratus"* were from north of this overlap zone and, therefore, are referable to the name *A. intermedius*. *Artibeus lituratus* is appropriately considered as the sister species to *A. intermedius*.

Artibeus jamaicensis may or may not be represented south of Colombia; I have treated South American *jamaicensis*-like bats as distinct species. One of these, occurring on the Pacific versant of the Andes, is *A. fraterculus*. At least two *jamaicensis*-like taxa occur east of the Andes: (1) *A. fuliginosus*, is a relatively small, dark-colored bat; (2) a larger bat has been identified as *A. planirostris* (the name I have used here). See Koopman (1978) for a discussion of these large South American *Artibeus*, as well as the status of names used by Patten (1971). Myers and Wetzel (1983) discussed a population that they believed would prove to represent a third *jamaicensis*-like bat east of the Andes, and indicated that the name *fimbriatus* should apply to it. I have followed them in treating this population as distinct from the other species of large *Artibeus*; however, the status of the name *fimbriatus* is left to consideration by other workers.

I have recognized seven species of small *Artibeus*. These are the six species recognized by Jones and Carter (1976) except that, following Koopman (1978) and Honacki *et al.* (1982), *A. anderseni* was considered distinct from *A. cinereus*.

CHARACTERS AND CODING

When possible, I took measurements and coded multistate characters from at least 10 specimens, five of each sex (Appendix I). My objective was to derive the best estimate of stenodermatine phylogeny obtainable from external and osteological characteristics. Accordingly, suites of continuous and discrete-state characters were coded, and several analytic methods were employed.

A total of 22 discrete-state external, cranial, mandibular, and dental characters was coded for each specimen. Postcranial characters were not used because full skeletons were unavailable for 18 of the 64 species studied. The 22 characters are listed, their character states described, and an unrooted character-state tree is given for each in Appendix II. I assigned the external character states of *Phyllops falcatus* to *P. vetus* (known only from fossil remains). For five of the six characters these also were representative of *P. haitiensis*.

The 33 continuous-characters also measure aspects of the cranium, mandible, and teeth (Appendix III). Some were taken directly from, or adapted from, Freeman (1981); I developed additional characters representing consistently measurable distances between homologous points.

ESTIMATING THE ANCESTOR—OUTGROUP PROCEDURES

Two steps are critical in phylogenetic analyses. The first is inclusion of a monophyletic assemblage of taxa as the ingroup, and the second is determination of the character-state transformation series. One facet of the transformation series is the order of evolutionary change, or tree topology. I specified tree topologies "based on the assumption that the most evenly graded series of changes is the evolutionarily-most-probable hypothesis" (Kluge, 1976).

A second facet of the transformation series is the direction of evolutionary change, specified by the tree root. All proposed procedures for rooting character-state trees are simply indirect methods of estimating the suite of character states comprising the most recent common ancestor of the study group. Watrous and Wheeler (1981) first formalized outgroup-comparison methodology and introduced the concept and terminology of functional ingroup and functional outgroup. Maddison *et al.* (1984) showed the relationship of the outgroup criterion to global and local parsimony, and developed arguments for the critical importance of outgroups with known relationships to each other and to the ingroup. They presented rules for resolution of outgroup relationships, and underscored the importance of using more than one outgroup taxon simultaneously in order to determine correctly both the position and direction of character-state changes in the ingroup phylogeny. I have followed Maddison *et al.* (1984) in my use of outgroups in the analysis.

Phyllostomid subfamilial relationships are poorly understood, especially the affinities of the Stenodermatinae. However, recent evidence (Honeycutt, 1981; Hood and Smith, 1982; Honeycutt and Sarich, 1987) indicates that the subfamily Carolliinae is the sister group to the stenodermatines. I, therefore, included the four species of *Carollia* among my outgroup taxa.

In order to strengthen the outgroup process of character-state tree construction, I used an additional outgroup species chosen on the basis of its presumed similarity to the hypothetical primitive phyllostomid. *Macrotus waterhousii* has been suggested as primitive for the family, not

only karyotypically (Bourlière, 1955; Patton and Baker, 1978) but also on the bases of general morphology (Winge, 1892), osteology (Walton and Walton, 1968), dentition (Slaughter, 1970), and fetal membrane structure (Luckett, 1980).

ANALYSES OF DISCRETE-STATE CHARACTERS

The six external and 16 cranial characters coded for each specimen are listed and described in Appendix II. The number of coded states for the discrete-state characters ranges from two (postglenoid foramen) to nine (dental formula). Some of these characters were intraspecifically variable in some species (Owen, 1987: appendix A1). To choose the character state that would most appropriately represent each species in the analyses, I used the modal, or most commonly encountered, state. If two states were equally common, I used the more plesiomorphic of the two. This is the conservative estimate in that I did not postulate a synapomorphy unless a uniquely modal state was found. After determining the representative character states for each of the outgroup species, a plesiomorphic state for the ingroup was considered as the one that is (in order of descending importance): (1) carried by all *Carollia* species; (2) shared by *Carollia* (one or more species) and *Macrotus*; (3) the modal state among the four *Carollia* species; (4) the modal state among the four *Carollia* species and *Macrotus*; or (5) in case of a modal tie in (4), the co-mode carried by *Macrotus*. Criteria 2 through 5 were needed in only a few cases. Even if these criteria were invoked in some other reasonable sequence, there would be few, if any, different assignments of character states to species.

Once the representative character states were determined for each species (Table 1), I transformed them into two-state (presence or absence) characters using additive binary coding (Sneath and Sokal, 1973). The 22 multistate characters thus were transformed into 72 two-state characters.

Wagner analysis.—Wagner analysis is a method of estimating a phylogeny through construction of the most parsimonious (shortest), rooted branching network that reflects the character states of the taxa under study. It is an approximation of the Hennigian phylogenetic method that is used appropriately when a synapomorphy scheme (Nelson, 1979) cannot be determined. The reasons for use of the parsimony criterion have been well documented (Camin and Sokal, 1965; Kluge and Farris, 1969; Estabrook, 1978; Farris, 1982; Panchen, 1982; Maddison *et al.*, 1984; Rohlf, 1984).

Maddison *et al.* (1984) described a method whereby successively smaller clades of a group of taxa may be studied, thus allowing the investigator to search for locally parsimonious solutions within the previously established constraints of a global parsimony solution. I have followed their general method of: (1) determining stable portions of the cladogram; (2) determining unstable portions in need of further analysis; and (3) establishing and confirming the ancestor estimate for these successive analyses.

TABLE 1.—*Discrete-state character values for stenodermatine and outgroup species examined. See Appendix II for description of characters, character states, and character-state trees. Characters are listed here in the same order as in Appendix II.*

Species	Character																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
STENODERMATINAE																						
Ametrida centurio	4	2	3	5	1	2	4	0	1	1	2	2	2	3	1	2	1	0	1	0	1	0
Ardops nichollsi	6	3	3	5	2	2	3	0	2	2	2	3	2	3	1	3	1	1	0	0	1	0
Ariteus flavescens	4	2	3	5	2	2	3	0	2	2	1	2	2	3	2	2	1	1	0	0	3	0
Artibeus anderseni	4	5	2	1	1	2	3	0	1	1	2	2	1	1	2	2	1	0	1	0	5	2
Artibeus aztecus	6	4	2	1	2	2	3	0	1	2	2	2	2	2	2	2	1	0	0	0	5	2
Artibeus cinereus	4	4	2	1	1	2	3	0	1	2	2	3	2	1	2	2	1	0	0	0	5	2
Artibeus concolor	4	3	3	0	1	3	3	0	1	2	2	1	2	3	1	2	0	0	0	0	1	0
Artibeus fimbriatus	4	3	2	1	1	2	3	0	1	2	2	3	2	3	2	2	0	0	0	0	3	0
Artibeus fraterculus	4	3	2	1	1	2	3	0	1	2	2	3	3	3	2	2	0	0	0	0	3	1
Artibeus fuliginosus	4	3	2	0	1	2	3	0	0	2	2	2	2	3	1	2	0	0	0	1	1	1
Artibeus glaucus	4	5	2	1	1	2	3	0	1	1	1	2	3	2	2	2	1	0	0	0	3	1
Artibeus hirsutus	4	3	2	1	1	2	3	0	1	3	2	2	2	3	1	2	1	0	0	0	1	1
Artibeus inopinatus	4	3	2	1	1	2	3	0	1	2	2	3	2	3	1	2	1	0	0	0	1	0
Artibeus intermedius	4	3	2	1	1	2	3	0	1	2	2	3	1	3	2	2	0	0	0	0	3	1
Artibeus jamaicensis	4	3	2	1	1	2	3	0	1	2	2	2	2	3	2	2	0	0	0	0	3	1
Artibeus phaeotis	6	5	2	1	1	2	3	0	1	2	2	3	2	2	2	1	1	0	0	0	5	2
Artibeus planirostris	4	3	2	1	1	2	3	0	1	2	2	3	1	3	1	2	0	0	0	0	1	1
Artibeus toltecus	6	5	2	1	1	2	3	0	1	1	2	3	2	2	2	1	0	0	0	0	5	2
Artibeus watsoni	6	5	2	1	1	2	3	0	1	2	2	2	3	2	2	2	0	0	0	0	3	1
Centurio senex	5	1	3	6	1	2	1	0	2	1	1	2	2	3	2	2	1	1	0	0	5	2
Chiroderma doriae	2	2	3	1	0	1	3	1	0	3	3	3	1	0	2	3	1	0	2	2	5	0
Chiroderma improvisum	4	2	2	2	0	2	1	0	0	0	2	3	0	2	0	2	1	0	2	2	5	2
Chiroderma salvini	6	4	3	3	0	2	3	1	0	2	2	2	2	0	2	2	1	0	2	1	5	2
Chiroderma trinitatum	4	4	3	3	1	2	3	1	0	0	2	2	2	2	0	2	1	0	2	2	5	2
Chiroderma villosum	4	3	3	1	0	2	3	2	0	3	2	2	1	1	2	2	1	0	2	2	5	2
Ectophylla alba	3	2	1	0	1	2	1	0	1	1	2	3	4	0	2	1	1	0	1	0	5	2
Enchisthenes hartii	4	2	2	1	2	2	3	0	1	1	2	3	3	2	0	2	1	0	1	0	1	0
Mesophylla macconnelli	4	4	3	0	1	2	3	1	1	3	2	1	3	0	2	1	1	0	1	1	3	1
Phyllops falcatus	6	2	3	5	2	2	3	0	2	2	2	3	2	3	1	1	0	1	0	0	1	0
Phyllops haitiensis	6	1	3	5	2	2	1	0	2	1	2	3	1	3	1	1	0	1	0	0	1	0
Phyllops vetus	6	2	3	5	2	2	3	0	2	2	2	3	3	2	1	2	1	1	0	0	1	0
Pygoderma bilabiatum	6	2	3	5	0	2	3	0	1	2	2	3	2	3	2	3	1	0	0	1	5	2
Sphaeronycteris toxophyllum	6	1	3	5	1	2	2	0	2	1	2	2	2	3	1	2	1	0	1	2	1	1
Stenoderma rufum	4	5	3	5	1	2	4	0	2	2	1	3	2	2	1	2	0	1	1	3	1	0
Sturnira aratathomasi	4	3	3	0	3	1	4	0	1	1	1	3	3	0	1	2	1	0	1	1	1	0
Sturnira bidens	4	3	3	0	3	1	3	0	1	2	1	1	2	0	0	2	1	0	1	0	2	0
Sturnira bogotensis	4	2	3	0	3	0	3	0	1	1	1	2	3	0	0	1	1	0	1	1	1	0
Sturnira erythromos	4	2	3	0	3	1	3	0	1	1	1	2	4	0	0	2	1	0	1	0	1	1
Sturnira lilium	3	2	3	0	3	1	3	0	1	2	1	3	3	0	1	1	1	0	1	1	1	0
Sturnira ludovici	4	2	3	0	3	1	3	1	1	1	1	3	2	0	0	1	1	0	1	1	1	0
Sturnira luisi	4	2	3	0	3	1	3	1	1	1	1	2	3	0	0	2	1	0	1	1	1	0
Sturnira magna	4	2	3	0	3	1	3	0	0	2	1	3	3	1	1	2	1	0	1	0	1	1
Sturnira mordax	4	2	3	0	3	1	3	0	1	1	1	3	3	0	0	1	1	0	1	1	1	0

TABLE 1.—*Continued.*

Species	Character																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Sturnira nana	4	3	3	0	3	2	3	0	0	2	1	2	2	0	0	1	1	0	1	0	2	0
Sturnira thomasi	4	2	3	0	3	0	3	0	0	1	1	3	4	0	0	1	1	0	1	1	8	2
Sturnira tildae	4	2	3	0	3	1	3	0	1	1	1	3	4	0	0	2	1	0	1	1	1	0
Uroderma bilobatum	6	4	2	3	1	2	1	0	0	2	2	3	1	3	1	2	1	0	0	0	1	1
Uroderma magnirostrum	4	3	2	3	1	3	1	0	0	2	2	3	2	2	0	2	1	0	0	0	1	0
Vampyressa bidens	4	5	3	4	1	2	3	1	0	3	2	2	2	0	2	2	1	0	1	1	7	1
Vampyressa brocki	4	4	3	1	1	2	3	1	0	3	2	2	2	0	2	2	1	0	1	1	5	2
Vampyressa melissa	4	5	3	1	2	2	1	1	0	2	2	2	4	0	2	2	1	0	1	1	3	1
Vampyressa nymphaea	4	4	3	2	1	2	3	1	1	2	2	1	2	0	2	2	1	0	1	1	5	2
Vampyressa pusilla	4	5	3	1	1	2	3	1	1	2	2	2	3	0	2	2	1	0	1	1	5	2
Vampyrodes caraccioli	4	2	2	4	2	2	3	1	0	2	2	2	3	1	2	3	1	0	1	2	3	0
Vampyrops aurarius	4	5	2	4	2	2	3	1	0	1	2	1	3	0	1	2	1	0	1	1	1	0
Vampyrops brachycephalus	6	4	2	4	2	2	3	1	1	2	2	1	3	1	1	2	1	0	1	1	1	0
Vampyrops dorsalis	4	3	3	4	2	2	3	1	0	1	2	2	2	1	1	2	1	0	1	2	1	0
Vampyrops helleri	4	4	2	4	2	3	1	1	1	2	2	1	3	1	1	2	1	0	1	1	1	0
Vampyrops infuscus	4	5	2	3	2	2	3	1	0	2	2	2	3	0	1	2	1	0	1	1	1	0
Vampyrops lineatus	6	3	2	4	2	2	3	1	1	2	2	2	2	0	1	2	1	0	1	1	1	0
Vampyrops nigellus	6	4	2	4	2	2	3	1	1	1	2	1	3	1	1	2	1	0	1	1	1	0
Vampyrops recifinus	3	3	2	2	1	2	1	1	1	2	2	1	3	0	1	2	0	0	1	1	1	0
Vampyrops umbratus	3	5	2	3	2	2	3	1	1	1	2	1	2	1	1	2	1	0	1	1	1	0
Vampyrops vittatus	4	4	2	4	2	2	3	1	1	1	2	3	3	0	1	2	1	0	1	1	1	0
CAROLLIINAE																						
Carollia brevicauda	4	4	3	0	0	0	3	1	0	2	1	2	4	0	0	2	1	0	0	0	1	0
Carollia castanea	4	3	3	0	0	0	1	1	0	2	1	2	4	0	0	2	1	0	0	0	1	0
Carollia perspicillata	4	3	3	0	0	0	1	1	0	2	1	2	3	0	0	1	1	0	0	0	1	0
Carollia subrufa	4	2	3	0	0	0	1	1	0	3	1	2	3	0	0	1	1	0	0	0	1	0
PHYLLOSTOMINAE																						
Macrotus waterhousii	8	2	2	0	0	0	5	1	1	3	1	1	2	1	0	2	1	0	1	0	0	0

I used the WAGNER78 computer program supplied by J. S. Farris. For each analysis (all taxa together first, and then successively smaller subsets of the taxa), I ran the Wagner program 50 times, each time entering the taxa in a different order. This is especially crucial in initial analyses of all taxa because of the vast number of possible tree topologies, and concomitant low likelihood of finding the shortest in a particular run. Another important aspect of this procedure is that it allows the investigator to examine a large number of tree topologies for "stable" portions (that is, portions that do not differ among the alternate trees being examined). This procedure thus adds a robustness to the phylogenetic estimate and, simultaneously, identifies portions of the tree in need of additional analysis. For any particular analysis, I arranged the results in order of total tree length and examined the shortest 25 of the 50 trees plus any others of the

same length as those included in the group. This group is referred to as the "shortest half" of the trees. I considered as stable only those portions of the tree that did not differ among the shortest half of the trees.

The initial analysis established the major clades among stenodermatine bats; successive analyses then were performed on "unstable" (thus unresolved) portions of the tree. In each case, a monophyletic portion of the tree was analyzed and, following Maddison *et al.* (1984), the ancestral state was estimated using those two taxa found to be the shortest distance from the hypothetical ancestor of the clade being reanalyzed. Although this method of repeated ancestor estimation for successively smaller portions of the tree might be suspected of leading to accumulated error, it should be emphasized that no locally parsimonious solution was accepted that was not concordant with one of the globally parsimonious solutions previously determined (that is, the shortest half of the trees found in the initial analysis).

Analysis using Weighted Invariant Step Strategy.—In contrast to the Wagner method, the Weighted Invariant Step Strategy (WISS) is a "top-down" type of clustering algorithm (that is, the terminal taxa with the greatest degree of similarity are clustered first, on the assumption that their shared similarities are uniquely derived). Farris *et al.* (1970) first formalized this method and discussed its relationship to parsimony (including Wagner) methods. The procedure, simply stated, is to select a subset of species for inclusion in a monophyletic group that is "best founded" in the sense that it shares at least as many derived steps as does any other possible subset of species; delete the subset from the set of species under consideration; replace it with the Hypothetical Taxonomic Unit (HTU) that represents the most recent common ancestor of the members of the subset; and repeat the process until the tree is specified. The program used was HENNIG, a Fortran IV program supplied by J. S. Farris.

ANALYSES OF CONTINUOUS CHARACTERS

Considerable controversy exists concerning the value of and methodologies for use of continuous (mensural) data in phylogenetic analyses. Wood (1983) pointed out that there is substantial information in such characters, but the problem is to extract mathematically the information that distinguishes systematically between taxa from the overall body of information contained in the data set. I use "information" to mean "stored information" rather than the "potential information" of Weaver (1949) or the "entropy" of Shannon (1949). In his studies of cranes, storks, and grassland sparrows, Wood (1983) found that the useful information typically represented only five to 10 percent of the total variation in the data set, and that the remaining 90 to 95 percent of the variation was common to all members of the data set and, hence, not useful. Below I describe a series of transformations and other manipulations of mensural characters that I believe allow a credible phylogenetic analysis from such a data set.

As pointed out by Jolicoeur *et al.* (1984), "the statistical model generally most appropriate in biological morphometrics is the lognormal distribution (in its univariate, bivariate, or multivariate versions)." Accordingly, all values in this study first were transformed to their natural logarithms. As biological size relationships typically are allometric, the log transformation has the effect of linearizing (but not reducing) the effect of size in the data matrix. The first principal component, therefore, will have a higher eigenvalue than it would have without the log transformation, and the remaining components will reflect less of the size relationships among taxa. The log transformation has the additional function of legitimizing arithmetic means and other linear statistics of the data (Humphries *et al.*, 1981).

As sexual dimorphism is known to exist to varying degrees among stenodermatine bats, the number of characters was doubled by using the male and female mean value of each character as separate characters (Table 2). Although this results in mostly redundant variation, the nonredundant portion (that is, the part reflecting sexual dimorphism) may have systematic usefulness (see Schnell *et al.*, 1978).

The result of the procedures described above is a matrix of appropriately transformed and averaged character-state values for each taxon. The remaining problem is to extract the useful information from the matrix and, from this reduced matrix, to construct an estimate of the phylogeny. I used two methods of data reduction to extract useful information.

Size-free analysis.—One method used was a "size-out" procedure. After averaging (for each sex) the log-transformed values, a matrix of character correlations was calculated, and a principal components analysis was performed on the matrix. From this, the matrix of projections of each species on each component was calculated based on unstandardized data. The vector of projections on the first component was deleted from the matrix, and the remaining vectors of projections were taken to be character-state values for a newly created suite of characters; thus, the effect of principal component I is removed from the matrix. In the case of the transformation described above, this component mostly reflects size relationships. More importantly, the converse also is true, and the remaining matrix should contain essentially size-free information. A Wagner analysis was then performed on this matrix. Unlike the case of discrete-state information, "ties" in calculated distances (and, thus, in the order of inclusion of species in the tree) are highly improbable; therefore, the same tree is generated regardless of order of species entry into the tree-generating procedure. This single tree then represents the best phylogenetic estimate for the group based on the size-free data matrix.

