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Patricia W. Freeman

University of Nebraska-Lincoln, pfreeman1@unl.edu

Cliff A. Lemen

University of Nebraska-Lincoln, clemen2@unl.edu

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Morphometrics of the Family Emballonuridae

PATRICIA W. FREEMAN¹ AND CLIFF A. LEMEN²

ABSTRACT

Morphometric analysis revealed three distinctive groups among the genera of emballonurids. *Taphozous-Saccolaimus* is a group distinctive in size and shape, particularly cranially. Diclidurids are distinctive in appendicular characters only, especially those in the wing. The third group includes

all other emballonurids. Phylogenetic studies also separated *Taphozous-Saccolaimus* as distinctive but included diclidurids among other New World species. Compared with molossids, emballonurids are morphometrically quite homogeneous.

INTRODUCTION

Miller (1907) thoroughly described most of the extant families of bats and illustrated several of the genera with exquisite line drawings. His work remains valuable for its clarity and for establishing a description of and qualitative differences among the morphologies of families and genera of Chiroptera.

We have been interested for some years in the quantitative morphological differences among genera within families and among families (Freeman, 1981; Lemen and Freeman, 1981, 1984). In this morphometric treatment of the family Emballonuridae, the sheath-tailed bats, we examine the quantitative differences among the species and genera within the family, compare the morphometric groupings with groupings from two phylogenetic studies, and describe the morphometric variation between the families Emballonuridae and Molossidae, the free-tailed bats.

Early generic treatments of emballonurids include Troughton's (1925) revision of the Australasian genera *Taphozous* and *Saccolaimus*, Sanborn's (1937) study of American species, and Tate and Archbold's (1939) examination of the genus *Emballonura*. More

recently Barghoorn (1977) examined cranial morphology of a fossil genus, *Vespertiliavus*, and all Recent genera for their possible phylogenetic relationships, and Robbins and Sarich (1988) produced a phylogenetic study of the family using protein electrophoresis and immunology.

METHODS

Thirty-eight meristic characters (27 cranial and 11 appendicular) were studied on 37 species of emballonurid bats. These are standard measurements and, for the most part, a subset of those in Freeman (1981). There are some changes, however, because of structural differences between molossids and emballonurids. Because there is no comparable third phalanx and cartilaginous tip of digit III in emballonurids, the quantity measured for both families is the length from the second phalanx to the tip of that digit. Postorbital and interorbital breadths in some emballonurids had to be measured inferior to any supraorbital bone overhanging those breadths in order to measure the least constriction. This was particularly true with the diclidu-

¹ Curator of Zoology and Associate Professor, Division of Zoology, University of Nebraska State Museum, Lincoln, Nebraska 68588-0514.

² Research Associate, Division of Zoology, University of Nebraska State Museum, Lincoln, Nebraska 68588-0514.

rids. The quantity SIZE equals the sum of the natural logs of greatest skull length (which differs slightly from condylocanine length; used in Freeman, 1984, 1988), zygomatic breadth, and height of braincase. SIZE correlates well with weight of the animal (Freeman, 1988).

Both bivariate and multivariate analyses were used to assess the data, including principal components analysis with and without a "shearing" function. The shear method described by Bookstein et al. (1985) is particularly useful in our analysis because it generates a size factor based on within-genus comparisons and not the first principal component of the entire data set, as used in "size-out." The distinction between the sizeout approach and shearing is particularly important in this data set because the bats in the *Taphozous-Saccolaimus* group are much larger than the majority of Emballonuridae. The sizeout approach will tend to define shape differences between *Taphozous-Saccolaimus* and other bats as size-related differences. This would indicate that bats of the *Taphozous-Saccolaimus* group are not different in shape. Shearing does not use the size differences among groups in its definition of size, and in this case *Taphozous-Saccolaimus* is found to have considerable shape differences compared to other Emballonuridae (fig. 1). Finally, simple regression analyses were performed on each character versus the SIZE quantity.

We examined the following species for this study: a. *Balantiopteryx io*, b. *Balantiopteryx plicata*, c. *Centronycteris maximiliani*, d. *Coleura afra*, e. *Cormura brevirostris*, f. *Diclidurus albus*, g. *Diclidurus ingens*, h. *Diclidurus isabella*, i. *Diclidurus scutatus*, j. *Emballonura alecto*, k. *Emballonura atrata*, l. *Emballonura beccarii*, m. *Emballonura monticola*, n. *Emballonura nigrescens*, o. *Emballonura raffrayana*, p. *Emballonura semicaudata*, q. *Emballonura sulcata*, r. *Peropteryx leucoptera*, s. *Peropteryx kappleri*, t. *Peropteryx macrotis*, u. *Peropteryx trinitatis*, v. *Rhynchonycteris naso*, w. *Saccopteryx bilineata*, x. *Saccopteryx canescens*, y. *Saccopteryx leptura*, A. *Taphozous australis*, B. *Taphozous hamiltoni*, C. *Taphozous hildegardeae*, D. *Taphozous longimanus*, E. *Taphozous mauritianus*, F. *Taphozous melan-*

opogon, G. *Taphozous nudiventris*, H. *Taphozous perforatus*, I. *Taphozous theobaldi*, J. *Saccolaimus flaviventris*, K. *Saccolaimus peli*, and L. *Saccolaimus saccolaimus*.

The following measurements were taken (descriptions and illustrations are in Freeman, 1981): **Cranial:** greatest skull length, palatal length, maxillary tooththrow, upper molariform row, lacrimal width, interorbital width, postorbital width (POSTORB), zygomatic breadth, breadth at mastoids, breadth of braincase, height of braincase, height of upper canine, length M3 (M3LENGTH), width M3, width at upper canines, width at upper molars, dentary length, dentary-condylocanine length, condyle to M3 length, lower tooththrow, moment arm of temporal, moment arm of masseter, height of coronoid, dentary thickness, height of condyle above tooththrow, height of lower canine, and length of condyle; **Appendicular:** tibia, forearm, third metacarpal, third metacarpal first phalanx (PHAL1M3), third metacarpal second phalanx to tip, fourth metacarpal, fourth metacarpal first phalanx, fourth metacarpal second phalanx, fifth metacarpal, fifth metacarpal first phalanx (PHAL1M5), and fifth metacarpal second phalanx.

Abbreviations used in the text include PC1, principal component one; PC2, principal component two; PC3, principal component three; H2, sheared component 2; and H3, sheared component 3.

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