Common-part-removed analysis.—Wood (1983) described a transformation for phenetic analysis of continuous data. This transformation involves regression of the vector of the character values of each species studied on the character-value vector(s) of one or more closely related species. He

TABLE 2.—*Character means (mm) for each sex of stenodermatine bat species. See Appendix III for descriptions of characters. Dash indicates missing value.*

Species	Sex	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Sturnira lilium	F	22.18	20.18	9.73	6.05	5.87	13.28	11.80	10.18	8.90	12.67	9.32	6.42	5.27	2.98	5.08	1.95
	M	22.50	20.57	10.17	6.43	6.05	13.83	12.30	10.50	9.05	12.60	9.47	6.55	5.35	2.98	5.08	1.95
Sturnira thomasi	F	24.02	23.08	11.52	5.98	5.72	12.18	11.66	9.84	8.82	12.76	10.84	6.92	5.62	3.06	4.84	2.08
	M	24.90	23.75	12.30	6.40	5.80	12.50	12.00	9.90	8.90	12.60	10.90	7.05	5.85	3.00	5.25	1.80
Sturnira tildae	F	23.58	21.74	11.08	6.72	6.22	14.50	12.82	10.92	9.12	12.68	10.22	6.82	5.54	3.00	5.14	1.98
	M	23.99	22.10	11.39	7.01	6.39	14.66	12.91	10.89	9.31	12.80	10.61	7.07	5.63	3.07	5.39	2.23
Sturnira magna	F	27.00	24.96	12.70	7.14	6.74	16.06	14.50	12.40	10.18	14.60	11.66	7.08	5.60	3.52	5.76	2.38
	M	27.72	25.27	12.93	7.69	7.07	16.74	14.92	12.44	10.42	14.62	12.07	7.33	5.80	3.70	5.99	2.49
Sturnira mordax	F	23.82	21.68	11.28	5.92	5.83	12.82	11.78	10.57	9.17	12.75	10.42	6.57	5.22	2.77	4.98	2.12
	M	24.21	22.36	11.44	6.19	6.07	13.22	12.19	10.66	9.21	13.09	10.86	6.62	5.38	2.92	4.90	2.21
Sturnira bidens	F	20.32	18.71	9.63	5.43	5.17	11.67	10.99	9.69	8.32	11.44	8.94	5.88	4.79	2.10	3.93	1.73
	M	20.83	18.88	9.83	5.66	5.26	11.84	11.10	9.83	8.30	11.63	9.10	5.86	4.74	2.03	3.98	1.79
Sturnira nana	F	18.52	16.82	8.86	4.84	4.66	10.07	9.32	8.48	7.22	10.26	8.12	4.86	4.02	2.00	3.62	1.64
	M	18.50	16.73	8.55	4.88	4.70	10.03	9.43	8.52	7.47	10.43	8.20	4.90	3.98	1.82	3.63	1.52
Sturnira aratathomasi	F	27.60	25.52	12.52	7.95	7.07	17.00	14.70	12.82	10.42	14.82	11.38	7.72	6.22	3.63	6.02	2.45
	M	27.60	25.80	12.87	8.07	7.23	17.10	14.97	13.03	10.37	14.77	11.43	7.80	6.17	3.67	5.80	2.73
Sturnira ludovici	F	21.88	20.04	10.04	6.24	5.92	13.10	11.65	10.11	8.86	12.49	8.99	6.22	5.14	2.74	4.87	1.86
	M	23.04	21.02	10.38	6.50	6.05	13.63	12.02	10.47	9.13	12.75	9.62	6.48	5.20	2.90	5.00	2.02
Sturnira erythromos	F	20.90	19.15	9.45	6.09	5.65	12.86	11.14	10.01	8.33	11.95	8.85	5.91	4.94	2.54	4.68	1.79
	M	20.93	19.12	9.30	6.09	5.69	12.81	11.21	9.90	8.33	12.08	8.91	5.88	4.87	2.48	4.68	1.88
Sturnira luisi	F	23.02	21.14	10.50	6.32	5.90	13.76	12.14	10.68	8.94	12.94	10.26	6.58	5.40	2.96	5.26	1.88
	M	23.16	21.24	10.66	6.38	5.96	13.98	12.30	10.70	9.02	13.02	10.34	6.82	5.46	3.06	5.26	2.08
Sturnira bogotensis	F	21.77	19.89	9.94	6.26	5.84	13.39	11.73	10.31	8.61	12.40	9.17	6.22	5.12	2.52	4.76	1.84
	M	22.18	20.33	10.05	6.37	5.92	13.62	11.80	10.40	8.77	12.82	9.42	6.25	5.18	2.52	4.78	1.87
Uroderma bilobatum	F	22.28	19.96	9.98	5.90	5.28	12.78	10.90	10.06	8.46	12.48	11.60	7.80	6.56	2.70	4.66	1.64
	M	22.82	20.35	10.43	6.05	5.33	13.23	11.00	10.00	8.53	12.87	11.62	8.08	6.75	2.70	4.88	1.47
Uroderma magnirostrum	F	23.10	21.34	10.47	6.45	5.80	13.02	11.10	9.74	8.20	13.15	12.19	7.91	6.60	2.94	5.11	1.65
	M	23.49	21.84	10.76	6.55	5.72	13.54	11.09	9.74	8.36	13.19	12.42	8.00	6.71	2.90	4.95	1.72
Vampyrops infuscus	F	29.83	27.43	14.61	6.94	6.56	17.93	14.61	12.39	10.34	15.26	15.69	11.88	9.94	3.93	7.77	2.37
	M	30.80	28.38	14.94	7.58	6.98	18.72	15.40	12.70	11.28	16.06	16.16	12.14	10.34	3.80	8.14	2.40
Vampyrops vittatus	F	31.77	29.44	15.67	8.21	7.49	19.01	15.27	12.97	11.00	16.49	16.24	12.47	10.61	4.17	8.63	2.54
	M	31.50	29.35	15.17	8.20	7.55	19.20	15.32	13.05	11.07	16.72	16.36	12.58	10.78	4.06	8.50	2.47
Vampyrops umbratus	F	27.84	25.35	13.15	6.69	6.52	16.81	13.81	11.89	10.01	15.05	14.20	10.55	8.80	3.71	6.84	2.01
	M	28.54	25.84	13.54	6.70	6.49	17.26	14.13	12.06	10.27	15.34	14.36	10.64	8.79	3.63	6.90	2.07

Species	Sex	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
												Character						
Sturnira lilium	F	2.27	1.18	1.48	2.53	14.26	13.73	10.34	7.24	10.31	6.86	4.97	3.47	5.21	3.41	2.23	2.17	2.17
	M	2.47	1.22	1.50	3.02	14.93	14.45	10.87	7.45	10.83	7.07	5.12	3.80	5.40	3.68	2.38	2.62	2.23
Sturnira thomasi	F	2.24	1.18	1.40	2.58	15.88	15.28	11.46	7.46	12.00	8.10	5.30	3.54	5.24	3.18	2.20	2.28	2.18
	M	2.40	1.20	1.40	3.15	16.35	15.75	11.60	7.65	12.55	8.55	5.50	3.80	5.30	3.35	2.60	2.80	2.30
Sturnira tildae	F	2.64	1.34	1.52	2.80	15.78	15.06	11.40	7.58	11.48	7.76	5.78	4.06	6.02	4.18	2.44	2.57	2.50
	M	2.67	1.31	1.59	3.14	15.99	15.41	11.56	7.64	11.69	7.63	5.76	4.19	6.01	3.90	2.66	2.90	2.47
Sturnira magna	F	2.98	1.14	1.42	3.02	17.98	17.00	12.96	8.16	13.42	9.08	6.62	4.74	7.16	4.50	2.92	2.76	2.54
	M	3.17	1.19	1.56	3.92	18.32	17.48	12.91	8.54	13.42	9.12	6.88	4.78	7.26	4.59	3.09	3.59	2.66
Sturnira mordax	F	2.35	1.17	1.33	2.60	15.25	14.87	11.10	7.37	11.72	7.80	5.45	3.63	5.13	3.53	2.20	2.37	2.02
	M	2.41	1.20	1.39	3.11	15.83	15.50	11.74	7.43	11.86	8.20	5.81	3.63	5.48	3.60	2.44	3.10	2.00
Sturnira bidens	F	2.02	0.98	1.45	2.32	13.15	12.91	9.51	6.74	9.62	6.24	4.36	3.03	4.72	3.04	1.81	2.34	1.96
	M	2.09	0.97	1.39	2.44	13.38	13.08	9.89	6.79	10.09	6.41	4.49	3.12	4.72	2.82	1.86	2.44	1.90
Sturnira nana	F	1.82	0.76	1.10	1.90	11.88	11.50	8.86	5.60	9.18	6.13	4.00	2.58	3.96	2.54	1.56	1.64	1.48
	M	1.78	0.80	1.07	2.03	11.72	11.42	8.92	5.60	9.05	6.03	3.90	2.60	3.90	2.68	1.62	1.90	1.48
Sturnira aratathomasi	F	2.75	1.50	1.90	4.13	17.65	17.17	12.77	9.00	12.35	8.57	6.55	4.42	7.60	4.63	3.25	3.75	2.55
	M	2.87	1.57	1.90	4.33	17.73	17.37	12.80	8.90	12.40	8.63	6.67	4.67	7.57	5.00	3.40	3.90	2.40
Sturnira ludovici	F	2.19	1.14	1.53	2.46	13.92	13.39	10.16	6.89	9.82	6.65	5.01	3.52	5.24	3.69	2.13	2.16	2.13
	M	2.30	1.20	1.53	2.75	14.55	14.17	10.65	7.32	10.72	6.93	5.38	3.60	5.53	3.75	2.38	2.48	2.13
Sturnira erythromos	F	2.22	1.10	1.39	2.32	13.66	13.19	9.88	6.80	9.89	6.59	4.80	3.22	5.08	3.30	2.04	2.06	2.21
	M	2.26	1.13	1.36	2.41	13.56	13.12	9.83	6.78	9.91	6.56	4.87	3.38	5.13	3.30	1.97	2.13	2.18
Sturnira luisi	F	2.46	1.34	1.60	2.80	15.14	14.54	10.96	7.52	11.08	7.15	5.32	3.58	5.38	3.60	2.42	2.43	2.12
	M	2.38	1.36	1.56	3.14	15.36	14.88	11.20	7.70	11.50	7.30	5.32	3.72	5.44	3.70	2.44	2.82	2.18
Sturnira bogotensis	F	2.51	1.20	1.48	2.14	14.19	13.69	10.36	6.90	10.51	6.96	5.00	3.41	5.51	3.44	2.17	2.00	2.33
	M	2.40	1.20	1.53	2.70	14.53	13.93	10.57	7.13	10.70	6.87	5.08	3.60	5.40	3.77	2.23	2.45	2.23
Uroderma bilobatum	F	2.50	1.66	2.14	2.82	14.78	14.48	10.10	8.48	11.42	—	4.80	2.96	5.30	2.88	2.54	2.88	2.38
	M	2.55	1.73	2.20	3.15	15.05	14.80	10.30	8.70	11.57	6.00	4.87	2.98	5.27	2.95	2.42	3.00	2.55
Uroderma magnirostrum	F	2.52	1.64	1.98	2.91	15.26	14.91	10.69	8.53	11.76	6.42	4.75	2.84	5.16	2.75	2.05	2.60	2.48
	M	2.54	1.65	2.00	2.86	15.59	15.06	10.85	8.64	12.01	6.70	4.90	2.89	5.16	2.76	2.05	2.60	2.49
Vampyrops infuscus	F	3.74	2.87	2.86	4.71	21.59	21.14	15.20	13.01	16.88	8.07	6.53	3.98	7.65	4.28	3.06	4.22	3.78
	M	3.44	2.94	2.94	5.16	22.26	21.68	15.50	13.48	17.28	8.28	6.80	4.38	8.24	4.56	3.32	4.68	3.82
Vampyrops vittatus	F	3.59	3.03	2.91	4.69	23.20	22.54	16.60	13.73	17.87	8.83	6.87	4.33	7.96	4.56	3.13	4.59	3.80
	M	3.57	3.06	2.92	4.80	22.84	22.32	16.12	13.62	17.54	8.72	6.84	4.40	7.72	4.60	3.06	4.66	3.66
Vampyrops umbratus	F	3.15	2.52	2.51	4.65	19.79	19.36	13.97	11.69	15.09	7.74	6.10	3.66	7.23	4.10	2.70	4.10	3.22
	M	3.47	2.43	2.47	4.84	20.11	19.74	14.31	11.94	15.29	7.99	6.23	3.89	7.41	4.39	2.86	4.31	3.37

TABLE 2.—Continued.

Species	Sex	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Vampyrops aurarius	F	28.70	26.42	14.24	7.06	6.68	17.32	14.22	11.94	10.22	15.00	14.80	11.08	9.30	3.32	7.36	2.10
	M	28.48	26.16	13.92	7.12	6.70	16.96	14.20	11.84	10.10	15.22	14.86	10.92	9.20	3.44	7.44	2.10
Vampyrops nigellus	F	25.13	22.91	12.23	6.31	6.07	14.31	12.17	10.73	8.91	13.97	12.43	9.40	7.94	2.96	6.26	1.67
	M	24.85	22.78	11.88	6.17	5.95	14.35	12.23	10.67	8.88	13.57	12.08	9.22	7.93	2.87	6.15	1.73
Vampyrops brachycephalus	F	21.20	19.10	9.80	5.60	5.30	12.60	10.75	9.45	8.40	12.20	9.50	7.30	6.05	2.60	5.40	1.40
	M	21.23	19.07	9.72	5.75	5.55	12.93	10.87	9.77	8.57	12.00	9.23	7.50	6.42	2.63	5.43	1.47
Vampyrops helleri	F	22.30	20.40	10.48	5.56	5.36	12.48	10.74	9.38	8.08	12.38	10.40	7.96	6.84	2.74	5.24	1.40
	M	21.86	20.06	10.32	5.66	5.48	12.44	10.78	9.40	8.16	12.32	10.48	7.76	6.70	2.66	5.14	1.40
Vampyrops lineatus	F	24.69	22.39	11.81	6.74	6.27	14.40	12.36	10.87	9.04	13.69	12.11	8.80	7.29	2.90	6.00	1.70
	M	24.71	22.46	11.55	6.61	6.25	14.29	11.94	10.65	9.21	13.96	11.85	8.82	7.35	2.92	6.02	1.72
Vampyrops recifinus	F	24.85	23.25	12.05	6.05	5.65	14.80	12.20	10.30	8.75	13.25	12.20	9.35	8.00	3.10	6.70	1.70
	M	24.00	22.07	11.32	6.25	5.82	14.20	11.82	10.17	8.97	13.32	11.72	8.80	7.27	2.97	6.20	1.60
Vampyrops dorsalis	F	27.54	25.42	13.54	6.74	6.22	16.40	13.50	11.42	9.78	14.54	14.32	10.86	9.24	3.30	7.24	2.12
	M	28.58	26.50	13.84	6.84	6.48	16.84	13.90	11.62	10.02	14.92	15.12	11.34	9.58	3.52	7.44	2.16
Vampyrodes caraccioli	F	27.34	24.32	12.74	7.20	6.52	17.28	13.84	11.60	9.88	15.24	13.92	9.70	8.12	3.22	6.38	2.08
	M	27.61	24.72	12.69	7.20	6.70	17.29	14.02	11.64	10.11	15.13	13.97	9.90	8.25	3.30	6.31	2.06
Vampyressa pusilla	F	18.13	16.37	7.70	4.77	4.68	10.68	9.25	8.50	7.25	10.42	8.32	5.88	4.67	2.07	4.32	1.20
	M	17.93	16.45	8.00	4.80	4.72	10.62	9.08	8.40	7.28	10.40	8.33	5.75	4.47	2.20	4.28	1.13
Vampyressa melissa	F	20.84	19.54	9.48	5.30	5.10	12.62	10.38	8.96	7.66	11.60	10.45	6.74	5.48	2.52	4.90	1.50
	M	20.86	19.44	9.70	5.44	5.12	12.17	10.28	9.22	7.80	11.52	9.82	6.70	5.32	2.50	5.00	1.42
Vampyressa nymphaea	F	20.76	18.46	9.78	4.86	4.74	12.18	10.32	9.04	7.88	11.30	10.02	6.98	5.83	2.48	4.88	1.48
	M	21.07	18.70	9.52	5.00	4.88	12.48	10.37	9.33	8.20	11.70	10.22	7.33	5.97	2.50	5.06	1.58
Vampyressa brocki	F	17.92	15.97	8.00	4.92	5.30	10.72	9.35	8.15	7.13	10.32	8.10	5.75	4.60	2.10	4.30	1.20
	M	18.10	16.20	8.40	5.40	5.30	10.70	9.50	8.40	7.10	10.60	8.30	5.80	4.60	2.10	4.20	1.10
Vampyressa bidens	F	20.00	17.97	9.23	5.32	5.28	12.10	10.25	9.18	7.75	11.48	9.48	6.38	5.18	2.52	4.88	1.45
	M	19.88	17.60	9.02	5.30	5.30	11.98	10.26	9.24	7.92	11.46	9.52	6.34	5.16	2.42	4.97	1.42
Chiroderma doriae	F	27.70	26.00	13.30	7.80	6.50	18.00	13.70	11.30	9.40	14.50	15.00	10.10	8.70	3.30	7.20	2.20
Chiroderma improvisum	F	28.70	27.60	14.30	7.20	6.50	18.80	14.30	12.80	10.10	15.00	16.10	11.00	8.90	3.60	7.60	3.10
	M	29.40	27.70	13.30	7.40	6.50	18.90	14.20	12.70	10.50	16.10	16.60	10.80	8.90	3.40	7.20	2.70
Chiroderma villosum	F	23.44	21.60	10.88	6.06	5.68	15.18	11.62	10.24	8.50	12.86	12.48	8.26	7.12	2.86	5.64	1.98
	M	23.42	21.30	10.52	6.18	5.80	15.30	11.78	10.54	8.70	13.30	12.44	8.18	6.78	2.86	5.60	1.90
Chiroderma salvini	F	25.65	23.57	12.01	6.86	6.04	16.03	12.47	11.00	9.05	14.13	13.78	9.03	7.50	3.16	6.07	2.09
	M	26.36	24.26	11.96	7.02	6.06	16.48	12.70	11.02	9.14	14.56	13.84	9.38	7.86	3.26	6.22	2.16
Chiroderma trinitatum	F	22.22	19.73	10.15	5.83	5.57	13.80	11.03	10.22	8.18	12.58	11.50	7.63	6.37	2.47	5.32	1.73
	M	21.62	19.30	9.64	5.82	5.36	13.32	10.78	9.84	8.14	12.46	11.14	7.32	6.12	2.42	5.12	1.64

| Species | Sex | Character | | | | | | | | | | | | | | | | |
		17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Vampyrops aurarius	F	3.50	2.84	2.90	4.20	20.28	19.72	14.16	12.10	15.52	7.84	6.04	3.78	7.30	4.34	2.92	3.74	3.40
	M	3.48	2.82	2.84	4.42	19.90	19.56	14.22	11.92	15.22	7.84	6.22	3.82	7.26	4.40	2.92	4.02	3.34
Vampyrops nigellus	F	2.81	2.31	2.30	3.32	17.37	16.97	12.40	10.33	13.16	6.83	5.19	3.23	5.83	3.41	2.26	3.00	2.63
	M	2.78	2.37	2.27	3.43	17.05	16.65	12.30	10.05	12.97	6.77	5.07	3.18	5.73	3.43	2.20	3.02	2.67
Vampyrops brachycephalus	F	2.50	1.85	1.80	2.80	13.70	13.20	9.40	7.80	10.30	5.50	4.10	2.80	4.30	2.70	1.70	2.40	2.40
	M	2.38	1.92	2.05	2.93	14.10	13.77	9.68	8.30	10.53	5.58	4.40	2.73	4.87	2.92	1.98	2.58	2.33
Vampyrops helleri	F	2.32	1.94	2.06	2.90	15.06	14.78	10.36	8.84	11.68	6.16	4.68	2.68	5.14	2.82	1.94	2.74	2.30
	M	2.22	1.96	2.02	2.92	14.64	14.36	10.28	8.40	11.08	6.14	4.52	2.32	4.88	2.80	1.95	2.64	2.30
Vampyrops lineatus	F	2.80	2.20	2.14	3.10	16.74	16.26	11.77	10.20	12.86	6.76	5.06	3.19	5.97	3.11	2.04	2.78	2.76
	M	2.76	2.13	2.13	3.22	16.63	16.15	11.26	9.84	12.64	6.56	4.97	3.17	5.90	3.22	2.15	2.89	2.61
Vampyrops recifinus	F	2.80	2.30	2.30	3.30	17.10	16.70	11.95	10.20	13.25	6.60	5.40	3.00	5.85	3.25	2.40	3.35	2.60
	M	2.65	2.13	2.10	3.43	16.27	15.77	11.38	9.25	12.60	6.30	5.02	2.90	5.57	2.77	2.17	3.17	2.55
Vampyrops dorsalis	F	3.32	2.90	2.60	3.90	19.52	19.08	13.94	11.60	15.20	7.34	5.90	3.72	6.84	3.80	2.50	3.97	3.10
	M	3.26	2.78	2.72	4.50	20.44	19.88	14.56	12.36	15.86	7.78	6.24	3.86	7.20	4.04	2.78	4.28	3.38
Vampyrodes caraccioli	F	3.84	2.80	2.86	3.86	18.54	18.14	12.96	11.14	14.18	7.10	6.12	4.16	8.18	4.36	2.82	3.42	3.94
	M	3.77	2.75	2.96	3.94	18.50	18.08	12.67	11.21	14.20	6.93	5.97	4.13	7.90	4.27	2.72	3.61	3.79
Vampyressa pusilla	F	1.98	1.25	1.60	2.05	11.60	11.17	7.43	6.22	8.07	4.90	3.62	2.12	3.38	2.78	1.82	2.03	1.73
	M	1.92	1.22	1.60	2.00	11.30	11.02	7.30	6.23	8.03	4.94	3.78	2.08	3.77	2.45	1.63	2.15	1.98
Vampyressa melissa	F	2.58	1.76	2.08	2.00	13.62	13.16	9.42	7.48	9.78	5.66	4.54	2.72	5.20	3.14	1.98	2.20	2.64
	M	2.58	1.64	2.06	2.07	13.56	13.12	8.98	7.48	9.62	5.72	4.60	2.66	5.18	3.04	2.00	2.25	2.54
Vampyressa nymphaea	F	2.00	1.63	1.98	2.87	13.78	13.28	9.48	7.73	10.38	5.62	3.98	2.55	4.42	2.70	1.85	2.47	2.07
	M	2.02	1.65	1.98	2.45	13.96	13.58	9.28	7.78	10.52	5.82	4.08	2.70	4.30	2.88	1.90	2.62	2.20
Vampyressa brocki	F	2.00	1.17	1.60	2.27	11.42	11.02	7.40	6.35	8.65	4.82	3.47	2.17	3.67	2.40	1.52	2.13	1.85
	M	2.20	1.10	1.70	2.50	11.20	11.10	7.50	6.10	8.50	5.20	3.70	2.10	3.80	2.40	1.30	2.60	1.90
Vampyressa bidens	F	2.27	1.40	1.86	2.52	12.77	12.52	8.60	7.14	9.65	5.36	3.95	2.58	4.45	2.48	1.92	2.38	2.12
	M	2.16	1.40	1.82	2.70	12.86	12.60	8.60	7.28	9.20	5.30	4.02	2.58	4.36	2.84	1.88	2.50	2.14
Chiroderma doriae	F	3.40	2.70	2.70	3.30	19.60	19.40	14.00	11.00	14.60	8.40	6.20	4.20	8.50	4.70	2.80	3.10	3.50
Chiroderma improvisum	F	3.80	2.70	2.90	4.00	21.20	20.90	15.00	12.10	16.00	8.90	7.10	5.90	8.60	4.30	4.10	3.80	3.60
	M	3.60	2.70	3.20	3.80	21.40	20.90	15.10	11.70	16.20	8.90	6.80	6.00	8.70	4.30	3.70	3.80	3.50
Chiroderma villosum	F	2.52	2.14	2.64	3.55	16.16	15.74	11.44	9.28	12.18	6.62	5.16	3.76	6.14	3.70	2.12	3.10	2.74
	M	2.56	2.16	2.56	3.22	15.82	15.44	11.26	9.06	11.86	6.40	4.96	3.72	5.84	3.86	2.22	3.00	2.80
Chiroderma salvini	F	2.86	2.44	2.80	3.53	17.53	17.13	12.29	10.17	13.70	7.17	5.36	3.93	6.53	3.50	2.50	3.27	2.93
	M	2.90	2.46	3.00	3.93	18.24	17.84	12.68	10.64	14.12	7.34	5.76	4.10	6.56	3.64	2.50	3.47	3.14
Chiroderma trinitatum	F	2.58	2.07	2.38	2.72	14.82	14.60	10.35	8.30	11.30	6.35	4.48	4.02	5.53	3.23	2.30	2.48	2.60
	M	2.50	2.14	2.26	2.66	14.36	14.10	10.04	8.08	10.96	5.80	4.42	3.74	5.36	3.06	2.10	2.60	2.64

TABLE 2.—Continued.

Species	Sex	Character															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Ectophylla alba	F	16.27	15.37	7.89	4.46	4.21	10.25	8.51	7.90	6.38	8.76	8.54	6.07	5.01	2.09	4.41	1.19
	M	16.52	15.55	7.97	4.53	4.32	10.32	8.62	7.93	6.38	8.82	8.42	6.07	5.02	2.20	4.47	1.27
Mesophylla macconelli	F	18.55	16.85	8.58	4.72	4.63	10.77	9.52	8.28	6.92	10.20	8.18	6.37	5.42	2.35	4.43	1.25
	M	18.46	16.64	8.52	4.64	4.58	10.54	9.46	8.48	7.06	10.28	8.08	6.26	5.26	2.28	4.50	1.18
Artibeus cinereus	F	20.24	18.72	8.76	5.40	5.00	12.35	10.54	9.14	8.16	11.68	9.40	6.60	5.68	2.74	4.52	1.38
	M	20.56	19.14	8.98	5.58	5.08	12.22	10.64	9.30	8.18	11.92	9.76	6.70	5.80	2.80	4.62	1.42
Artibeus glaucus	F	20.01	18.24	9.08	5.73	5.12	11.67	10.41	9.17	7.66	11.39	9.13	6.37	5.57	2.58	4.44	1.36
	M	20.04	18.56	9.31	5.71	5.14	11.88	10.59	9.23	7.86	11.29	9.31	6.44	5.63	2.74	4.49	1.39
Artibeus watsoni	F	19.10	17.40	8.38	5.55	4.63	11.20	9.92	8.80	7.65	10.92	8.55	6.17	5.40	2.55	4.32	1.45
	M	19.62	17.96	8.74	5.72	4.88	11.44	10.26	9.06	7.80	11.18	9.24	6.34	5.46	2.64	4.52	1.32
Artibeus phaeotis	F	18.86	16.94	8.19	4.93	4.70	11.67	10.11	9.06	7.97	10.83	8.31	5.85	5.08	2.63	4.27	1.34
	M	18.80	16.80	7.82	5.10	4.70	11.50	10.07	8.98	7.72	11.25	8.25	5.97	5.07	2.67	4.23	1.37
Artibeus toltecus	F	19.98	18.18	9.00	5.54	5.04	12.16	10.80	9.50	8.18	11.42	9.48	6.58	5.66	2.82	4.62	1.36
	M	19.93	18.27	9.00	5.37	4.88	12.12	10.67	9.45	8.20	11.58	9.27	6.63	5.65	2.83	4.67	1.42
Artibeus aztecus	F	22.66	20.62	9.72	5.78	5.38	13.64	11.84	10.68	9.02	12.88	10.48	7.56	6.58	3.20	5.56	1.66
	M	21.90	19.84	9.66	5.99	5.49	13.01	11.38	10.13	8.79	12.76	9.76	7.16	6.24	2.94	5.26	1.51
Artibeus hirsutus	F	26.66	23.81	13.05	7.00	6.65	16.45	14.06	11.91	10.31	13.74	13.15	9.52	8.20	3.12	5.61	2.05
	M	26.30	23.66	12.94	7.05	6.75	16.46	14.10	12.06	10.44	13.71	13.06	9.61	8.15	3.06	5.44	2.00
Artibeus inopinatus	F	25.09	22.17	12.34	6.09	5.50	15.78	13.81	11.59	9.97	13.24	12.11	8.73	7.33	3.04	5.53	1.87
	M	24.95	22.00	12.02	6.05	5.52	15.47	13.88	11.48	9.93	13.58	12.42	8.73	7.32	3.07	5.47	1.88
Artibeus concolor	F	21.68	19.40	9.58	6.00	5.50	13.26	11.30	9.88	8.58	12.78	9.68	6.96	6.02	2.84	5.10	1.54
	M	21.26	18.84	9.06	5.68	5.44	13.24	11.40	9.96	8.82	12.82	9.32	6.80	5.94	2.90	4.98	1.52
Artibeus jamaicensis	F	27.48	24.97	13.30	7.90	6.95	17.12	14.80	12.18	10.45	14.12	13.37	9.80	8.08	3.58	6.47	2.05
	M	27.84	25.04	13.54	7.69	7.01	16.90	14.84	12.40	10.34	14.30	13.56	9.84	8.19	3.53	6.21	2.01
Artibeus intermedius	F	29.50	26.50	15.00	7.30	6.30	19.00	16.10	13.30	10.90	14.80	14.10	10.50	8.60	4.00	6.90	2.30
	M	28.85	26.03	13.90	7.78	6.45	18.47	16.27	13.42	10.87	14.95	13.80	10.18	8.42	3.70	6.77	2.25
Artibeus planirostris	F	31.44	28.36	15.59	9.06	7.65	19.75	17.25	13.59	11.12	15.90	15.72	11.71	10.05	4.15	7.29	2.35
	M	31.80	28.49	15.57	9.09	7.56	20.01	17.49	13.42	11.41	16.07	15.89	11.73	10.01	4.30	7.33	2.51
Artibeus anderseni	F	18.02	16.42	7.76	4.82	4.56	10.92	9.42	8.68	7.44	10.68	8.02	5.58	4.84	2.46	4.18	1.22
	M	18.16	16.36	7.80	4.84	4.48	11.20	9.56	8.72	7.50	10.82	8.18	5.68	4.98	2.56	4.28	1.24
Artibeus fuliginosus	F	27.72	24.90	13.62	7.12	6.50	16.62	14.30	12.30	10.20	14.64	13.92	10.06	8.66	3.76	6.40	2.14
	M	27.00	24.26	13.02	6.96	6.50	16.46	14.44	12.26	10.34	14.48	13.22	9.66	8.30	3.52	6.18	2.12
Artibeus fraterculus	F	26.78	24.00	13.14	7.26	6.66	16.14	14.34	11.76	10.14	13.96	12.96	9.36	8.12	3.46	6.28	2.02
	M	26.44	23.56	13.22	7.22	6.60	16.04	14.32	11.80	10.16	13.84	12.70	9.28	8.10	3.38	5.90	1.96

Species	Sex	Character																
		17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Ectophylla alba	F	1.59	1.46	1.56	1.73	11.10	10.81	7.27	6.47	8.39	4.37	3.19	2.49	3.44	2.71	1.48	1.75	1.80
	M	1.65	1.52	1.53	1.80	11.12	10.77	7.32	6.37	8.28	4.33	3.05	2.42	3.47	2.72	1.48	2.75	1.80
Mesophylla macconnelli	F	1.77	1.50	1.57	1.80	11.82	11.38	7.70	7.13	9.10	4.52	3.32	2.22	3.87	2.27	1.53	1.83	1.83
	M	1.74	1.44	1.56	1.88	11.50	11.30	7.52	6.98	9.28	4.46	3.34	2.16	3.72	2.28	1.60	1.80	1.78
Artibeus cinereus	F	2.32	1.62	2.10	2.73	13.26	12.90	9.42	6.86	10.32	5.94	4.62	2.98	5.34	2.58	2.10	2.43	2.18
	M	2.36	1.60	2.08	2.70	13.52	13.26	9.86	6.92	10.42	6.28	4.68	3.04	5.40	2.76	2.14	2.43	2.26
Artibeus glaucus	F	2.16	1.54	1.97	2.59	12.79	12.41	9.18	6.99	9.36	5.59	4.43	2.66	5.30	2.72	2.02	2.47	2.09
	M	2.14	1.50	2.06	2.58	13.07	12.63	9.17	6.99	9.86	5.76	4.50	2.64	5.30	2.74	2.07	2.52	2.11
Artibeus watsoni	F	1.95	1.45	1.90	2.50	12.52	12.22	8.72	6.77	9.63	5.45	4.17	2.75	4.65	2.45	1.88	2.50	2.02
	M	2.08	1.60	1.98	2.96	12.80	12.50	9.08	7.08	9.50	5.48	4.22	2.66	4.82	2.54	1.98	2.78	2.02
Artibeus phaeotis	F	2.14	1.45	1.98	2.57	12.17	11.84	8.50	6.20	9.31	5.53	4.17	2.73	4.89	2.66	1.89	2.36	2.10
	M	2.08	1.47	2.08	2.67	11.93	11.60	8.35	6.35	8.77	5.30	4.12	2.58	4.65	2.72	1.78	2.57	2.12
Artibeus toltecus	F	2.18	1.68	2.26	2.53	13.18	12.74	9.30	6.90	10.04	5.74	4.50	2.76	5.32	2.70	1.06	2.40	2.10
	M	2.20	1.62	2.27	2.78	13.00	12.60	9.08	6.92	9.85	5.60	4.32	2.72	5.27	2.48	2.03	2.63	2.25
Artibeus aztecus	F	2.28	1.86	2.48	3.08	14.76	14.36	10.44	7.92	11.12	6.38	4.92	3.14	5.82	3.06	2.28	2.84	2.44
	M	2.49	1.88	2.39	3.03	14.07	13.66	9.85	7.59	10.57	6.16	4.65	3.04	5.52	2.89	2.20	2.81	2.38
Artibeus hirsutus	F	3.15	2.34	2.90	3.47	17.61	17.12	12.17	10.15	13.49	6.88	5.97	3.70	7.67	3.91	2.73	3.53	3.25
	M	3.13	2.41	2.86	3.68	17.55	17.08	11.98	10.24	13.35	6.70	5.95	3.71	7.58	4.03	2.83	3.71	3.25
Artibeus inopinatus	F	3.33	2.01	2.56	3.60	16.73	16.23	11.56	9.47	13.00	6.73	5.61	4.04	7.34	3.49	2.59	3.36	3.33
	M	3.27	2.05	2.62	3.78	16.52	16.12	11.25	9.52	12.92	6.42	5.48	4.13	7.32	3.62	2.75	3.56	3.23
Artibeus concolor	F	2.48	1.70	2.16	2.92	14.14	13.64	9.92	7.74	10.40	6.00	4.88	2.96	5.88	3.30	2.50	2.70	2.50
	M	2.40	1.64	2.20	2.86	13.68	13.30	9.48	7.46	10.30	5.78	4.56	3.06	5.80	3.06	2.40	2.58	2.48
Artibeus jamaicensis	F	3.32	2.30	2.95	4.22	19.00	18.55	13.27	10.85	14.52	7.67	6.48	4.35	8.23	4.22	2.97	3.97	3.42
	M	3.20	2.37	3.16	4.27	19.07	18.56	13.29	10.73	14.51	7.79	6.23	4.21	8.20	4.17	3.04	4.00	3.24
Artibeus intermedius	F	3.70	2.30	3.20	4.80	20.20	19.60	13.90	11.60	15.00	8.00	6.50	6.00	9.90	5.30	3.20	4.00	3.60
	M	3.32	2.22	3.13	4.40	20.13	19.65	13.90	11.50	15.23	8.35	6.75	5.32	9.60	4.63	3.22	4.13	3.43
Artibeus planirostris	F	3.91	2.44	3.40	5.00	22.01	21.45	15.25	12.68	16.99	8.70	7.32	5.01	9.84	4.86	3.41	4.56	3.95
	M	3.86	2.84	3.69	5.10	22.25	21.59	15.25	12.92	16.94	8.54	7.35	4.93	9.82	5.03	3.49	4.89	3.97
Artibeus anderseni	F	2.08	1.38	1.82	2.48	11.40	11.08	7.86	5.98	8.44	5.14	3.84	2.48	4.66	2.48	1.82	2.32	2.00
	M	2.12	1.30	1.98	2.60	11.62	11.28	7.96	6.02	8.58	5.28	3.88	2.56	4.56	2.40	1.84	2.40	2.10
Artibeus fuliginosus	F	3.22	2.32	2.90	4.14	18.78	18.22	13.02	10.72	14.52	7.28	6.38	4.08	7.98	3.94	2.96	3.78	3.18
	M	3.06	2.14	2.80	4.10	17.32	17.86	12.66	10.58	13.70	7.38	6.14	4.12	7.92	4.12	3.02	3.80	3.08
Artibeus fraterculus	F	2.98	2.38	2.84	3.88	18.00	17.46	12.52	10.30	13.62	6.92	5.84	3.92	7.44	3.94	2.76	3.54	3.06
	M	2.76	2.28	2.80	4.07	17.76	17.28	12.20	10.26	13.56	6.76	5.78	3.82	7.72	3.86	2.78	3.70	3.02

TABLE 2.—Continued.

Species	Sex	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Artibeus fimbriatus	F	29.73	26.94	14.94	8.32	7.29	18.31	15.73	13.14	10.82	5.37	14.79	10.62	9.16	4.07	7.07	2.18
	M	30.00	27.09	14.90	8.23	7.31	18.51	16.17	13.46	11.20	15.59	15.29	10.87	9.39	4.06	6.99	2.24
Enchisthenes hartii	F	20.65	19.03	9.21	5.98	5.70	12.42	10.85	9.45	8.21	11.81	9.50	6.76	5.90	2.59	4.61	1.45
	M	20.63	18.80	9.24	5.86	5.71	12.44	10.66	9.60	8.31	11.83	9.41	6.89	5.94	2.59	4.61	1.39
Ardops nichollsi	F	23.10	20.39	10.50	6.64	5.71	15.16	12.33	10.32	9.21	12.49	5.23	7.51	6.68	2.27	4.50	1.50
	M	21.65	18.65	9.28	6.18	5.67	14.22	11.90	9.92	9.42	12.25	4.48	6.52	5.86	2.04	4.08	1.52
Phyllops falcatus	F	20.65	18.85	8.20	5.65	5.50	14.15	12.25	10.20	8.55	13.10	5.10	6.15	5.50	2.70	5.10	1.25
	M	—	—	7.80	5.80	5.20	—	—	—	—	—	4.90	5.90	5.30	2.80	4.90	1.30
Phyllops haitiensis	F	20.21	18.49	7.64	5.74	5.53	13.69	12.10	10.14	8.46	12.80	5.19	5.99	5.17	2.73	4.84	1.33
	M	19.58	17.76	7.26	5.50	5.38	13.30	11.54	9.80	8.40	12.82	4.80	5.74	5.02	2.70	4.88	1.34
Phyllops vetus	F	19.73	17.60	7.45	5.98	5.30	13.25	11.57	10.10	8.80	12.87	4.32	5.78	4.97	2.30	4.40	1.22
Ariteus flavescens	F	20.30	17.28	8.30	5.26	4.84	14.45	11.76	9.46	8.40	11.74	4.06	6.02	5.38	2.36	4.16	1.36
	M	18.72	15.98	7.36	4.94	4.82	7.40	11.22	9.44	8.44	11.70	3.40	5.44	4.74	2.20	3.98	1.38
Stenoderma rufum	F	22.62	19.72	9.84	6.02	5.66	15.48	12.82	10.66	10.20	13.02	4.30	6.88	6.42	2.74	5.48	1.60
	M	22.08	19.14	9.14	5.88	5.54	14.94	12.32	10.64	9.84	13.12	4.14	6.56	6.02	2.64	5.28	1.36
Pygoderma bilabiatum	F	20.85	19.25	9.94	8.88	7.65	14.20	12.45	10.47	9.13	11.04	7.33	6.07	5.05	2.91	3.95	1.29
	M	20.15	17.63	9.39	8.50	7.59	13.69	12.17	10.42	9.23	11.10	6.94	5.55	4.56	2.78	3.67	1.13
Ametrida centurio	F	16.08	13.76	6.94	4.18	4.16	11.30	9.76	8.44	7.44	10.06	5.00	4.44	4.06	2.36	5.36	0.98
	M	14.70	12.54	5.80	3.44	3.40	10.52	9.10	8.24	6.98	9.34	4.32	3.98	3.62	2.10	4.94	0.86
Sphaeronycteris toxophyllum	F	16.68	14.92	5.92	6.58	5.85	12.33	10.38	9.37	8.58	11.33	4.42	4.63	4.10	2.25	4.17	1.08
	M	16.20	14.30	5.57	6.27	5.60	12.08	10.03	9.07	8.45	11.00	4.17	4.37	3.85	2.18	4.10	1.00
Centurio senex	F	18.03	15.24	6.38	5.72	5.85	15.26	12.05	10.31	9.47	11.27	4.16	5.15	4.34	3.10	6.74	1.39
	M	17.50	14.60	6.12	5.43	5.62	14.70	11.70	10.28	9.58	11.23	3.82	4.73	4.18	3.08	6.63	1.33
Macrotus waterhousii	F	23.92	21.13	11.50	5.47	4.10	11.57	10.52	8.97	8.30	12.30	10.95	9.13	8.05	1.50	3.02	1.47
	M	22.95	20.35	11.20	5.32	4.32	11.13	10.13	8.95	8.22	12.00	10.25	8.57	7.57	1.45	3.02	1.40
Carollia perspicillata	F	22.57	20.40	10.80	6.40	5.59	11.38	11.19	9.59	8.37	12.04	10.10	7.51	6.11	2.17	4.14	1.80
	M	22.63	20.78	10.93	6.45	5.53	11.52	11.17	9.62	8.50	12.17	10.25	7.55	6.20	2.23	4.13	1.88
Carollia brevicauda	F	22.08	20.12	10.58	6.14	5.22	11.02	10.80	9.28	8.14	11.74	10.08	7.06	5.82	2.16	4.24	1.82
	M	21.88	19.82	10.38	6.28	5.38	11.30	10.94	9.38	8.24	11.62	10.16	7.06	5.88	2.36	4.34	1.70
Carollia subrufa	F	20.92	18.88	10.08	6.32	5.24	10.78	10.54	9.24	7.90	11.30	9.42	6.68	5.48	2.16	4.08	1.54
	M	20.85	18.82	9.98	6.25	5.27	10.82	10.77	9.25	7.98	11.17	9.37	6.77	5.50	2.18	4.00	1.57
Carollia castanea	F	19.82	17.60	9.80	6.16	5.34	10.10	9.96	8.84	7.76	10.78	8.90	6.30	5.52	2.04	3.92	1.44
	M	19.94	17.78	9.60	6.20	5.36	10.24	10.40	9.00	7.66	10.68	8.80	6.32	5.50	2.14	4.02	1.52

Species	Sex	Character																
		17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Artibeus fimbriatus	F	3.73	2.57	3.10	4.13	19.73	20.00	14.28	11.70	15.79	8.12	6.78	4.79	8.82	4.40	3.14	3.96	3.67
	M	3.71	2.71	3.21	4.53	20.91	20.29	14.27	12.21	16.24	7.93	6.80	4.61	9.07	4.46	3.24	4.27	3.69
Enchisthenes hartii	F	2.22	1.59	1.95	2.54	13.30	12.93	9.54	7.27	10.05	5.68	4.32	2.46	5.03	2.71	2.06	2.38	2.15
	M	2.23	1.56	2.00	2.63	13.23	12.81	9.56	7.24	9.94	5.36	4.34	2.69	4.89	2.77	2.21	2.43	2.20
Ardops nichollsi	F	3.14	2.04	2.83	1.95	14.13	13.76	10.40	7.74	10.50	5.99	5.62	2.97	7.18	3.37	2.82	2.57	3.60
	M	2.68	1.76	2.48	2.55	12.54	12.16	9.28	6.60	9.34	5.42	5.12	2.80	6.44	2.98	2.52	2.10	3.36
Phyllops falcatus	F	2.50	1.35	1.75	2.50	12.75	12.30	8.85	6.60	8.80	5.80	4.65	3.00	6.15	3.80	2.10	2.40	2.65
	M	2.50	1.30	1.60	2.50	12.20	11.80	8.30	6.30	8.90	5.30	4.50	2.70	6.00	3.60	2.00	2.50	2.50
Phyllops haitiensis	F	2.53	1.30	1.70	2.32	12.53	12.00	8.67	6.31	9.06	5.66	4.86	2.89	6.09	3.44	2.04	2.50	2.57
	M	2.30	1.20	1.62	2.20	11.88	11.44	8.32	6.16	8.50	5.26	4.64	2.68	5.90	3.22	1.92	2.24	2.46
Phyllops vetus		2.60	1.20	1.57	—	11.80	11.20	8.00	5.70	8.30	5.10	4.50	2.10	5.50	3.60	1.80	—	2.50
Ariteus flavescens	F	2.94	1.72	2.46	2.38	12.42	12.00	8.66	6.72	8.94	5.16	4.86	2.82	6.42	3.24	2.36	2.50	3.12
	M	2.30	1.52	2.10	2.12	11.10	10.72	7.88	5.88	7.90	4.86	4.42	2.54	5.90	3.14	2.22	2.28	2.82
Stenoderma rufum	F	3.32	1.80	2.36	2.50	13.88	13.42	10.04	7.28	9.78	6.02	5.50	3.42	7.68	4.48	2.92	2.54	3.40
	M	3.36	1.68	2.24	2.50	13.22	12.78	9.68	7.06	9.48	5.64	5.04	3.28	7.48	4.48	2.80	2.60	3.42
Pygoderma bilabiatum	F	2.19	1.28	1.65	2.91	12.73	12.33	8.19	6.30	9.36	5.98	4.52	2.47	5.75	3.55	2.72	2.66	2.36
	M	2.07	1.17	1.41	2.72	12.06	11.68	7.64	5.74	8.72	5.82	4.29	2.31	5.38	3.40	2.59	2.55	2.20
Ametrida centurio	F	1.58	1.02	1.30	2.20	9.24	8.82	6.28	5.04	6.84	3.88	3.04	1.76	3.66	2.12	1.88	2.18	1.72
	M	1.44	0.86	1.12	2.16	8.36	8.00	5.62	4.54	6.18	3.54	2.76	1.72	3.34	2.32	1.66	2.08	1.56
Sphaeronycteris toxophyllum	F	1.75	1.08	1.78	2.45	9.53	9.27	6.38	5.10	6.75	4.08	3.43	1.90	4.05	2.53	1.70	2.20	1.85
	M	1.62	0.92	1.58	2.35	9.20	8.87	6.05	4.82	6.37	3.97	3.20	1.85	3.85	2.73	1.63	2.10	1.70
Centurio senex	F	2.11	1.54	2.15	2.47	11.06	10.47	7.19	5.89	7.84	4.54	3.52	2.16	4.14	3.38	2.45	2.35	2.13
	M	1.72	1.42	2.02	2.37	10.45	9.90	6.75	5.65	7.38	4.40	3.40	2.18	3.98	3.35	2.42	2.17	2.12
Macrotus waterhousii	F	2.20	1.95	1.97	2.15	15.35	14.95	10.40	9.77	12.65	5.30	4.40	3.15	6.17	3.65	1.70	2.02	2.50
	M	2.17	1.80	1.95	2.05	14.65	14.25	7.60	9.32	11.85	5.15	4.17	2.82	5.95	3.42	1.88	1.85	2.35
Carollia perspicillata	F	2.11	1.36	1.67	2.13	15.07	14.49	10.36	8.21	11.69	6.53	4.47	3.14	5.33	3.13	2.03	1.98	1.77
	M	2.12	1.32	1.67	2.27	15.20	14.65	10.63	8.07	11.72	6.63	4.68	3.25	5.67	3.27	2.13	2.00	1.87
Carollia brevicauda	F	2.10	1.22	1.58	1.95	14.62	14.02	10.42	7.88	11.10	6.54	4.40	3.08	5.32	2.82	1.92	1.80	1.84
	M	2.18	1.26	1.58	2.26	14.42	13.90	9.92	7.70	11.10	6.36	4.40	2.98	5.30	3.46	2.08	2.04	1.94
Carollia subrufa	F	1.92	1.14	1.54	2.16	13.64	13.06	9.32	7.28	10.54	5.90	4.08	3.08	4.68	2.82	1.74	2.00	1.70
	M	1.98	1.15	1.55	2.57	13.77	13.10	9.28	7.38	10.72	5.85	4.03	3.08	4.80	2.77	1.77	2.17	1.68
Carollia castanea	F	1.74	1.06	1.42	2.10	12.96	12.34	8.92	6.90	10.06	5.64	3.66	2.68	4.10	2.42	1.68	1.98	1.50
	M	1.96	1.06	1.42	2.34	13.00	12.42	8.86	6.90	9.98	5.60	3.68	2.82	4.30	2.54	1.68	2.04	1.50

termed this method the common-part transformation. Although he did not offer it as a cladistic procedure, Wood's (1983) justification of the method clearly suggests that, if the regression were made on an appropriate outgroup, this would be a reasonable method of ancestor estimation in a phylogenetic analysis of morphometric data.

While following Wood's (1983) general idea, I have modified the procedure somewhat for several reasons: (1) to meet more fully the assumptions of linear regression; (2) to follow more closely outgroup methodology; and (3) to allow for meaningful comparison between common-part-removed and size-free methods. As in the size-free analysis, I first log-transformed the individual values. The arithmetic mean of each character then was calculated for both sexes of each species, thus readying the data for the common-part transformation.

The vector of character values for each species was regressed on the vector for *Carollia brevicauda* as the outgroup. This regression defines a common-part vector for each species, containing the portion of the stenodermatine variation that is predictable by the species' membership in the stenodermatine-carolliine clade. For each stenodermatine species, the vector of residual values was retained, and these vectors were combined as the transformed data matrix. Standard Wagner analysis then was applied to the residuals matrix, with the tree being rooted in the transformed ancestor estimate (that is, a composite taxon with a residuals vector of all zeros, representing the regression-predicted ancestral value for each character).

Tree Comparison and Consensus Procedure

To compare trees and define areas of congruence, I used the tree-consensus procedure of Adams (1972). As pointed out by Rohlf *et al.* (1983), Adams described two different procedures, one for trees with labeled nodes and one for trees with unlabeled nodes. As none of the trees in my analyses had labeled nodes, and because of the pragmatic and theoretic properties described below, I used the procedure described for unlabeled nodes (the Adams-2 tree of Rohlf *et al.*, 1983).

A cladogram may be viewed as a set of the included terminal taxa and of their relationships as defined by the branching arrangement. An Adams-2 consensus tree is simply the intersection of two such sets and, in fact, conforms to the usual properties of set intersection (Meyer, 1970; Runyon and Haber, 1971). Properties that are specifically important to the tree-consensus operaton are a redundancy identity property and the associative property. The redundancy identity (Fig. 1) means that a particular tree may be entered into the consensus procedure more than one time without further affecting the consensus product. Entering two identical trees into a multiple-tree consensus procedure will have the same outcome as entering only one of them. One interpretation of this property is that there is no weighting factor (either actual or potential) in the consensus procedure.
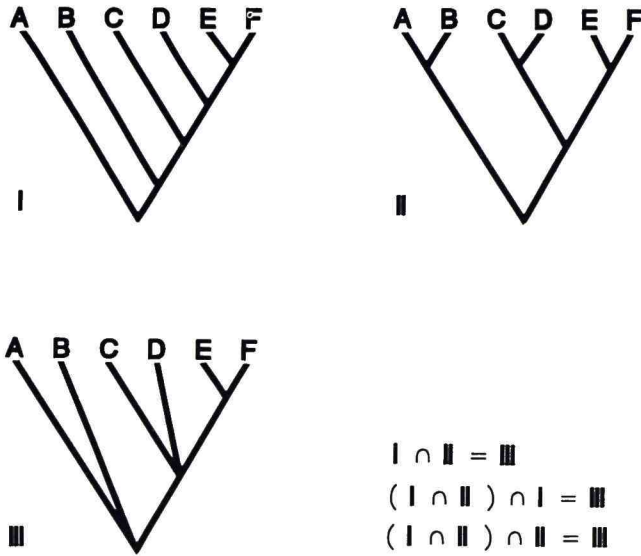
FIG. 1.—Conformance of the Adams-2 consensus operation to the redundancy identity property of set intersection. Repetition of inclusion in two-tree consensus has no effect. "∩", set intersection; "=", set equivalence.

The associative property (Fig. 2) means that order of tree entry into a multiple-tree consensus procedure does not affect the outcome. Clearly, this property is imperative in comparisons of three or more trees.

Four additional points should be made concerning what can and cannot be gained by the Adams-2 consensus procedure. Fig. 3 illustrates the first three of the four points. First, sister position on the tree may not indicate true sister status. A member of a more basal, unresolved furcation on the consensus tree may have sister position in one of the component trees; thus, it may be the true sister, although this will have been contradicted by at least one other component tree. Second, nonsister status on the consensus tree, if due only to lower resolution, does not necessarily imply true nonsister status. Third, nonsister status on a consensus tree due to inclusion in a different clade strongly implies true nonsister status, due to consensus aspect of both clades in all component trees. Fourth, the Adams-2 consensus procedure is an operational method of hypothesis testing in phylogenetics. A phylogenetic hypothesis (cladogram) is tested by the introduction of new data or a new analysis that has resulted in a competing hypothesis. The attractive aspect of this particular procedure is that only the falsified portions of the component trees are rejected (reconstructed, actually), and the nonfalsified portions are retained.

RESULTS OF DISCRETE-STATE CHARACTER ANALYSES

Wagner analysis.—The primary analysis used *Macrotus* as the root taxon, and included the *Carollia* species to assure further the correct rooting of the
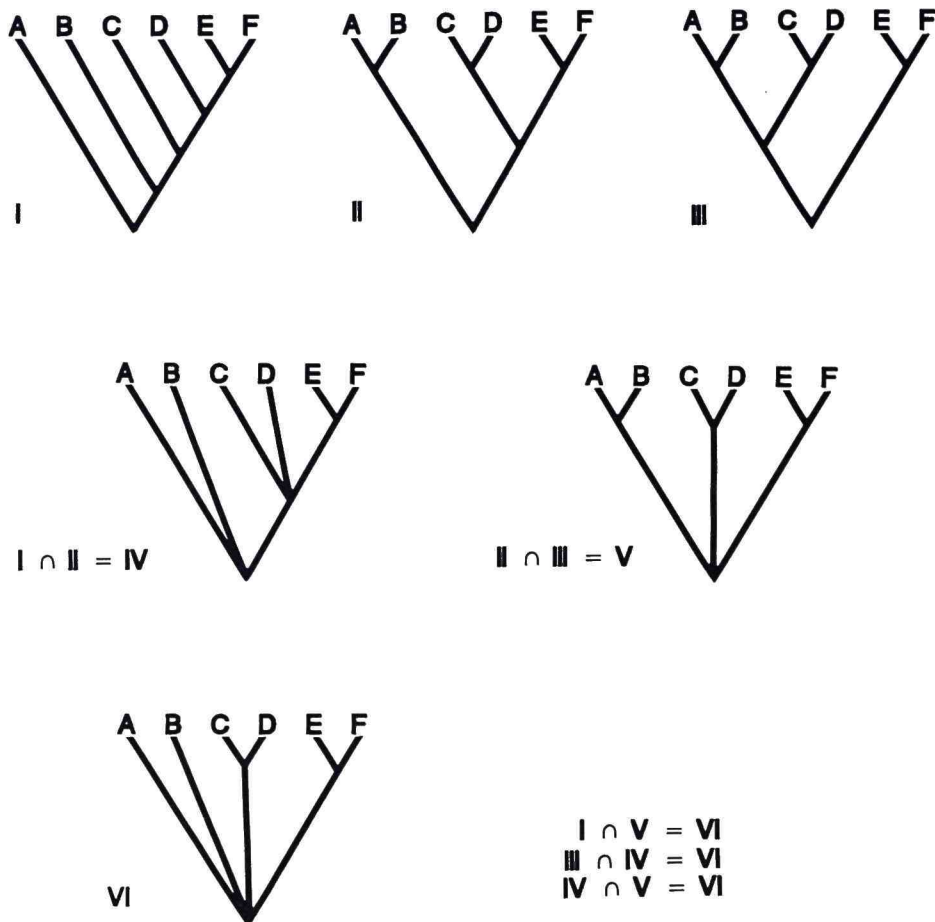
FIG. 2.—Conformance of the Adams-2 consensus operation to the associative property of set intersection. Order of inclusion in three-tree consensus has no effect. "∩", set intersection; "=", set equivalence.

character-state trees at this level of analysis. Among the shortest half (actually 27 of 50) of the trees obtained, stability is exhibited only near the base of the tree (that is, a number of equally-parsimonious and nearly-as-parsimonious topologies exist). The stable portion of the tree (Fig. 4) includes the *Carollia* species as sister to the Stenodermatinae, and the *Sturnira* species as a convex group (Duncan, 1980) basal to the remainder of the stenodermatines. Within *Sturnira*, the clade of *S. nana* and *S. bidens* is shown to be the sister-group to the remainder (Fig. 4), with *S. ludovici*, *S. luisi*, and *S. bogotensis* the next most basal taxa.

Among the trees obtained in the primary analysis, few clades are found that correspond to currently recognized genera or genus groups. Two factors probably contribute to this result. First, rather than bifurcating symmetrically, the trees tend to "chain" taxa together sequentially. Second,
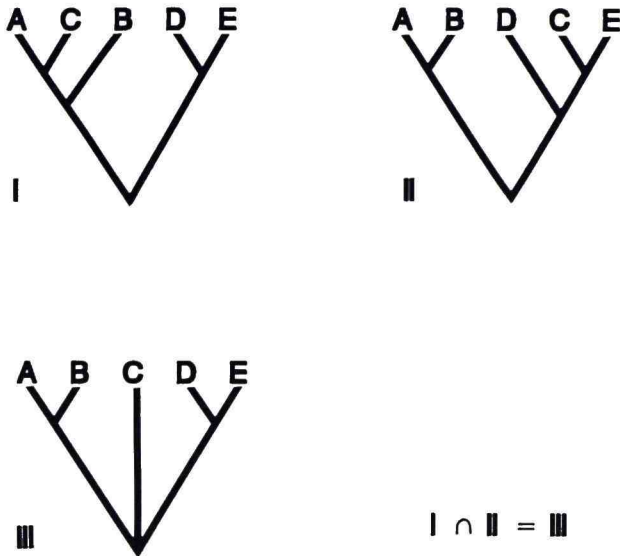
FIG. 3.—Valid and invalid inferences from an Adams-2 consensus tree. Given that either tree I or II might be true, true sister status of A with B or D with E may not validly be inferred from tree III. However, inferred nonsister status of A with D or E, and of B with D or E, is valid. "∩", set intersection; "=", set equivalence.

four currently recognized genera do not form convex groups (Duncan, 1980) in most of the trees. To be convex in the primary analysis, *Artibeus* must include *Uroderma* (and not *Enchisthenes*), *Vampyressa* must include *Chiroderma* and *Ectophylla* (*Mesophylla*) *macconnelli*, and *Vampyrops* must include *Vampyrodes*. Fig. 5 shows the general arrangement of these groups on the primary cladogram.

The secondary analysis included the remainder of *Sturnira* and all other stenodermatine species. *Sturnira luisi* was used as the outgroup, as it was separated from the hypothetical common ancestor of the stenodermatines by one less character-state change than was *S. bogotensis*. In order that the taxon subset be monophyletic, *S. bogotensis* also was included in the secondary analysis. Among the shortest half of the trees, the general arrangement of species groups is concordant with that in Fig. 5. The stable portion of the tree (Fig. 6) includes *Artibeus* (*Enchisthenes*) *hartii* as the sister taxon to all non-*Sturnira* stenodermatines, the eight short-faced genera as a convex group (two clades), and *Uroderma* embedded within the otherwise convex *Artibeus* species. Among these shortest trees, the relationship of several species of *Sturnira* is unresolved. The sister status of *S. tildae* with *S. thomasi* and *S. erythromos* remains stable, but the cladogeny of *S. lilium*, *S. magna*, *S. mordax*, and *S. aratathomasi* is uncertain. The positions of the short-faced stenodermatines are stable, as are those of the middle-sized and large *Artibeus*, as well as the two species of *Uroderma*.
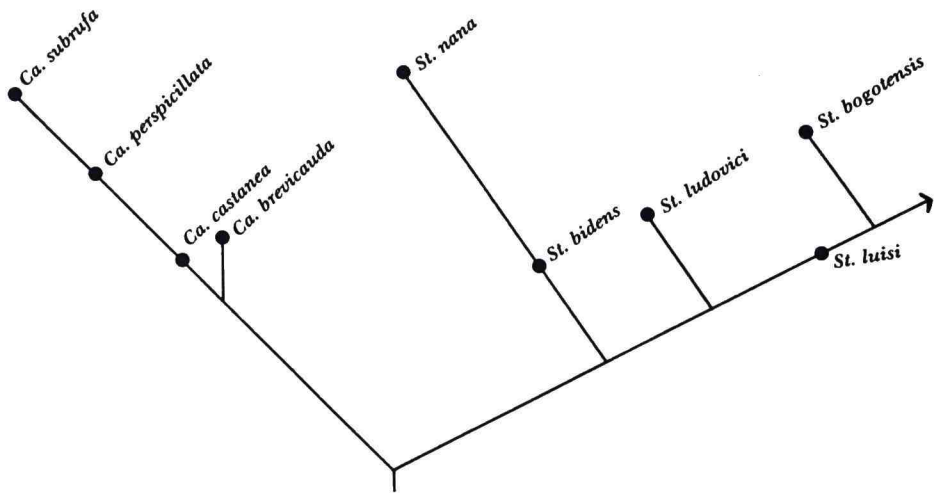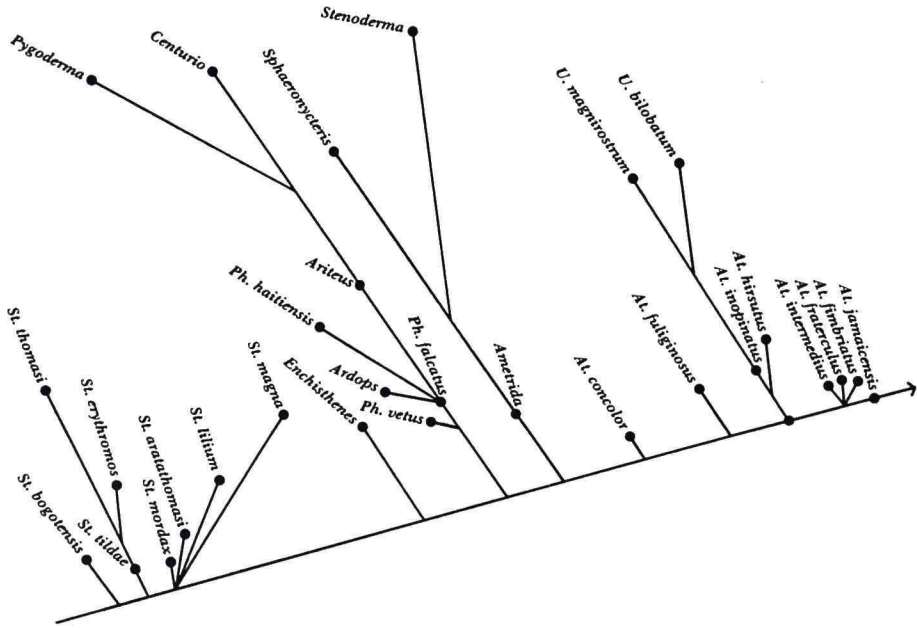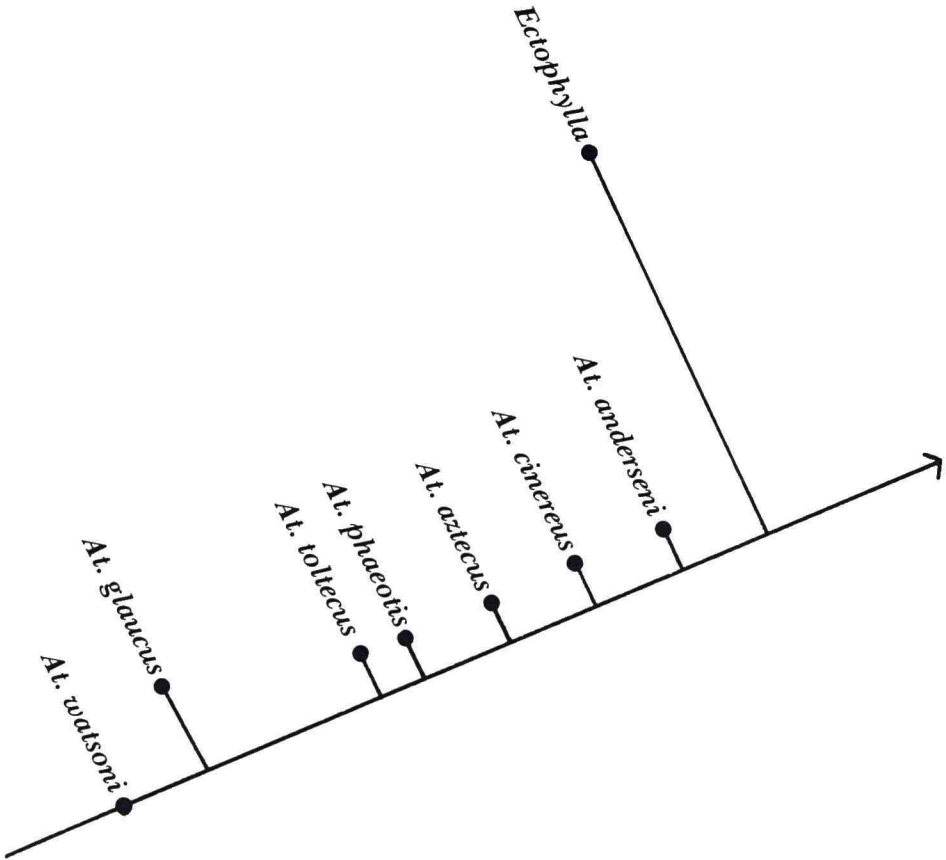
FIG. 4.—Stable portion of cladogram (scaled in character state units) from primary Wagner analysis of discrete-state data. Arrow represents all remaining stenodermatine species in this analysis. Generic abbreviations: *Ca., Carollia; St., Sturnira.*

The third analysis included the small *Artibeus*, *Ectophylla* (including *Mesophylla*), *Vampyressa*, *Chiroderma*, *Vampyrops*, and *Vampryodes*. *Artibeus jamaicensis* was used as the outgroup. Among the shortest half of the trees, the positions of the small *Artibeus* are found to be stable, with *A. anderseni* the sister to the remaining genera (Fig. 7). Also, *Ectophylla alba* is seen as sister to the included non-*Artibeus* genera. For the fourth analysis, *A. anderseni* was used as the outgroup because it is separated by fewer character-state changes from the hypothetical ancestor of the *Vampyressa-Vampyrodes* clade than is *Ectophylla* (seven as compared with 13).

The fourth analysis supports *Ectophylla alba* as sister to the *Vampyressa* and *Vampyrops* group (Fig. 8). Another stable portion includes the five species of *Chiroderma*, which represent a monophyletic group. The relationship of this genus to *Vampyressa melissa*, *V. nymphaea*, and *V. brocki* (and of these three species to each other) is unresolved, however. An additional stable portion of the tree shows *Ectophylla* (*Mesophylla*) *macconnelli* to be sister to *Vampyressa melissa*, *V. bidens*, and *Vampyrops-Vampyrodes*; further, *Vampyrops infuscus* is sister to the remaining *Vampyrops* and *Vampyrodes*.

The fifth Wagner analysis on discrete-state data included the 10 recognized species of *Vampyrops* and the monotypic genus *Vampyrodes*, with *Vampyrops infuscus* as the outgroup (Fig. 9). In this tree, *V. helleri* and *V. recifinis* form a clade. Also, *V. lineatus*, *V. dorsalis*, and *Vampyrodes* form a clade, with *V. lineatus* sister to the other two. As mentioned, *V. infuscus* is sister to all other *Vampyrops* and *Vampyrodes*. Next, *V. vittatus*, *V. umbratus*, and *V. aurarius* comprise an unresolved sister-group to the remaining seven species. Further, *V. nigellus*, *V. brachycephalus*, *V. helleri*,
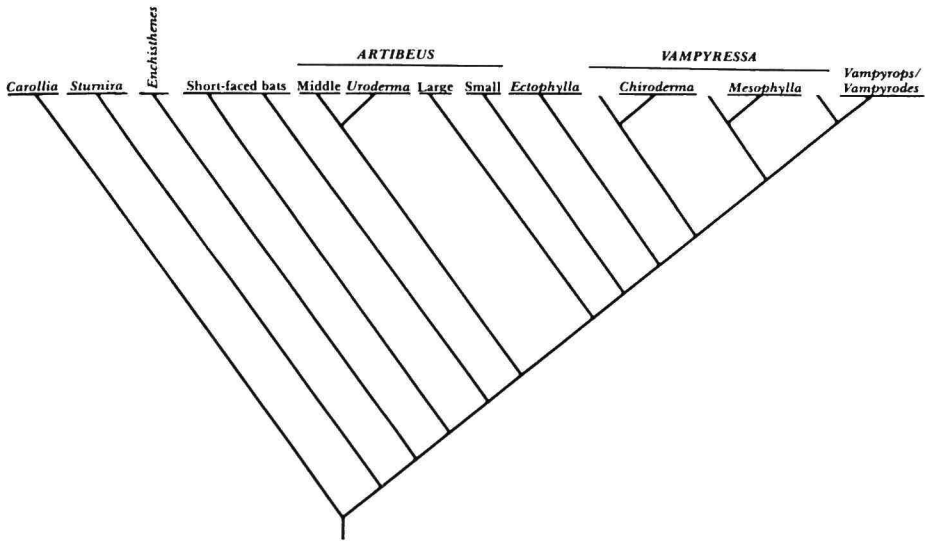
FIG. 5.—Globally-parsimonious arrangement of species groups from primary Wagner analysis of discrete-state data, showing topology only. Names not italicized are group common names (for instance, large *Artibeus*); italicized names in upper and lower case are genera that are monophyletic on the tree; and italicized names in upper case designate genera that are polyphyletic on tree (for instance, *VAMPYRESSA*).

and *V. recifinus* form a group that is unresolved except for the sister status of *V. helleri* and *V. recifinus*. This group is sister to the remaining clade of *V. lineatus*, *V. dorsalis*, and *Vampyrodes*.

The complete cladogram derived from Wagner analysis of discrete-state cranial and external data is shown in Fig. 10. This cladogram, which shows topology only, combines the global and local parsimony solutions of Figs. 4-9.

WISS analysis.—The general result of the "top-down" procedure of the WISS algorithm is that homoplasy is placed nearer the base in the branching pattern than it is in a Wagner tree. The relationships of the major clades, therefore, are less likely to be accurate, or even consistent among the most parsimonious trees, although the arrangements within the clades are more likely to be consistent. This generality was clearly reflected in the relationships of the major clades. However, the following groups are monophyletic on all topologies represented among the shortest half of the trees: *Carollia*, *Sturnira*, *Vampyrops* (including *Vampyrodes*), *Chiroderma*, *Vampyressa* (including *Mesophylla*), the large *Artibeus*, *Uroderma*, the small *Artibeus* (including *Ectophylla alba*), and the short-faced genera. Two exceptions are found. First, in one topology *Enchisthenes* and *Ectophylla alba* are within the *Sturnira* clade. Second, in one instance each, *Chiroderma salvini* and *C. doriae* are placed in the *Vampyressa* clade.

Further, a number of stable areas are found within the monophyletic groups mentioned. *Carollia perspicillata* and *C. subrufa* are sister species, as are *C. brevicauda* and *C. castanea*. The two species pairs are sister taxa.
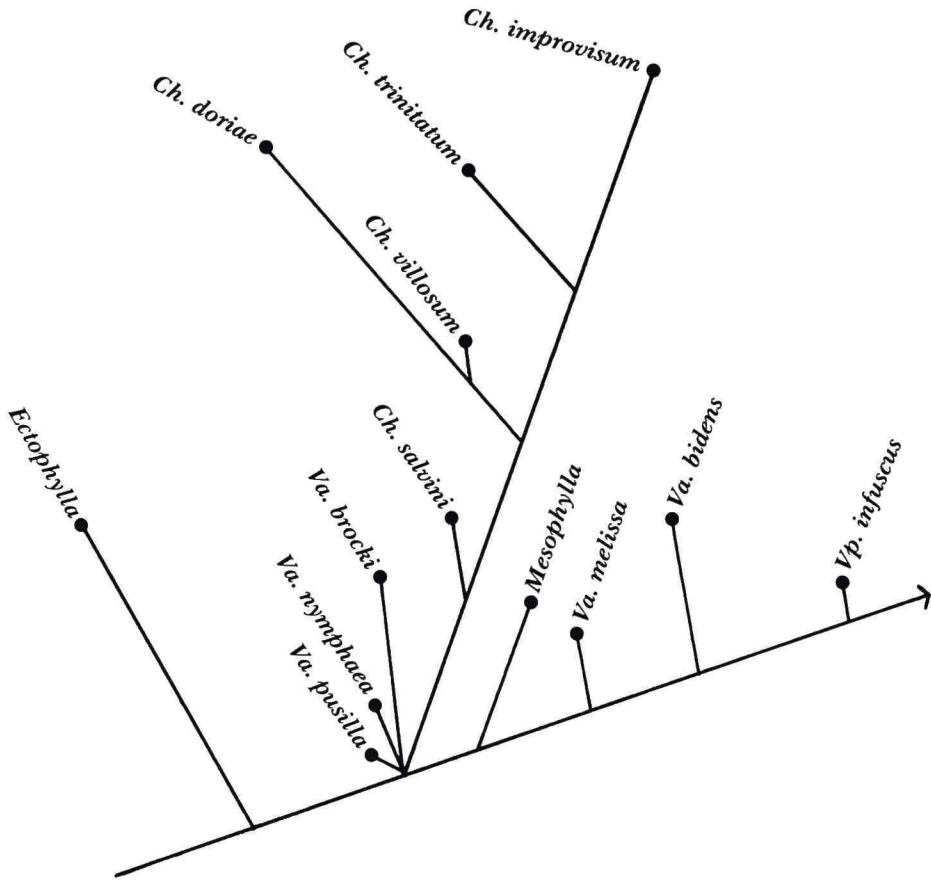
FIG. 6.—Stable portion of cladogram (scaled in character-state units) from secondary Wagner analysis of discrete-state data. Arrow represents all remaining stenodermatine species in this analysis. Generic abbreviations: *At.*, *Artibeus*; *Ph.*, *Phyllops*; *St.*, *Sturnira*; *U.*, *Uroderma*.

Within *Sturnira*, *S. bidens* and *S. nana* are sister species, and (with one exception each) *S. thomasi* is paired with *S. tildae* and *S. mordax* with *S. aratathomasi*. The relationship of species of *Vampyrops* (including *Vampyrodes*) is always monophyletic and is stable, with two exceptions (see Fig. 11). Among the shortest half of the trees, alternative arrangements are found in which *V. umbratus* or *V. brachycephalus* is sister to *V. nigellus*. In this arrangement, *Vampyrodes* is the sister species to *Vampyrops dorsalis*.

Chiroderma improvisum, the Antillean member of the genus, is the sister species to *C. trinitatum*. Although the species of *Vampyressa* were always monophyletic and always included *Mesophylla*, no consistent arrangement of *Vampyressa* species was found. The two *Uroderma* are sister species, and are arranged as the sister taxon to the clade of large and middle-sized *Artibeus*. Within this clade, *A. hirsutus* is sister to the remaining eight species, with *A. inopinatus* being next most basal on the clade. The terminal portion of this clade is represented by *A. lituratus* and *A. fraterculus*, with *A. jamaicensis* as sister to the pair. Among small *Artibeus*, *A. glaucus* and *A. watsoni* are sister species, as are *A. phaeotis* and *A. toltecus*. Among the eight short-faced genera, the two extant species of *Phyllops* are paired, with *P. vetus* and *Ardops* being successively basal sister taxa. Two other pairs are *Ametrida* and *Sphaeronycteris*, and *Ariteus* and *Centurio*.

Fɪɢ. 7.—Stable portion of cladogram (scaled in character-state units) from tertiary Wagner analysis of discrete-state data. Arrow represents all remaining stenodermatine species in this analysis. Generic abbreviation: *At., Artibeus.*

After conducting the analyses described above, I deleted *Macrotus* and used *Carollia brevicauda* as the outgroup. As no global parsimony constraint was derived from the primary WISS analysis, results from this secondary analysis were examined for areas of stability among all of the shortest half of the trees. In this analysis, *Sturnira* is shown as sister to the remaining stenodermatines, thus allowing for meaningful analysis of each of these two sister groups separately. In both of these subsequent analyses, then, *Carollia brevicauda* was retained as the outgroup because it represented the fewest number of steps from the subgroup's hypothetical common ancestor in the secondary analysis.

The third WISS analysis examined the 12 species of *Sturnira*. Among the shortest half of the generated trees, the only completely stable relationship is the sister status of *S. bidens* and *S. nana*. In all trees of the shortest

FIG. 8.—Stable portion of cladogram (scaled in character-state units) from quaternary Wagner analysis of discrete-state data. Arrow represents all remaining stenodermatine species in this analysis. Generic abbreviations: *Ch.*, *Chiroderma*; *Va.*, *Vampyressa*; *Vp.*, *Vampyrops*.

length, *S. mordax* and *S. aratathomasi* are sister taxa, with *S. tildae* sister to them and *S. erythromos* sister to all three.

The fourth WISS analysis examined the remaining stenodermatine species, and revealed stability only among the trees of shortest length. Among these trees, the *Vampyrops* group is stable, with *Vampyrodes* a sister to *V. dorsalis*. The *Vampyressa* group (including *Mesophylla*) is monophyletic, but the only stable portion is the sister status of *V. melissa* to the other species. The five species of *Chiroderma* form a stable and monophyletic group as do the small *Artibeus* (including *Ectophylla alba*) with one exception—the interchanging of *A. anderseni* and *A. cinereus* in the cladogram.

Because little stability of major clades was found among WISS results, I produced a consensus tree from the four most parsimonious WISS topologies (representing the two shortest total tree lengths). This procedure
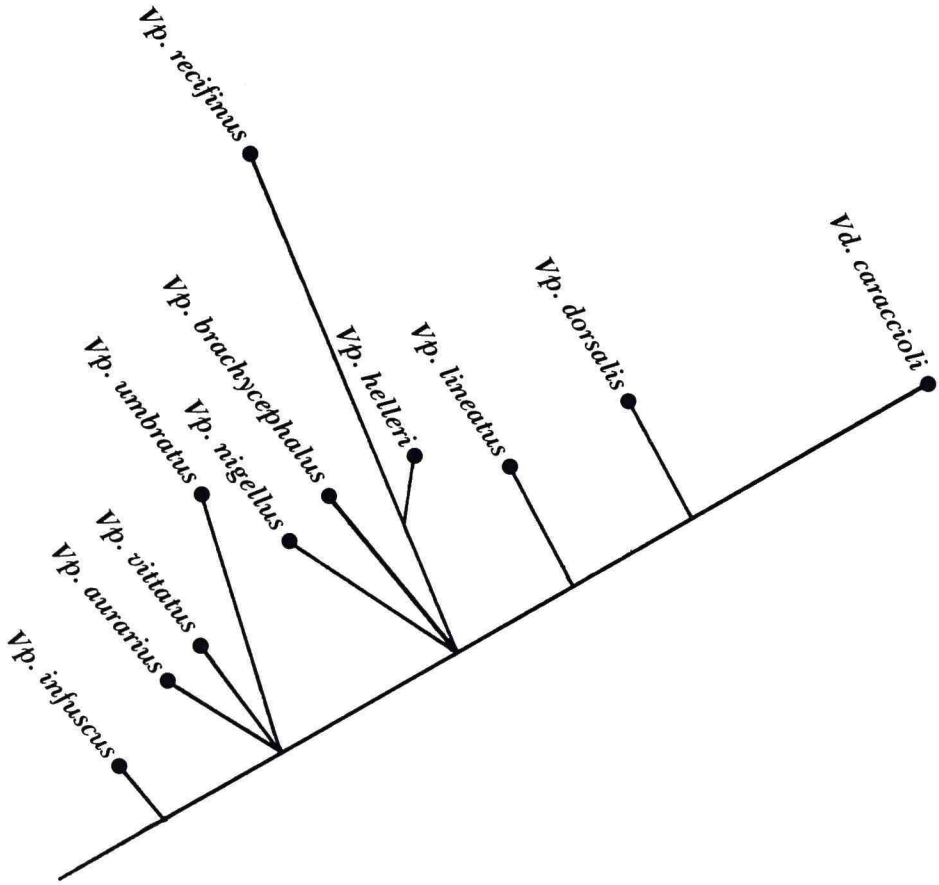
FIG. 9.—Cladogram (scaled in character-state units) from final Wagner analysis of discrete-state data. Generic abbreviations: *Vd.*, *Vampyrodes*; *Vp.*, *Vampyrops*.

resulted in several unresolved nodes in the tree but revealed areas of congruence among these shortest WISS trees (Fig. 12). Monophyletic clades are formed by the species of *Sturnira*, *Chiroderma*, *Vampyrops* (including *Vampyrodes*), *Vampyressa* (including *Mesophylla*), the small *Artibeus* (including *Ectophylla*), and the large *Artibeus* (excluding *A. fuliginosus*).

RESULTS OF CONTINUOUS-CHARACTER ANALYSES

Size-free analysis.—The first principal component of the log-transformed morphometric data explains 82.2 percent of the variation, and all characters have positive loadings on this component (Table 3). The second through fifth components explain 5.4, 4.9, 1.8, and 1.2 percent, respectively. Remaining components each account for less than one percent of the variance. After removal of the first-component projections, the Wagner analysis was conducted on projections from the remaining 65 components.

Ca. subrufa
Ca. perspicillata
Ca. castanea
Ca. brevicauda
St. nana
St. bidens
St. ludovici
St. luisi
St. bogotensis
St. thomasi
St. erythromos
St. tildae
St. mordax
St. aratathomasi
St. lilium
St. magna
Enchisthenes
Centurio
Pygoderma
Ariteus
Ardops
Ph. haitiensis
Ph. falcatus
Ph. vetus
Sphaeronycteris
Stenoderma
Ametrida
At. concolor
At. fuliginosus
U. magnirostrum
U. bilobatum
At. inopinatus
At. hirsutus
At. planirostris
At. fraterculus
At. intermedius
At. fimbriatus
At. jamaicensis
At. watsoni
At. glaucus
At. toltecus
At. phaeotis
At. aztecus
At. cinereus
At. anderseni
Ectophylla
Va. pusilla
Va. nymphaea
Va. brocki
Ch. improvisum
Ch. trinitatum
Ch. villosum
Ch. doriae
Ch. salvini
Mesophylla
Va. melissa
Va. bidens
Vp. infuscus
Vp. aurarius
Vp. vittatus
Vp. umbratus
Vp. nigellus
Vp. brachycephalus
Vp. recifinus
Vp. helleri
Vp. lineatus
Vp. dorsalis
Vd. caraccioli

FIG. 10.—Cladogram (showing topology only) combining global and local parsimony solutions from Wagner analyses of discrete-state data. Generic abbreviations; *At.*, *Artibeus*; *Ca.*, *Carollia*; *Ch.*, *Chiroderma*; *Ph.*, *Phyllops*; *St.*, *Sturnira*; *U.*, *Uroderma*; *Va.*, *Vampyressa*; *Vd.*, *Vampyrodes*; *Vp.*, *Vampyrops*.
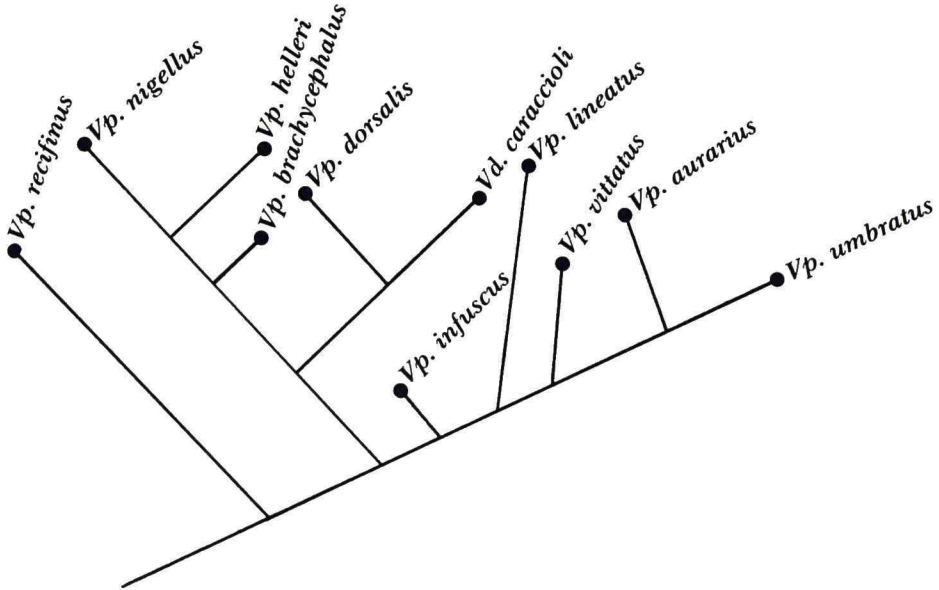
Fig. 11.—Cladogram (scaled in character-state units) from WISS analysis of discrete-state data for *Vampyrops* and *Vampyrodes* species. Among the shortest half of the trees, alternative arrangements are found in which either *V. umbratus* or *V. brachycephalus* is the sister of *V. nigellus*. Generic abbreviations: *Vd.*, *Vampyrodes*; *Vp.*, *Vampyrops*.

This Wagner tree (Fig. 13) is more nearly concordant with traditional stenodermatine taxonomy than are those trees based upon discrete-state characters. The genus *Sturnira* is monophyletic and is sister to all other stenodermatines. The next most basal clade contains the short-faced taxa, with the Antillean and mainland species forming separate clades within the group. The genus *Uroderma* is monophyletic and not associated with any *Artibeus* species. The genera *Ectophylla* and *Mesophylla* are a monophyletic group and associated with *Vampyressa nymphaea*. *Chiroderma* is monophyletic only if *Vampyrodes* is included, and *Vampyrops* forms a convex, though not entirely monophyletic, group. The small species of *Artibeus* form a clade basal to the subfamily exclusive of *Sturnira* and the short-faced bats, whereas the large *Artibeus* species form one of the two terminal sister clades. *Artibeus concolor* is alone in a position just basal to the small species of *Artibeus*, and *Enchisthenes* is unassociated with either *Artibeus* clade.

Common-part-removed analysis.—Linear regressions of character vectors of each of the species on that of the outgroup (*Carollia*) revealed that the portion of the vector variance accounted for by the outgroup (ancestor estimate) ranged from 86.2 (*Centurio senex*) to 98.7 (*Sturnira bogotensis*) percent (Table 4). Thus, the Wagner analysis was performed on residuals vectors representing from 1.3 to 13.8 percent of the original variance in the data from each species.
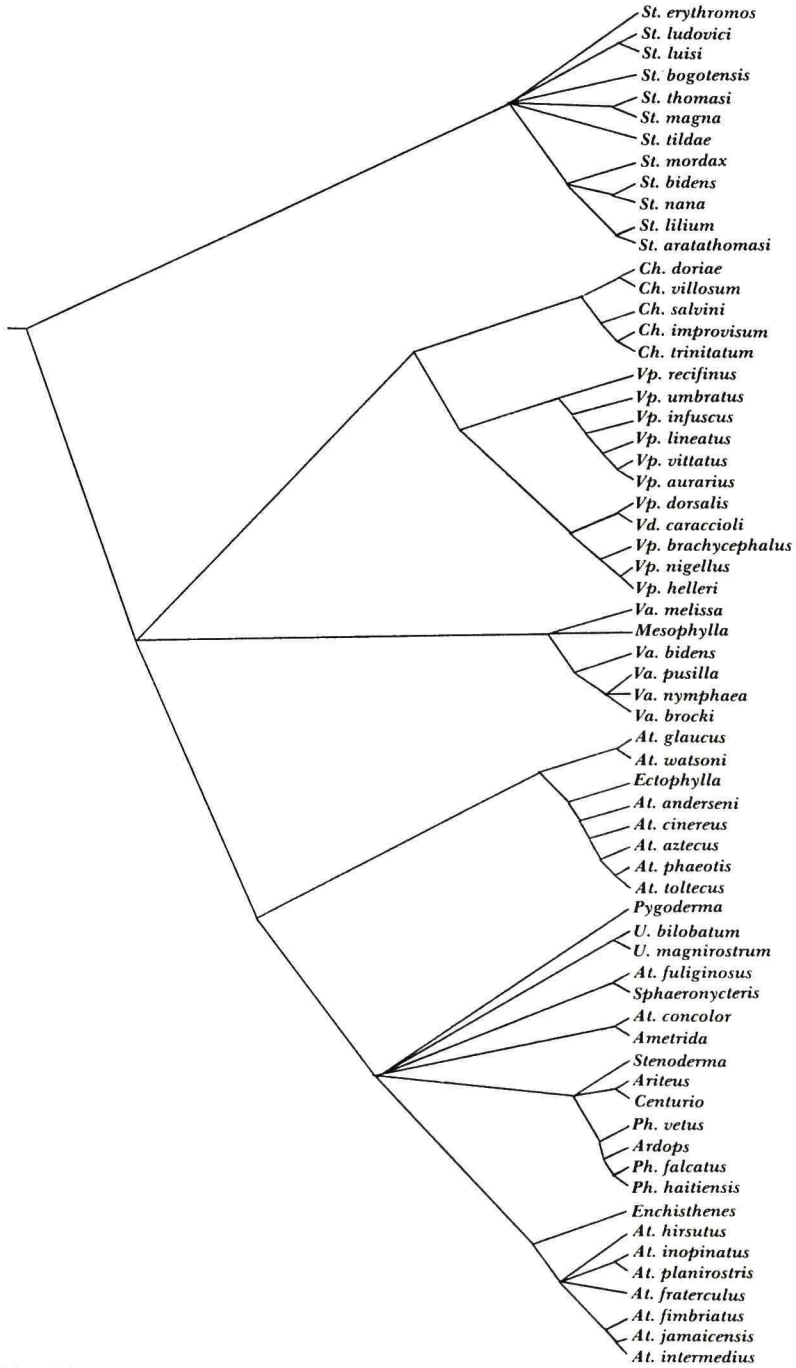
FIG. 12.—Adams-2 consensus cladogram from four most-parsimonious WISS trees. Generic abbreviations as for Fig. 10.

A number of similarities occur between this Wagner tree (Fig. 14) and the one described for the size-free data. Both *Sturnira* and the short-faced bat group are monophyletic assemblages, with the island as opposed to mainland division maintained in the short-faced species. *Ectophylla* and *Mesophylla* are sister taxa, although found associated with the otherwise monophyletic *Vampyrops* clade. *Chiroderma* is monophyletic, and *Vampyrodes* is included among the large *Artibeus*. *Vampyressa nymphaea* is again unassociated with its congeners, which otherwise form a convex group. The two species of *Uroderma* do not form a convex group in this case. As with the size-free results, there is a wide division between the large and small *Artibeus*. Neither *Artibeus concolor* nor *Enchisthenes* is a member of either *Artibeus* clade although, in this and the size-free results, both *A. concolor* and *Enchisthenes* are convex with the small *Artibeus* group.

Discussion and Conclusions

The discrete-state and continuous morphologic data sets, each analyzed by two methods (WISS and Wagner; size-free and common-part-removed), produced different cladograms of stenodermatine bats. A consensus tree was produced from the results of the two analyses of discrete-state data (Wagner and WISS—Figs. 10 and 12), as was one from the two trees representing analyses of continuous data (size-free and common-part-removed—Figs. 13 and 14). These two consensus trees (Figs. 15 and 16) represent the best available estimates of stenodermatine phylogeny based on discrete-state and continuous data, respectively.

From these, a final consensus tree (Fig. 17) was produced to represent the best phylogenetic hypothesis based on all data considered in this study. As is expected from a multiple consensus tree based on considerably different component trees, a number of unresolved nodes occur on this cladogram. A number of species groups may be discerned, however. *Sturnira* (with the possible exception of the subgenus *Corvira*) is a monophyletic group. The small *Artibeus* (possibly including *A. concolor* or *Enchisthenes* or both, but not *A. inopinatus* or *A. hirsutus*) are monophyletic and are most closely related to the eight genera of short-faced bats. Of these, the Antillean genera (possibly excepting *Stenoderma*) are derived from a single lineage. Fig. 17 does not support or refute *Vampyressa* as a monophyletic group. However, if this genus is in fact monophyletic, *Mesophylla macconnelli* must be included in it. *Chiroderma* is monophyletic, as is *Vampyrops*, except that either might include *Vampyrodes*. The large *Artibeus* (including *A. inopinatus* and *A. hirsutus*) form a clade with close relationship to *Uroderma* and *Ectophylla*.

In Appendix IV, I give an annotated Linnaean classification (Wiley, 1981) based upon a strict interpretation of the topology of Fig. 17. Because this classification ignores the *incertae sedis* status of a number of taxa in Fig. 17, I do not recommend adoption of the classification in Appendix IV.

TABLE 3.—*Character loadings on first five principal components from character correlation matrix. Characters with prefix "F" (34-66) are values from female measurements; those without the prefix (1-33) are from males. Characters are listed and defined in Appendix III.*

Character	Principal Components				
	I	II	III	IV	V
1 SKULL	0.985	−0.029	0.143	−0.027	−0.022
2 CONBAS	0.966	−0.069	0.214	−0.028	−0.023
3 ROST	0.927	−0.168	0.280	−0.037	−0.085
4 LACR	0.864	0.283	0.119	0.105	−0.340
5 POST	0.859	0.290	0.107	0.163	−0.311
6 ZYGO	0.859	0.103	−0.031	0.250	0.022
7 MAST	0.945	0.279	−0.050	0.042	0.023
8 BRAINB	0.952	0.256	−0.031	0.081	0.044
9 BRAINH	0.912	0.327	−0.117	0.069	−0.04
10 BRAINL	0.959	0.091	−0.026	−0.019	0.031
11 PALAT	0.737	−0.467	0.418	0.133	−0.065
12 MAXIL	0.930	−0.346	−0.011	−0.003	−0.064
13 MOLAR	0.922	−0.340	−0.108	−0.010	−0.055
14 WCAN	0.896	0.059	−0.020	0.297	0.121
15 WMOL	0.855	0.155	−0.142	0.264	0.302
16 MFOSL	0.880	0.069	0.366	−0.081	0.144
17 MFOSW	0.938	0.013	−0.087	−0.211	−0.020
18 UM2L	0.813	−0.440	−0.332	−0.034	−0.017
19 UM2W	0.764	−0.327	−0.463	−0.076	−0.045
20 UCAN	0.919	−0.054	0.035	0.273	0.036
21 DENTL	0.966	−0.150	0.193	−0.007	−0.001
22 CONCAN	0.965	−0.167	0.193	−0.009	−0.007
23 CONM1	0.951	−0.120	0.246	−0.071	0.030
24 TOOTH	0.938	−0.321	0.032	0.031	−0.009
25 MFAD	0.950	−0.219	0.203	−0.010	−0.009
26 CONMOL	0.871	0.064	0.453	−0.054	0.020
27 TEMMOM	0.950	0.138	0.172	−0.139	−0.002
28 MASMOM	0.898	0.085	0.273	−0.154	0.173
29 CORONH	0.938	0.172	−0.127	−0.200	−0.016
30 ANGPRO	0.865	0.370	0.019	−0.039	0.109
31 DENTTH	0.910	0.266	−0.037	−0.014	0.080
32 LCANH	0.930	−0.057	−0.036	0.186	0.043
33 CONDL	0.888	−0.024	−0.357	−0.223	−0.022
34 FSKULL	0.990	−0.003	0.058	−0.043	−0.024
35 FCONBAS	0.981	−0.034	0.133	−0.041	−0.036
36 FROST	0.945	−0.140	0.182	−0.071	−0.055
37 FLACR	0.842	0.338	−0.021	0.130	−0.353
38 FPOST	0.850	0.355	0.004	0.213	−0.266
39 FZYGO	0.917	0.216	−0.286	0.020	0.059
40 FMAST	0.926	0.312	−0.141	0.032	0.023
41 FBRAINB	0.940	0.281	−0.076	0.070	0.041
42 FBRAINH	0.889	0.366	−0.162	0.076	0.023
43 FBRAINL	0.948	0.123	−0.065	0.001	0.027
44 FPALAT	0.755	−0.476	0.370	0.122	−0.066
45 FMAXIL	0.933	−0.315	−0.102	−0.021	−0.073
46 FMOLAR	0.915	−0.312	−0.197	−0.038	−0.071
47 FWCAN	0.905	0.081	−0.089	0.283	0.130
48 FWMOL	0.854	−0.119	−0.222	0.256	0.276

TABLE 3.—*Continued.*

49 FMFOSL	0.895	0.065	0.338	−0.080	0.134
50 FMFOSW	0.913	0.078	−0.252	−0.234	0.004
51 FUM2L	0.777	−0.420	−0.435	−0.036	−0.021
52 FUM2W	0.726	−0.271	−0.566	−0.087	−0.077
53 FUCAN	0.912	−0.060	−0.176	0.224	−0.001
54 FDENTL	0.981	−0.129	0.104	−0.039	−0.002
55 FCONCAN	0.980	−0.146	0.098	−0.042	−0.016
56 FCONM1	0.970	−0.094	0.161	−0.093	0.021
57 FTOOTH	0.938	−0.308	−0.051	0.001	−0.034
58 FMFAD	0.962	−0.212	0.114	−0.024	−0.024
59 FCONMOL	0.898	0.111	0.393	−0.101	0.025
60 FTEMMOM	0.950	0.181	0.065	−0.178	−0.002
61 FMASMOM	0.900	0.093	0.205	−0.200	0.146
62 FCORONH	0.913	0.196	−0.196	−0.225	−0.029
63 FANGPRO	0.860	0.386	−0.059	−0.104	0.091
64 FDENTTH	0.872	0.282	−0.182	−0.044	0.071
65 FLCANH	0.903	−0.072	−0.284	0.162	−0.008
66 FCONDL	0.866	0.053	−0.409	−0.224	−0.032

Classification recommendations are given in the final paragraph of this paper and in Appendix VI.

De la Torre (1961: fig. 4) was the first author to construct a phyletic tree representing all currently recognized stenodermatine genera (Fig. 18A). This arrangement was based on his study of dental features in phyllostomid bats, and the subfamily comprised four distinct lineages. One was the *Brachyphylla*-line, consisting only of this genus. Interestingly, this line crosses that of the Carolliinae (from a point near the origin of the *Erophylla-Phyllonycteris* lineage) to arrive within the stenodermatine clade. The other three clades are the *Chiroderma*-line (*Chiroderma, Vampyressa, Mesophylla,* and *Ectophylla*), the *Vampyrodes*-line (*Vampyrodes, Vampyrops, Sturnira, Enchisthenes, Uroderma,* and *Artibeus*), and the *Pygoderma*-line (*Pygoderma, Ardops, Phyllops, Ariteus, Stenoderma, Sphaeronycteris, Centurio,* and *Ametrida*).

Baker (1973: fig. 5) constructed an arrangement based primarily on standard karyotypic data and secondarily on morphological features (Fig. 18B). His tree comprises three basal stock groups and three divergent lineages. *Sturnira* is split between two of the basal stocks, as are *Artibeus* and *Vampyrops. Uroderma* occupies one of the divergent groups alone; the eight short-faced genera occupy another; and *Chiroderma, Vampyressa,* and *Mesophylla* comprise the third. Smith (1976: fig. 2) also proposed a phylogeny for the stenodermatine genera, arranging them to include two main lineages separated according to face (rostral) length (Fig. 18C). His short-faced group included *Artibeus, Enchisthenes,* and the eight genera termed short-faced herein. His proposed phylogeny showed the mainland and Antillean short-faced genera to be of different origins, with the Antillean bats more closely related to *Artibeus.* He further suggested that *Vampyrodes, Vampyrops,* and *Vampyressa* share a common ancestor.
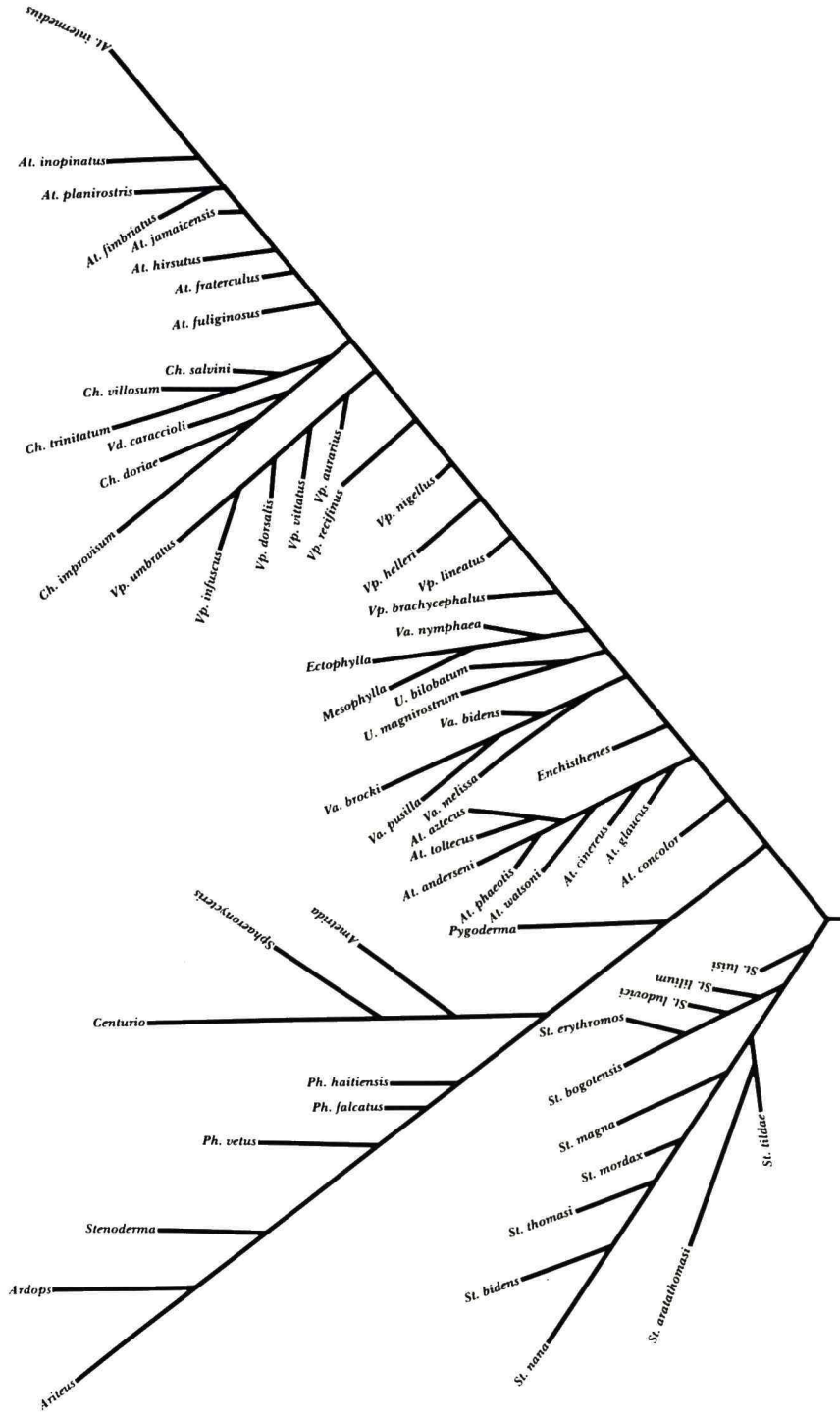
FIG. 13.—Cladogram (scaled to character-value lengths) from Wagner analysis of size-free continuous-state data. Generic abbreviations as for Fig. 10.

TABLE 4.—R^2 *values (adjusted for error degrees of freedom) from linear regression of each study species on an outgroup* (Carollia brevicauda). *Values indicate percentage of original variance for each species' data vector explained by outgroup; Wagner analysis performed on vectors of residuals from these regressions.*

Species	R^2	Species	R^2
Sturnira lilium	.984	Chiroderma villosum	.974
Sturnira thomasi	.984	Chiroderma salvini	.972
Sturnira tildae	.982	Chiroderma trinitatum	976
Sturnira magna	.964	Ectophylla alba	.975
Sturnira mordax	.980	Ectophylla macconnelli	.975
Sturnira bidens	.985	Artibeus cinereus	.978
Sturnira nana	.985	Artibeus glaucus	.980
Sturnira aratathomasi	.967	Artibeus watsoni	.976
Sturnira ludovici	.984	Artibeus phaeotis	.973
Sturnira erythromos	.985	Artibeus toltecus	.972
Sturnira luisi	.985	Artibeus aztecus	.971
Sturnira bogotensis	.987	Artibeus anderseni	.974
Uroderma bilobatum	.977	Artibeus hirsutus	.974
Uroderma magnirostrum	.981	Artibeus inopinatus	.969
Vampyrops infuscus	.958	Artibeus concolor	.977
Vampyrops vittatus	.963	Artibeus jamaicensis	.974
Vampyrops umbratus	.961	Artibeus lituratus	.968
Vampyrops aurarius	.964	Artibeus planirostris	.970
Vampyrops nigellus	.970	Artibeus fuliginosus	.971
Vampyrops brachycephalus	.969	Artibeus fraterculus	.976
Vampyrops helleri	.967	Artibeus fimbriatus	.975
Vampyrops lineatus	.976	Enchisthenes hartii	.980
Vampyrops recifinus	.960	Ardops nichollsi	.909
Vampyrops dorsalis	.958	Phyllops falcatus	.934
Vampyrodes caraccioli	.966	Phyllops haitiensis	.939
Vampyressa pusilla	.977	Phyllops vetus	.919
Vampyressa melissa	.978	Ariteus flavescens	.889
Vampyressa nymphaea	.974	Stenoderma rufum	.899
Vampyressa brocki	.968	Pygoderma bilabiatum	.929
Vampyressa bidens	.979	Ametrida centurio	.911
Chiroderma doriae	.976	Sphaeronycteris toxophyllum	.900
Chiroderma improvisum	.973	Centurio senex	.863

Gardner (1977: fig. 8) included a dendrogram based upon similarity of standard karyotypes (Fig. 18D). He disagreed with Smith (1976) on several points, showing: (1) the short-faced genera as monophyletic; (2) *Vampyressa* associated with *Chiroderma* and *Mesophylla*, rather than *Vampyrops* and *Vampyrodes*; and (3) *Ectophylla* as unrelated to *Mesophylla*. With the exception of the relation between *Mesophylla* and *Chiroderma*, my Fig. 17 is in agreement with Gardner (1977) on these points.

In the introduction of this paper, I listed seven aspects of stenodermatine phylogeny that are in special need of clarification. My results provide insight into some of these questions; the discussion follows the order in which the questions were listed in the introduction.

FIG. 14.—Cladogram (scaled to character-value lengths) from Wagner analysis of common-part-removed continuous-state data. Subtree at lower left is a continuation (in smaller scale) from arrow at right. Scale markers at bottom indicate equivalent character-value lengths for two portions of tree. Generic abbreviations as for Fig. 10.

Little is revealed in Fig. 17 concerning the relationships of the species of *Sturnira* to each other or to the other genera. These results certainly do not agree with de la Torre (1961), Smith (1976), or Gardner (1977), each of whom showed this genus as part of an internal clade within the subfamily (Fig. 18 A,C,D). The apparent separation of *S. bidens* and *S. nana* (the subgenus *Corvira*) from other *Sturnira*, is supported only by the Wagner analysis of discrete-state data (Fig. 10). Pending additional evidence, I follow Gardner and O'Neill (1969, 1971) and retain subgeneric status for *Corvira*. Nothing in any of my analyses suggests distinctiveness above the

FIG. 15.—Adams-2 consensus cladogram from Wagner discrete-state cladogram (Fig. 10) and WISS consensus tree (Fig. 12). Generic abbreviations as for Fig. 10.

St. luisi
St. lilium
St. tildae
St. magna
St. aratathomasi
St. ludovici
St. erythromos
St. bogotensis
St. mordax
St. bidens
St. thomasi
St. nana
At. concolor
Enchisthenes
At. glaucus
At. cinereus
At. watsoni
At. phaeotis
At. anderseni
At. toltecus
At. aztecus
Pygoderma
Ametrida
Sphaeronycteris
Centurio
Ph. haitiensis
Ph. falcatus
Ph. vetus
Stenoderma
Ardops
Ariteus
Va. melissa
Va. bidens
Va. pusilla
Va. brocki
U. bilobatum
U. magnirostrum
Vd. caraccioli
At. inopinatus
At. hirsutus
At. fuliginosus
At. fraterculus
At. jamaicensis
At. intermedius
At. planirostris
At. fimbriatus
Va. nymphaea
Ectophylla
Mesophylla
Ch. salvini
Ch. villosum
Ch. trinitatum
Ch. doriae
Ch. improvisum
Vp. brachycephalus
Vp. lineatus
Vp. helleri
Vp. recifinus
Vp. nigellus
Vp. aurarius
Vp. vittatus
Vp. infuscus
Vp. umbratus
Vp. dorsalis

Fig. 16.—Adams-2 consensus cladogram from size-free cladogram (Fig. 13) and common-part-removed cladogram (Fig. 14). Generic abbreviations as for Fig. 14.

FIG. 17.—Adams-2 consensus cladogram from discrete-state consensus tree (Fig. 15) and continuous-state tree (Fig. 16). Generic abbreviations as for Fig. 10.
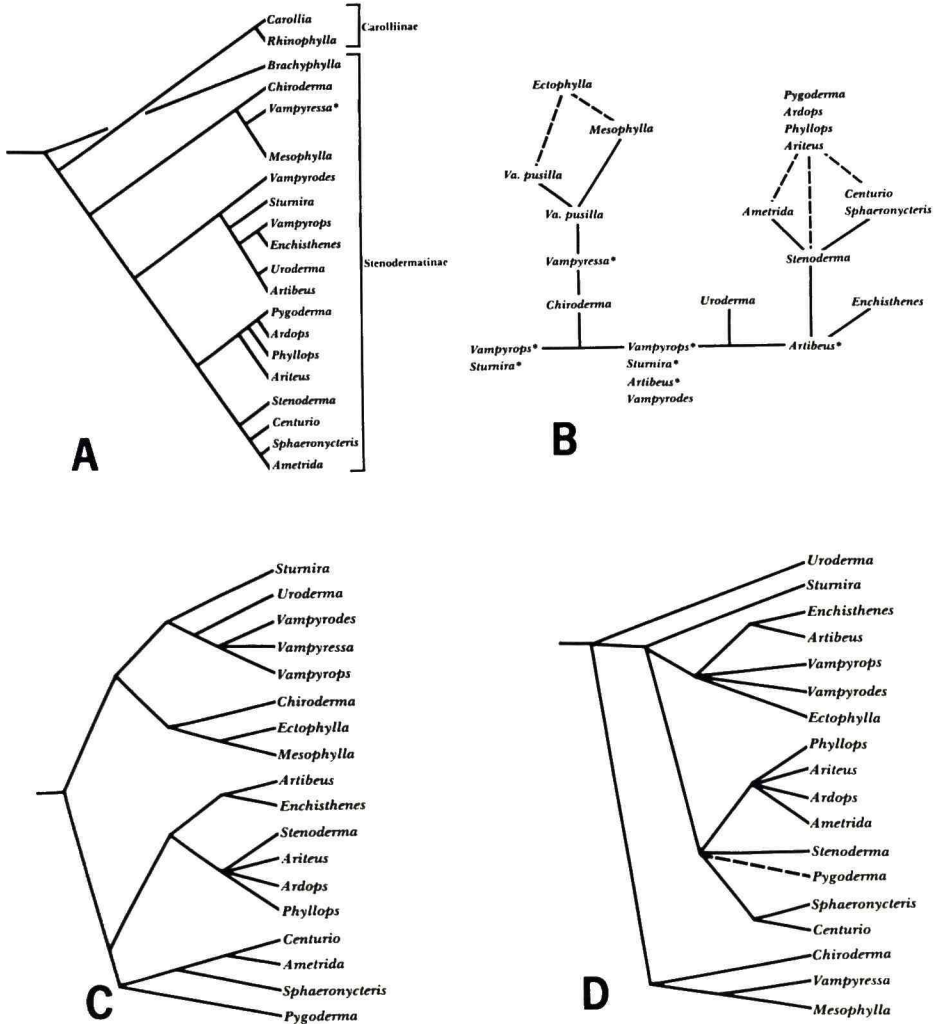
Fig. 18.—Phylogenies (redrawn) from four published arrangements of stenodermatine genera. (A) de la Torre (1961: fig. 4); (B) Baker (1973: fig. 5); (C) Smith (1976: fig. 2); (D) Gardner (1977: fig. 8). Asterisk indicates only part of genus in a particular position. Dashed line indicates alternate or uncertain phylogeny.

species level for *S. mordax*—recognition of *Sturnirops* is not supported even as a subgenus.

Within *Vampyrops*, Fig. 17 indicates at least two lineages. One contains *V. nigellus*, *V. helleri*, and *V. dorsalis*; the other includes *V. vittatus*, *V. aurarius*, *V. lineatus*, and *V. umbratus*. The status of the remaining three species is unclear. Although Gardner and Carter (1972a) agreed with Sanborn (1955) in considering *V. umbratus* a synonym of *V. dorsalis*, my study indicates that Panamanian and Colombian specimens (probably

referable to the name *umbratus*) represent a species distinct from *V. dorsalis* of Perú.

Tuttle (1970), in a review of Peruvian bats, included *V. infuscus* within *V. vittatus*, but Gardner and Carter (1972*a*) and Koopman (1978) recognized *V. infuscus* as specifically distinct. Koopman also disagreed with the description by Gardner and Carter (1972*b*) of *V. nigellus* as a distinct species; Koopman regarded this taxon as a subspecies of *V. lineatus*. Although my results provide little insight into the distinctness of *V. infuscus*, they do show *V. lineatus* and *V. nigellus* in different clades, implying full specific status for *V. nigellus*.

The relationship of *Uroderma* to other stenodermatine genera has been a matter of dispute at least since Burt and Stirton (1961) suggested (without explanation) that the genus probably should be regarded as a subgenus of *Artibeus*. They noted that "the differences are rather subtle," but their suggestion has not been generally accepted, particularly in light of Baker's (1967, 1973) finding of karyotypic differences that separated *Uroderma* from all other stenodermatines known karyotypically at that time. Based presumably on this and other evidence, Smith (1976) arranged *Uroderma* as the sister taxon to *Vampyressa*, *Vampyrodes*, and *Vampyrops*. Gardner (1977), who also examined standard karyotypes, considered a high diploid number to be the primitive condition and placed *Uroderma* essentially as an outgroup to the remaining stenodermatines (including *Sturnira*).

In studies of G- and C-banded chromosomes to determine homologous segments, Johnson (1979) and Baker *et al.* (1979) again found *Uroderma* to be quite different from *Artibeus* and, in fact, were unable to ascertain a close relationship between *Uroderma* and any other group. An analysis of electrophoretic data (Koop and Baker, 1983) also failed to find *Uroderma* to be closely related to any of the six *Artibeus* species included in the study. In my results, *Uroderma* appears to be a sister taxon to the species group of the large *Artibeus* and *Ectophylla*. The status of the genus certainly requires further study, but it is prudent at present to retain generic rank for *Uroderma*.

Eight of the 17 stenodermatine genera belong to a group of short-faced bats with characteristic white epaulettes. All but one of these genera currently are regarded as containing but one species (Jones and Carter, 1976; Honacki *et al.*, 1982). Four of the genera are Antillean endemics, and the remainder occur on the mainland from Mexico to Argentina. Investigators have not agreed on the interspecific relationships of the group, or whether the 10 living species even constitute a natural assemblage. Jones and Schwartz (1967), in their review of the genus *Ardops*, stated that the four Antillean genera (*Ardops*, *Ariteus*, *Phyllops*, and *Stenoderma*) are related, with *Ardops* probably most closely related to *Ariteus*. Koopman (1968) agreed that they are all closely related, but noted that, "*Ardops* seems rather closely related to, and possibly congeneric with, *Phyllops*. . . ." He also

postulated that the derivation of the group was probably from a form of *Artibeus* or a close relative.

Baker (1973) believed that the eight genera comprised a natural assemblage, but his chromosomal data suggested that *Stenoderma* was less closely related to *Ardops*, *Phyllops*, and *Ariteus* than to some of the mainland genera. *Pygoderma* was depicted (Baker, 1973: fig. 5) as being the closest mainland relative of the Antillean genera *Ardops*, *Phyllops*, and *Ariteus*, and the entire lineage of eight genera was postulated as having been derived (along with *Enchisthenes*) from the *Artibeus* group possessing the 30-31 diploid number. Nagorsen and Peterson (1975) published a karyotype of *P. haitiensis* and agreed with Baker's (1973) assessment of the phylogeny of this group. Varona (1974), however, followed Simpson (1945) in synonomizing *Ariteus*, *Ardops*, and *Phyllops* under the genus *Stenoderma*, thus making all Antillean species congeneric.

Greenbaum *et al.* (1975), with additional standard karyotype data, stated that the four Antillean genera represent a single invasion from the mainland and, further, that the eight short-faced genera together share a common evolutionary history exclusive of other stenodermatines. Smith (1976) agreed that the Antillean species share a common ancestor, but believed them to be more closely related to *Artibeus* and *Enchisthenes* than to the mainland short-faced taxa. Gardner (1977) agreed with Baker's (1973) exclusion of *Stenoderma* from the monophyletic Antillean assemblage, indicating that this group might instead be more closely related to the mainland *Ametrida*.

Baker and Genoways (1978) restated the belief that the four Antillean genera form a monophyletic group, and suggested that it is the second oldest bat taxon in the Caribbean region (after the endemic subfamily Phyllonycterinae). Johnson (1979) included a cladogram, based on G- and C-banded chromosomes, in which *Phyllops* was allied with *Artibeus* and *Vampyrops*, but not with *Centurio*, suggesting that the eight short-faced genera are not monophyletic.

The questions of systematic relationships among these eight genera thus can be reduced to two general categories—the monophyly of Antillean genera, and the monophyly of the group overall. My results (Fig. 17) indicate that the eight short-faced genera form a monophyletic assemblage (although one possible interpretation of this tree also involves the inclusion of *Enchisthenes* or *Artibeus concolor*, or both, in the lineage). The positions of *Pygoderma*, *Centurio*, and *Stenoderma* are unresolved in the clade, indicating that these data at least do not support synonomy of the Antillean species under the generic name *Stenoderma*. The relation of *Ardops* and *Ariteus* indicated in Fig. 17 is in agreement with the statement of Jones and Schwartz (1967). The close association of these two genera with *Phyllops* suggests that if the number of Antillean genera of this group were to be reduced, it should be reduced to two, with *Ardops* and *Phyllops* placed in synonomy under the older name *Ariteus*. However, given the

uncertain position of *Stenoderma* on the tree, and the continued uncertainty concerning the phylogeny of the mainland species, I believe it best in the interest of nomenclatorial stability to retain, for the present, the generic names *Ardops* and *Phyllops*.

Vampyressa and *Vampyriscus*, originally described as subgenera of *Vampyrops* (Thomas, 1900), both were raised to full generic rank by Miller in 1907. Simpson (1945) evidently disagreed, as he included both of these names (as well as *Vampyrodes*) within *Vampyrops*. Goodwin (1963), in a review of *Vampyressa*, did not include *Vampyriscus bidens*, considering it to be generically distinct. Peterson (1968), in another review, included *Vampyriscus* as a subgenus of *Vampyressa*, and described a new subgenus *Metavampyressa* to include *V.* (*M.*) *nymphaea* and *V.* (*M.*) *brocki*. Davis (1975), in a review of variation in *V. bidens*, placed *Metavampyressa* in synonomy under *Vampyriscus*, which he retained as a subgenus.

In 1968, Starrett and Casebeer departed from currently accepted taxonomy and returned *Mesophylla* to generic status, pointing out that the skull of *M. macconnelli* shows greater similarity to *Vampyressa pusilla thyone* than to *Ectophylla alba*. *Mesophylla*, described by Thomas (1901), had been placed in synonomy with *Ectophylla* by Laurie (1955) and Goodwin and Greenhall (1962). Starrett and Casebeer (1968) agreed that the three genera form a well-defined group, but regarded *Mesophylla* as sufficiently dissimilar from *Ectophylla* to be accorded generic rank.

Based primarily on standard karyotypic data, Baker (1973) suggested that *Mesophylla* was derived from the *Vampyressa* lineage (which in turn was derived from *Chiroderma*). Without knowing the karyotype at the time, he assumed that *Ectophylla* was closely related to *Mesophylla*. Also, Baker *et al.* (1973) found that standard karyotypic data indicate that *V. pusilla* is more closely related to *Mesophylla* than to the other *Vampyressa* species then known karyotypically. Greenbaum *et al.* (1975), reporting on the karyotype of *Ectophylla*, found it to be unlike that of *Mesophylla* or any species of *Vampyressa*, and suggested that *Ectophylla* might be more distantly related to the *Vampyressa-Mesophylla* stock than is the genus *Chiroderma*. Nevertheless, Jones and Carter (1976) retained *Ectophylla macconnelli* in their checklist, and implied that *Mesophylla* might have validity as a subgenus. In the same volume, Smith's (1976) phylogeny showed *Mesophylla* and *Ectophylla* as sister taxa, with *Vampyressa* in a separate clade along with *Vampyrops* and *Vampyrodes*.

Gardner (1977), in a review of chromosomal variation in *Vampyressa*, pointed out that the subgenera *Vampyressa* and *Vampyriscus* appear to be karyotypically valid. He also commented that the karyotypes of Peruvian *V. pusilla* (at least three karyotypic variants are known in this species) and *Mesophylla* are "remarkably similar," but declined to relegate *Mesophylla* to synonomy within *Vampyressa*. Recently, Anderson *et al.* (1982) recognized *Ectophylla macconnelli*, noting that recognition of *Mesophylla* as a distinct genus seems to be based more on karyology than on

morphology. Both treatments have been used in recent years and the question is still open.

A suite of interrelated questions thus remains concerning these genera, the status of the two currently recognized subgenera of *Vampyressa*, and the relationship of *Mesophylla* to this genus and to *Ectophylla*. My results for the *Vampyressa* species are the least well resolved of any group, as they do not even confirm the monophyly of the genus. Nor is the subgeneric question answered here, although there is a suggestion that the distinction is not valid.

The status of *Mesophylla* is quite clear, however, both from morphologic data and previously cited chromosomal data. Although the species of *Vampyressa* are not well resolved in Fig. 17, any interpretation of this tree indicates that if *Vampyressa* is a natural assemblage it includes *Mesophylla macconnelli*. Additionally, Fig. 17 does not strongly support subgeneric status for *Mesophylla*. I recommend therefore, that *Mesophylla* be placed in synonomy under *Vampyressa*, with the proper name of the single species being *Vampyressa macconnelli*. See Appendix V for additional nomenclatorial comments concerning taxa referable to this species.

Ectophylla is placed in Fig. 17 in association with *Uroderma* and the large species of *Artibeus*. Neither these results nor any previous work have questioned the generic validity of *Ectophylla* as applied to the single species *E. alba*, and this combination should remain in use.

Artibeus is the most species-rich genus currently recognized within the subfamily Stenodermatinae. The content of the genus was clarified by Miller (1907), who excluded from it the taxa referable to *Uroderma* and, agreeing with Andersen (1906, 1908), the one species referable to *Enchisthenes*. Miller also stated that he saw no reason to recognize subgenera within *Artibeus*. Simpson (1945) evidently regarded the differences between *Enchisthenes* and *Artibeus* to be minor, as he included *E. hartii* as a species of the latter. Gardner (1977), based on his own and other work (for example, Baker 1967, 1973), retained *Enchisthenes* at the generic level, showing it as the sister taxon to *Artibeus*. Koopman (1978) and Anderson *et al.* (1982), without explanation, synonomized *Enchisthenes* with *Artibeus*, as did Jones and Carter (1979) and Honacki *et al.* (1982), although Hall (1981) did not.

The last full revision of the genus *Artibeus* was by Andersen (1908). Subsequent systematic work on the smaller taxa of the genus has been undertaken by (among others) Hershkovitz (1949), Dalquest (1953), Davis (1958, 1970), Baker (1973) and Koopman (1978). The larger species of *Artibeus* also have been studied by a number of workers, including Patten (1971), Baker (1973), Koopman (1978), Myers and Wetzel (1979), Anderson *et al.* (1982), Davis (1984), and Koepcke and Kraft (1984).

Several recent studies have examined the relationship of the genus *Artibeus* to other stenodermatine taxa. Baker (1967) found *Artibeus* to be similar karyotypically to *Vampyrops* and *Sturnira*, and quite unlike *Uroderma*. Within the genus, he found *A. turpis* (= *phaeotis*) to differ from

A. jamaicensis, A. lituratus, and *A. toltecus* in the form of a chromosomal sex-determining mechanism. Straney *et al.* (1979) presented electrophoretic analyses of several phyllostomid bats that suggested *Artibeus* might be polyphyletic. Koop and Baker (1983), analyzing 22 electrophoretic loci, found apparent diphyly in *Artibeus,* with *A. concolor* and *A. jamaicensis* separate from the four small *Artibeus* species examined in the study. They also noted that *A. concolor* and *A. jamaicensis* were separated by relatively large genetic distance.

The results of my morphologic analyses strongly indicate that *Artibeus,* as presently understood, is a polyphyletic assemblage (Fig. 17). The large species constitute a natural group, which includes the populations recognized under the names *A. inopinatus, A. hirsutus, A. jamaicensis, A. planirostris, A. fraterculus, A. intermedius* (and presumably *A. lituratus*), as well as the Paraguayan taxon referred to in this study as *A. fimbriatus.* These bats should continue to be referred to under the generic name *Artibeus.*

The second natural group of *Artibeus* bats includes the species now recognized under the names *A. watsoni, A. glaucus, A. toltecus, A. cinereus, A. phaeotis, A. aztecus,* and *A. anderseni,* and possibly also *Enchisthenes hartii* and *A. concolor.* The oldest available generic name for this group is *Dermanura* Gervais 1855, and I recommend this name be applied to these bats at the generic level. Specific names ending in "us" would be changed to agree: *D. glauca, D. tolteca, D. cinerea,* and *D. azteca.* As pointed out above, the relationships of *A. (Enchisthenes) hartii* and *A. concolor* to the *Dermanura* bats are yet unclear. Koop and Baker (1983) and Tandler *et al.* (1986), for instance, noted that *A. concolor* is unlike the other species of *Artibeus* used in their studies. The generic validity of *Enchisthenes* has been in dispute since Andersen (1906) removed if from *Artibeus,* under which it was originally described. In the interest of stability I follow recent authors (for example, Koopman 1978; Jones and Carter, 1979; Anderson *et al.,* 1982), who have not recognized *Enchisthenes* at the generic level. Thus, until additional evidence is available, I suggest applying the name *Dermanura* to both *hartii* and *concolor,* as well as the other species listed above. The name combinations for the affected species thus would be *Dermanura hartii, Dermanura concolor, Dermanura watsoni, Dermanura glauca, Dermanura tolteca, Dermanura cinerea, Dermanura phaeotis, Dermanura azteca,* and *Dermanura anderseni.* See Appendix V for additional nomenclatorial comments concerning taxa referable to *Demanura.*

Within the reduced genus *Artibeus,* the question remains of the relationships and possible conspecific status of the South American taxa. My results (Fig. 17) suggest, but do not confirm, that neither *A. planirostris* nor *A. fraterculus* is conspecific with *A. jamaicensis,* and that *A. hirsutus* and *A. inopinatus* are not conspecific, as has been suggested (Honacki *et al.,* 1982). My results strongly indicate that *A. fuliginosus* is specifically

distinct from *A. jamaicensis*, notwithstanding the comments of Anderson *et al.* (1982). Within the genus *Dermanura*, the focal question concerns *D. glauca* and *D. watsoni*, and their relationship to *D. cinerea*. Koopman (1978), Jones and Carter (1979), and Anderson *et al.* (1982) all judged *glaucus* and *watsoni* to be synonyms of *A. cinereus*. My results suggest that this may not be the case, but do agree with statements by the same authors that *D. anderseni* is specifically distinct from *D. cinerea*.

Based on data and analyses leading to Fig. 17, I recommend that *Mesophylla macconnelli* be considered as congeneric with species of *Vampyressa*, and that the genus *Artibeus* (including *Enchisthenes*) be split into two genera, with the smaller taxa referred to under the name *Dermanura*. The recommended generic classification of all stenodermatine species is listed in Appendix VI, and also is indicated in Fig. 17.

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APPENDIX I—SPECIMENS EXAMINED

An asterisk indicates the type specimen of the species. Museum acronyms used are as follows: AMNH, American Museum of Natural History; CMNH, Carnegie Museum of Natural History; FMNH, Field Museum of Natural History; KU, Museum of Natural History, University of Kansas; LACM, Los Angeles County Museum of Natural History; LSU, Museum of Zoology, Louisiana State University; MCZ, Museum of Comparative Zoology, Harvard University; MSB, Museum of Southwestern Biology, University of New Mexico; MSU, The Museum, Michigan State University; MVZ, Museum of Vertebrate Zoology, University of California; OU, Stovall Museum of Science and History, University of Oklahoma; ROM, Royal Ontario Museum; TCWC, Texas Cooperative Wildlife Collections, Texas A&M University; TTU, The Museum, Texas Tech University; UA, Department of Biological Sciences, University of Arizona; UMMZ, Museum of Zoology, University of Michigan; USNM, United States National Museum of Natural History. Number in parentheses after localities indicates the number of specimens examined from that locality. Number in parentheses after species name indicates total number examined.

STENODERMATINAE

Ametrida centurio (17)—Trinidad (11): CMNH 45335; TTU 5215, 8766, 8769, 8771-72, 8811, 8888, 9545, 9548, 9557. Suriname (6): CMNH 63767, 63769, 63771-73, 68418.

Ardops nichollsi (14)—Montserrat (2): ROM 71463, 71467. Guadeloupe (3): TTU 20801, 20805, 20810. Dominica (7): KU 104805-10, 104813. Martinique (1): AMNH 213951. St. Lucia (1): USNM 110921.

Ariteus flavescens (13)—Jamaica (13): TTU 21714-21, 21763, 21772; USNM 534909-11.

Artibeus anderseni (10)—Bolivia (10): AMNH 209583, 210825-26, 210828-30, 210834, 210836-37, 210845.

Artibeus aztecus (13)—México (4): AMNH 203753-54, 203757; USNM 52050*. Guatemala (1): TCWC 17507. Costa Rica (7): LSU 12876; TTU 12907-08, 12910-11, 12913-14. Panamá (1): USNM 323455.

Artibeus cinereus (10)—Trinidad (10): TTU 5450, 5541, 5660, 5672, 5679, 8968-69, 8971, 8973, 8975.

Artibeus concolor (10)—Colombia (1): TCWC 26046. Venezuela (8): USNM 387379, 387381-82, 387386-88, 2 numbers lost. Brazil (1): AMNH 78859.

Artibeus fimbriatus (10)—Paraguay (10): UMMZ 125914, 125936, 125938, 125943-44, 133721, 133724-27.

Artibeus fraterculus (10)—Ecuador (10): AMNH 47248*; USNM 498940-41; 522472, 522474-75, 522478-81.

Artibeus fuliginosus (10)—Perú (10): USNM 364439, 499209-14, 499216-17, 499220.

Artibeus glaucus (16)—Ecuador (3): TCWC 12278, 12280-81. Perú (13): AMNH 37196-97, 214361, 233750-51, 236067; LSU 16602-05, 19184, 19186, 19706.

Artibeus hartii—see *Enchisthenes hartii;*.

Artibeus hirsutus (22)—México (22): LACM 9982, 9985, 9988, 13299-301, 13303, 13804, 34988, 58424; MSB 18407; TTU 8697, 8700-04, 10592-93; UA 6348-49; USNM 126449*.

Artibeus inopinatus (13)—Honduras (7): TCWC 9517*, 18407-08; TTU 7685, 7688-90. Nicaragua (6): TTU 12916, 12918, 12921-24.

Artibeus intermedius (7)—México (3): TTU 15564-65, 15568. El Salvador (4): TTU 12990-93.

Artibeus jamaicensis (13)—México (12): AMNH 12038/10469; TTU 8205, 8209-10, 8212, 8214, 8217, 8344, 10043, 10045, 15557; USNM 126554. Nicaragua (1): AMNH 28335.

Artibeus lituratus—see *A. intermedius*.

Artibeus phaeotis (12)—México (1): USNM 108176*. Guatemala (1): TCWC 14392. Honduras (10): TTU 12962, 12964, 12967-69, 12971-73, 12975, 12985.

Artibeus planirostris (25)—Guyana (1): TCWC 28739. Perú (24): LSU 12535-36, 12538, 12540, 12542, 12545, 12547-49, 12556, 24529, 24531; MVZ 153408-09, 154900-01, 154903-05, 154909-12, 157725.

Artibeus toltecus (11)—México (11): TCWC 6499; TTU 10022-23, 10025, 10133, 10204-05, 10207-08, 10210-11.

Artibeus watsoni (9)—Nicaragua (2): TTU 12968-69. Costa Rica (4): TTU 12979-82. Panamá (3): USNM 503666, 503668, 503673.

Centurio senex (17)—México (11): LACM 13476-80; MSB 25186; MSU 16490-91; UA 10807-08; USNM 511741. El Salvador (1): MVZ 130911. Panamá (4): USNM 310238, 310242, 310244, 503837. Trinidad (1): USNM 346847.

Chiroderma doriae (2)—Brazil (2): USNM 521053, 542616.

Chiroderma improvisum (2)—Montserrat (1): TTU 31403. Guadeloupe (1): TTU 19900*.

Chiroderma salvini (14)—México (5): MSU 16502; OU 14336-14337; TTU 9996; USNM 338711. Honduras (2): TTU 12800, 12802. Panamá (7): USNM 309930-34, 309946, 338044.

Chiroderma trinitatum (11)—Panamá (2): USNM 309903, 335295. Trinidad (9): AMNH 175325*; TTU 5223, 5265, 5336, 5382, 5675, 8989, 9014; UA 17070.

Chiroderma villosum (13)—El Salvador (10): TTU 12755, 12757-59, 12762-63, 12767, 12771, 12773-74. Trinidad (1): CMNH 45357. Suriname (2): CMNH 53793-94.

Ectophylla alba (13)—Costa Rica (4): LACM 14365-66; MSB 34204, 34251. Panamá (9): USNM 315563, 335317-24.

Ectophylla macconnelli (16)—Trinidad (13): AMNH 186433; CMNH 45358-59; TTU 5202, 5205, 5207-09, 5211-13, 5362, 5474. Suriname (3): CMNH 63829-30, 68430.

Enchisthenes hartii (18)—México (5): LACM 13529-30, 55911; MSU 15391; TTU 5581. Costa Rica (1): MSB 26805. Panamá (6): USNM 310214-17, 323539, 539813. Trinidad (2): TTU 5243, 5371. Colombia (1): MVZ 124036. Perú (3): LSU 21534, 27251; MVZ 135599.

Mesophylla macconnelli—see *Ectophylla macconnelli*.

Phyllops falcatus (4)—Cuba (4): AMNH 176190; USNM 123187, 143844, 300504.

Phyllops haitiensis (12)—Hispaniola (12): AMNH 236691-92, 236696; ROM 72797; UMMZ 123279; USNM 520534, 538339-42, 538345, 542273.

Phyllops vetus (6)—Cuba (6): AMNH 41001*, 41002-06.

Pygoderma bilabiatum (52)—Dutch Guiana (1): USNM 37502/14816. Bolivia (10): AMNH 246398-99, 246401-08. Brazil (2): FMNH 94716; ROM 70910. Paraguay (38): AMNH 234288, 234290-98; MCZ 28064; MVZ 144465-66; UMMZ 124373-75, 125804-12, 125824-25, 125828-29, 125833-37, 125841-43; USNM 105685. Argentina (1): CMNH 72333.

Sphaeronycteris toxophyllum (12)—Colombia (1): TTU 10277. Venezuela (9): FMNH 29445; USNM 370797-99, 370801, 370839-40, 405686, 455936. Bolivia (2): AMNH 209740-41.

Stenoderma rufum (10)—Puerto Rico (10): TTU 8861, 8864-66, 8869, 8875-76, 8879-80, 8884.

Sturnira aratathomasi (7)—Colombia (6): ROM 70874, 70876; USNM 395158*, 501064-66. Ecuador (1): ROM 46349.

Sturnira bidens (19)—Colombia (3): FMNH 58719-20, 113447. Venezuela (5): USNM 386557, 386559-60, 386567, 386570. Peru (11): AMNH 214349, 216114; LSU 14197-99, 16525, 18368, 18386, 18389, 20741-42.

Sturnira bogotensis (12)—Colombia (8): AMNH 207853, 207856-59, 207861-62; USNM 251989*. Bolivia (4): UMMZ 126752-53, 126836-37.

Sturnira erythromos (19)—Colombia (5): FMNH 58721-25. Perú (10): FMNH 75183, 75185, 110921; LSU 14191, 18960, 18975, 18992-94; MVZ 139521. Bolivia (4): AMNH 246569, 246571-72; UMMZ 126835.

Sturnira lilium (17)—México (5): OU 14423, 14430, 14433, 14436; USNM 126555. Dominica (1): USNM 361881. St. Vincent (1): USNM 361852. Trinidad (10): TTU 5367, 5408, 5415, 5648, 5651, 5669-71, 5677-78.

Sturnira ludovici (14)—México (13): MSU 8808; TCWC 37863, 37865, 37868-69, 37874-77; TTU 5584, 7341-42, 8221. Ecuador (1): AMNH 67328*.

Sturnira luisi (11)—Costa Rica (3): TCWC 9959*, 9992, 9998. Panamá (1): USNM 309565. Ecuador (4): TCWC 12112, 12120-22. Peru (3): TCWC 12125-27.

Sturnira magna (14)—Colombia (2): FMNH 113282-83. Perú (12): AMNH 230624; LSU 21484; MVZ 153366-69, 153371-72, 154842-43, 154856-57.

Sturnira mordax (13)—Costa Rica (13): LSU 11456, 12784; MSB 28345; TCWC 9978, 10034, 10042; UA 20814; UMMZ 111332, 111415, 112038, 112040-41; USNM 250310*.

Sturnira nana (11)—Peru (11): AMNH 219138, 219171-73; LSU 15683*, 16519, 16521-24; TCWC 28071.

Sturnira thomasi (7)—Guadeloupe (7): AMNH 234950; ROM 68118; TTU 19904-07; USNM 361883*.

Sturnira tildae (19)—Trinidad (3): AMNH 149625*; CMNH 45362; TTU 5402. Suriname (6): CMNH 63842-43, 63845-46, 63848, 63851. Perú (7): AMNH 213362, 213365, 213368-69, 213371-72, 213374. Bolivia (2): AMNH 209408-09. Brazil (1): USNM 361658.

Uroderma bilobatum (11)—México (1): TCWC 16603. El Salvador (10): TTU 12651-52, 12654-57, 12659-61, 12664.

Uroderma magnirostrum (18)—Honduras (1): TCWC 17189*. Perú (7): MVZ 136498-504. Bolivia (10): AMNH 210752, 210754-56, 210758, 210760-62, 210765, 210768.

Vampyressa bidens (11)—Venezuela (1): USNM 387190. Ecuador (4): AMNH 67997-98, 71656, 76090. Perú (4): AMNH 208072; LSU 21536; MVZ 136506, 153381. Brazil (2): USNM 361721, 393025.

Vampyressa brocki (8)—Colombia (3): TTU 8827, 8832, 9047. Guyana (2): ROM 38515*, 59745. Suriname (3): CMNH 63871-73.

Vampyressa melissa (10)—Peru (10): AMNH 233769; LSU 16580-83, 19100, 19102-03; MVZ 139983, 154869.

Vampyressa nymphaea (13)—Nicaragua (3): TTU 12612, 12905-06. Costa Rica (1): LSU 12829. Panamá (9): USNM 309882, 309885-89, 318130, 519695-96.

Vampyressa pusilla (12)—Honduras (1): TTU 12894. Nicaragua (4): TTU 12897-99, 12903. Costa Rica (2): MSB 34209; TTU 12892. Panamá (4): MSB 36397; USNM 173832, 503629, 503633. Ecuador (1): USNM 535095.

Vampyrodes caraccioli (15)—México (5): LACM 18631-33; UA 9400-01. Panamá (8): UA 7892; USNM 309771, 309773-74, 309805-06, 309813-14. Perú (2): AMNH 230654-55.

Vampyrops aurarius (10)—Venezuela (10): USNM 387143-44, 387146-47, 387149, 387159, 387163*, 387168, 387171-72.

Vampyrops brachycephalus (11)—Venezuela (1): USNM 408411. Suriname (3): CMNH 63874-76. Perú (5): AMNH 230639; LSU 12165-66, 12168; TCWC 12193*. Bolivia (1): MSU 28110.

Vampyrops dorsalis (10)—Perú (10): AMNH 214355, 233614, 233621; LSU 20734-35, 21451-52, 24775-77.

Vampyrops helleri (12)—Trinidad (12): OU 9808-09; TTU 5259, 5365, 5423, 5481, 5483, 5540, 5647, 5674, 5830, 5840.

Vampyrops infuscus (15)—Perú (15): AMNH 230645; LSU 16402, 19095-98; USNM 364397-405.

Vampyrops lineatus (16)—Brazil (6): LACM 28041, 28044-46; USNM 391085-86. Paraguay (10): UMMZ 125879-85, 125891, 125893-94.

Vampyrops nigellus (13)—Perú (9): AMNH 233646, 233686; LSU 16415*, 24773, 24783-84; MVZ 154875, 154877-78. Bolivia (4): AMNH 246616-18, 246620.

Vampyrops recifinus (8)—Brazil (8): FMNH 19516; USNM 27566/545001, 27959/545002, 542611, 542612-15.

Vampyrops umbratus (16)—Panamá (2): USNM 338025, 338027. Colombia (14): AMNH 233186-87, 235778-79; LACM 18695-99; USNM 483540-41, 483544-45, 483547.

Vampyrops vittatus (14)—Costa Rica (7): LSU 10220, 12891; MSB 26804; TTU 12888-91. Panamá (7): USNM 309720, 336031-36.

CAROLLIINAE

Carollia brevicauda (10)—México (10): AMNH 189732-33, 189736, 189739-42, 189745-46, 203693.

Carollia castanea (10)—Panamá (10): USNM 309421-22, 309424, 309439, 309450, 309452, 309461, 503521, 503528, 503835.

Carollia perspicillata (13)—Panamá (4): MVZ 114402, 118779-81. Venezuela (5): MVZ 160046-47, 160050, 160065-66. Perú (4): MVZ 157681, 157684, 157686, 157697.

Carollia subrufa (11)—Guatemala (5): USNM 502216, 502223, 502234, 502238-39. Honduras (5): TCWC 19192, 19979-82. El Salvador (1): TCWC 19978.

PHYLLOSTOMINAE

Macrotus waterhousii (18)—Isle of Pines, Cuba (10): CMNH 2376, 2379, 2381, 2383-89. Cayman Islands (6): USNM 538125, 538127, 538129, 539736-38. Jamaica (1): USNM 534883. Hispaniola (1): USNM 538336.

APPENDIX II—DISCRETE-STATE CHARACTERS

Discrete-state characters, with character-state values and tree topology for each. Nonlinear (bifurcating) character-state trees are shown in Fig. 19.

EXTERNAL CHARACTERS

1. *Ear shape.*—(1) Little or no posterior emargination (folding forward of latero-posterior border of pinna); pronounced indentation of medio-anterior border of pinna to point of attachment to head. (2) About one-fifth emarginated; pronounced indentation as in state 1. (3) About one-third emarginated; pronounced indentation as in state 1. (4) About one-half emarginated; pronounced indentation as in state 1. (5) About one-half emarginated; anterior lobe on pinna at medio-anterior point of attachment to head. (6) About three-fourths emarginated; pronounced indentation as in state 1. (7) About three-fourths emarginated; no medio-anterior indentation. (8) Completely emarginated; pronounced indentation as in state 1. Tree: see Fig. 19A.

2. *Leaf shape* (width measured at level of posterio-dorsal attachment; length measured from tip to point of posterio-dorsal attachment).—(1) Length less than width. (2) Length about equal to width. (3) Length greater than width. (4) Length about 1½ times width. (5) Length greater than 1½ times width. Tree: 1-2-3-4-5.

3. *Dorsal hair bands* (number of differentially colored bands on dorsal pelage).—(1) Hair uniformly colored. (2) Two bands. (3) Three bands. Tree: 1-2-3.

4. *Pelage pattern.*—(1) Pelage essentially uniformly colored (this state may include shoulder patches resulting from glandular secretions). (2) Paired white or pale-colored lines from nose leaf, above eye and ear; paired lines of same color from corner of mouth to base of tragus. (3) As in state 2, plus single middorsal line on posterior half of body. (4) As in state 3, with middorsal line extending nearly to neck. (5) As in state 4, with middorsal line extending to head. (6) As in state 1, with distinct white or near-white patch on shoulder near point of attachment of antebrachial membrane. (7) As in state 6, with ribbed pattern on patagium mediad to digit 4. Tree: 7-6-1-2-3-4-5.

5. *Uropatagium shape* (with legs extended so that uropatagium is uniformly stretched; measured along midline).—(1) Uropatagium long, extending one-half or more of distance from sacrum to base of calcar. (2) Uropatagium shorter, extending less than one-half of distance from sacrum to base of calcar. (3) Uropatagia connected at base of sacrum. (4) Uropatagia not connected to each other. Tree: 1-2-3-4.

6. *Plagiopatagial attachment to leg.*—(1) Attaches to tibial region. (2) Attaches to tarsal region. (3) Attaches to metatarsal region. (4) Attaches to metatarsal-phalangeal joint. Tree: 1-2-3-4.

CRANIAL CHARACTERS

7. *Incisive foramina development.*—(1) Absent or minute. (2) Small, not extending past posterior margin of canines. (3) Small (as in state 2), located farther caudad, between levels of P1 and P2. (4) Medium size, not extending farther caudad than posterior margin of P1. (5) Large, extending beyond posterior margin of P1. (6) Small (as in state 2), located between levels of C and P1. Tree: see Fig. 19B.

8. *Nasal septal foramen* (completely penetrates nasal septum in dorsal-ventral direction).—(1) Absent. (2) One present. (3) Two (occasionally three) present. Tree: 1-2-3.

9. *Hard palate posterior extent* (measured from anterior border of orbit; not including any medial posterior projection of palate).—(1) Extends farther caudad than least width of palate between orbits. (2) Extends caudad to anterior border of orbits, but no farther than least width of palate. (3) Does not extend caudad to anterior border of orbit. Tree: 1-2-3.

10. *Hard palate posterior border shape.*—(1) Essentially square. (2) V-shaped (sharp medial notch; lateral borders straight). (3) U-shaped (lateral borders curved; no distinct medial notch). (4) As in state 3, with median posterior projection. Tree: see Fig. 19C.
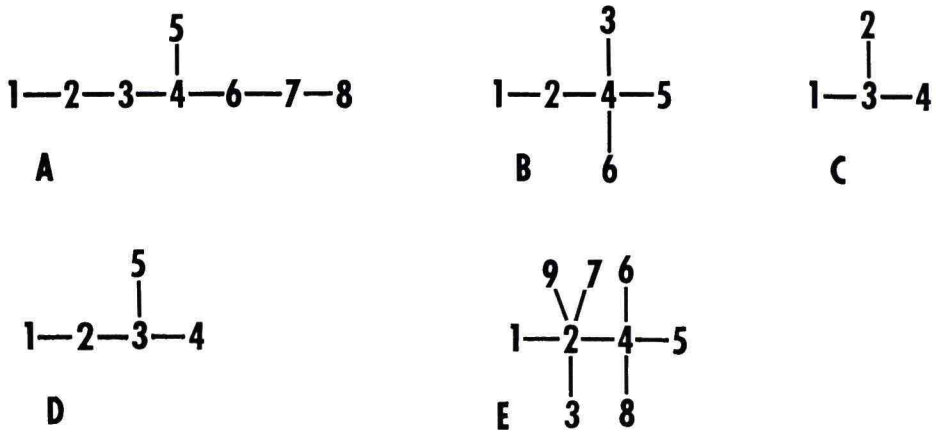
FIG. 19.—Topologies of nonlinear (bifurcating) character-state trees for discrete-state characters. See Appendix II for descriptions of characters and character states, as well as character-state trees for all discrete-state characters not shown here. (A) 1—ear shape; (B) 7—incisive foramina development; (C) 10—hard palate posterior border shape; (D) 16—hypoglossal foramen; (E) 21—dental formula.

11. *Parapterygoid foramina* (just lateral to pterygoid processes).—(1) One present (passes dorso-caudally into braincase). (2) Two present (second passes dorso-cranially). (3) Three present (anterior two are smaller, appear homologous to anterior one in state 2). Tree: 1-2-3.

12. *Paraoccipital process development.*—(1) No paraoccipital process. (2) Minimal development (little disturbance of contour of the region). (3) Moderate development (less well developed than mastoid process). (4) Pronounced development (developed as much or more than mastoid process). Tree: 1-2-3-4.

13. *Basisphenoid pit development.*—(1) Absent. (2) Shallow. (3) Moderate. (4) Deep. (5) Extremely deep. Tree: 1-2-3-4-5.

14. *M1 hypocone development.*—(1) Absent. (2) Slight protuberance. (3) Moderately developed. (4) Strongly developed. (5) Extremely strongly developed. Tree: 1-2-3-4-5.

15. *M3 development.*—(1) Well developed (cusps present). (2) Poorly developed (small, peglike). (3) Absent. Tree: 1-2-3.

16. *Hypoglossal foramen* (in occipital condyle; canal passes cranio-ventrally out of braincase).—(1) Absent. (2) Small. (3) Medium. (4) Large. (5) Two foramina present (appears as ossified division of medium-sized foramen). Tree: see Fig. 19D.

17. *Secondary foramen of occipital condyle* (canal passes cranio-laterally into braincase).—(1) Absent. (2) One present. (3) Two present. Tree: 1-2-3.

18. *Postglenoid foramen* (at posterior end of zygomatic arch, above mandibular condyle; canal passing ventrally from dorsal face of zygomatic arch).—(1) Absent. (2) Present. Tree: 1-2.

19. *External nares shape* (caudad extent of nares as viewed from dorsad to skull).—(1) Bony palate barely or not visible. (2) Bony palate clearly visible. (3) Nares extend caudad to level of anterior border of orbit. Tree: 1-2-3.

20. *Rostral shape* (dorsal border of frontal section at anterior border of orbit).—(1) Ridged or rounded convexly. (2) Flat or slightly troughed. (3) Moderately troughed. (4) Pronouncedly troughed. Tree: 1-2-3-4.

21. *Dental formula.*—(1) 2/2 1/1 2/3 3/3. (2) 2/2 1/1 2/2 3/3. (3) 2/1 1/1 2/2 3/3. (4) 2/2 1/1 2/2 3/3. (5) 2/2 1/1 2/1 2/3. (6) 2/2 1/1 2/2 2/2. (7) 2/2 1/1 1/1 3/3. (8) 2/1 1/1 2/2 2/3. (9) 2/2 1/1 2/2 3/2. Tree: see Fig. 19E.

22. *Development of m3.*—(1) Well developed (cusps present). (2) Poorly developed (small, peglike). (3) Absent. Tree: 1-2-3.

APPENDIX III—CONTINUOUS CHARACTERS

Continuous characters (abbreviations in capitals).

1. Skull length (SKULL)—Greatest length not including incisors.

2. Condylobasal length (CONBAS)—Occipital condyle to anterior border of incisive alveolus.

3. Rostral length (ROST)—Anterior border of braincase (in orbital recess) to anterior border of incisive alveolus.

4. Lacrimal width (LACR)—Greatest breadth across lacrimal protuberances.

5. Postorbital width (POST)—Least breadth of postorbital constriction.

6. Zygomatic width (ZYGO)—Greatest breadth across zygoma (all Stenodermatines have complete zygomatic arches).

7. Mastoid width (MAST)—Greatest breadth across mastoid processes.

8. Braincase width (BRAINB)—Greatest breadth of braincase, not including mastoid or paraoccipital processes.

9. Braincase height (BRAINH)—With calipers supporting antero-ventral border of foramen magnum and the hard palate, greatest cranial height excluding sagittal crest.

10. Braincase length (BRAINL)—Anterior border of braincase (in orbital recess) to posterior-most extension of occiput, excluding occipital crest.

11. Palatal length (PALAT)—Posterior palatal notch to anterior border of incisive alveolus.

12. Maxillary toothrow length (MAXIL)—Posterior border of molar alveolus to anterior border of canine alveolus.

13. Molariform toothrow length (MOLAR)—Posterior border of molar alveolus to anterior border of premolar alveolus.

14. Palate width at canines (WCAN)—Least width across palate between canines.

15. Palate width at second molar (WMOL)—Least width across palate between M2s.

16. Mandibular fossa length (MFOSL)—Greatest antero-posterior length of fossa.

17. Mandibular fossa width (MFOSW)—Greatest latero-medial length of fossa.

18. Upper second molar length (UM2L)—Greatest antero-posterior length at crown.

19. Upper second molar width (UM2W)—Greatest latero-medial width at crown.

20. Upper canine height (UCAN)—Length, on lateral aspect, from tip to dorsal edge of cingulum (not taken on noticeably worn or broken teeth).

21. Dentary length (DENTL)—Midpoint of mandibular condyle to anterior-most point of dentary.

22. Condylocanine length (CONCAN)—Midpoint of mandibular condyle to anterior border of canine alveolus.

23. Condyle to first molar length (CONM1)—Midpoint of mandibular condyle to anterior border of lower first molar alveolus.

24. Mandibular toothrow length (TOOTH)—Posterior-most border of molar alveolus to anterior border of canine alveolus.

25. Mandibular foramen to dentary anterior (MFAD)—Anterior border of mandibular foramen to anterior-most point of mandibular symphysis.

26. Condylomolar length (CONMOL)—Midpoint of mandibular condyle to posterior-most molar alveolus.

27. Temporal moment arm length (TEMMOM)—Midpoint of mandibular condyle to tip of coronoid process.

28. Masseter moment arm length (MASMOM)—Midpoint of mandibular condyle to tip of angular process.

29. Coronoid height (CORONH)—Perpendicular height from ventral mandibular border to tip of coronoid process.

30. Angular process length (ANGPRO)—Tip of angular process to nearest border of mandibular foramen.

31. Dentary thickness (DENTTH)—Vertical height of dentary at anterior base of second molar.

32. Lower canine length (LCANH)—Length, on lateral aspect, from tip to ventral edge of cingulum (not taken on noticeably worn or broken teeth).

33. Condyle length (CONDL)—Medio-lateral length of mandibular condyle.

Appendix IV—Linnaean Classification

Annotated Linnaean classification of the species of the subfamily Stenodermatinae based on Fig. 17. Classification conventions (including sequencing) follow Wiley (1981). This classification disregards the "*incertae sedis*" status of a number of taxa in Fig. 17, and is listed here for heuristic and comparative purposes only. For proposed generic classification of the Stenodermatinae, see end of text.

Subfamily Stenodermatinae (all taxa *sedis mutabilis*)
  Tribe Corvirini
    Genus *Corvira*
      Corvira bidens
      Corvira nana
  Tribe Sturnirini
    Genus *Sturnira* (all taxa *sedis mutabilis*)
      Unnamed subgenus
        Sturnira luisi
      Unnamed subgenus
        Sturnira erythromos
      Unnamed subgenus
        Sturnira ludovici
      Unnamed subgenus
        Sturnira bogotensis
      Unnamed subgenus
        Sturnira thomasi
      Unnamed subgenus
        Sturnira magna
      Unnamed subgenus
        Sturnira tildae
      Unnamed subgenus
        Sturnira mordax
      Subgenus *Sturnira*
        Sturnira lilium
        Sturnira aratathomasi
  Tribe Stenodermatini (all taxa *sedis mutabilis*)
    Subtribe Enchistheneini
      Genus *Enchisthenes*
        Enchisthenes hartii
    Unnamed subtribe
      Unnamed genus
        ____ *concolor*
    Subtribe Dermanurini
      Genus *Dermanura* (all taxa *sedis mutabilis*)
        Unnamed subgenus
          Dermanura watsoni
        Unnamed subgenus
          Dermanura glauca
        Subgenus *Dermanura* (all taxa *sedis mutabilis*)
          Unnamed infragenus
            Dermanura tolteca
          Infragenus *Dermanura*
            Dermanura cinerea
          Unnamed infragenus (all species *sedis* mutabilis)
            Dermanura phaeotis
            Dermanura azteca
            Dermanura anderseni

Subtribe Stenodermatini (all taxa *sedis mutabilis*)
  Genus *Pygoderma*
    Pygoderma bilabiatum
  Genus *Centurio*
    Centurio senex
  Genus *Stenoderma*
    Stenoderma rufum
  Genus *Ariteus* (all taxa *sedis mutabilis*
    Unnamed subgenus
      Ariteus vetus
    Subgenus *Phyllops*
      Ariteus falcatus
    Unnamed subgenus
      Ariteus haitiensis
    Subgenus *Ariteus*
      Ariteus nichollsi
      Ariteus flavescens
  Genus *Ametrida*
    Ametrida centurio
    Ametrida toxophyllum
Tribe Artibeini (all taxa *sedis mutabilis*)
  Unnamed subtribe
    Unnamed genus
    ———— *melissa*
  Subtribe Vampyressatini
    Genus *Vampyressa* (all species *sedis mutabilis*)
      Vampyressa pusilla
      Vampyressa brocki
      Vampyressa bidens
  Subtribe Mesophyllatini
    Genus *Mesophylla*
      Mesophylla nymphaea
      Mesophylla macconnelli
  Subtribe Chirodermini (all genera *sedis mutabilis*)
    Genus *Chiroderma* (all species *sedis mutabilis*)
      Chiroderma doriae
      Chiroderma salvini
      Chiroderma trinitatum
      Chiroderma improvisum
      Chiroderma villosum
    Genus *Vampyrodes*
      Vampyrodes caraccioli
    Genus *Vampyrops* (all taxa *sedis mutabilis*)
      Unnamed subgenus
        Vampyrops infuscus
      Unnamed subgenus
        Vampyrops recifinus
      Unnamed subgenus
        Vampyrops brachycephalus
      Subgenus *Vampyrops* (all species *sedis mutabilis*)
        Vampyrops vittatus
        Vampyrops aurarius
        Vampyrops lineatus
        Vampyrops umbratus

    Unnamed subgenus (all species *sedis mutabilis*)
        Vampyrops nigellus
        Vampyrops helleri
        Vampyrops dorsalis
Subtribe *Artibeini* (all genera *sedis mutabilis*)
    Genus *Ectophylla*
        Ectophylla alba
    Genus *Uroderma*
        Uroderma magnirostrum
        Uroderma bilobatum
    Genus *Artibeus* (all taxa *sedis mutabilis*)
        Unnamed subgenus
            Artibeus fuliginosus
        Unnamed subgenus
            Artibeus inopinatus
        Subgenus *Artibeus* (all taxa *sedis mutabilis*)
            Unnamed infragenus
                Artibeus hirsutus
            Unnamed infragenus
                Artibeus planirostris
            Unnamed infragenus
                Artibeus fraterculus
            Infragenus *Artibeus* (all species *sedis mutabilis*)
                Artibeus jamaicensis
                Artibeus intermedius
                Artibeus fimbriatus

APPENDIX V—NEW BINOMIAL AND TRINOMIAL COMBINATIONS

New binomial and trinomial combinations resulting from taxonomic changes proposed in text. Species and subspecies listed are those generally recognized at present. Inclusion is not intended to imply validity of the several taxa; rather, this list is presented simply for the purpose of providing the appropriate name combinations to facilitate subsequent work on these bats. The list is based on those in Jones and Carter (1976), Koopman (1978), and Anderson *et al.* (1982).

Dermanura anderseni
Dermanura azteca azteca
Dermanura azteca major
Dermanura azteca minor
Dermanura cinerea bogotensis
Dermanura cinerea cinerea
Dermanura cinerea pumilia
Dermanura cinerea solimoesi
Dermanura concolor
Dermanura glauca

Dermanura hartii
Dermanura phaeotis nana.
Dermanura phaeotis palatina
Dermanura phaeotis phaeotis
Dermanura tolteca hespera
Dermanura tolteca rava
Dermanura tolteca tolteca
Dermanura watsoni
Vampyressa macconnelli flavescens
Vampyressa macconnelli macconnelli

APPENDIX VI—RECOMMENDED GENERIC CLASSIFICATION

Recommended generic classification of species of the subfamily Stenodermatinae (taxa are listed alphabetically). This generic classification also is indicated in Fig. 17 by the names to the right of the cladogram. Name combinations are provided here to facilitate subsequent taxonomic work.

Ametrida centurio.

Ardops nichollsi.

Ariteus flavescens.

Artibeus fimbriatus, Artibeus fraterculus, Artibeus fuliginosus, Artibeus hirsutus, Artibeus inopinatus, Artibeus intermedius, Artibeus jamaicensis, Artibeus lituratus, Artibeus planirostris.

Centurio senex.

Chiroderma doriae, Chiroderma improvisum, Chiroderma salvini, Chiroderma trinitatum, Chiroderma villosum.

Dermanura anderseni, Dermanura azteca, Dermanura cinerea, Dermanura concolor, Dermanura glauca, Dermanura hartii, Dermanura phaeotis, Dermanura tolteca, Dermanura watsoni.

Ectophylla alba.

Phyllops falcatus, Phyllops haitiensis, Phyllops vetus.

Pygoderma bilabiatum.

Sphaeronycteris toxophyllum.

Stenoderma rufum.

Sturnira aratathomasi, Sturnira bidens, Sturnira bogotensis, Sturnira erythromos, Sturnira lilium, Sturnira ludovici, Sturnira luisi, Sturnira magna, Sturnira mordax, Sturnira nana, Sturnira thomasi, Sturnira tildae.

Uroderma bilobatum, Uroderma magnirostrum.

Vampyressa bidens, Vampyressa brocki, Vampyressa macconnelli, Vampyressa melissa, Vampyressa nymphaea, Vampyressa pusilla.

Vampyrodes caraccioli.

Vampyrops aurarius, Vampyrops brachycephalus, Vampyrops dorsalis, Vampyrops helleri, Vampyrops infuscus, Vampyrops lineatus, Vampyrops nigellus, Vampyrops recifinus, Vampyrops umbratus, Vampyrops vittatus.

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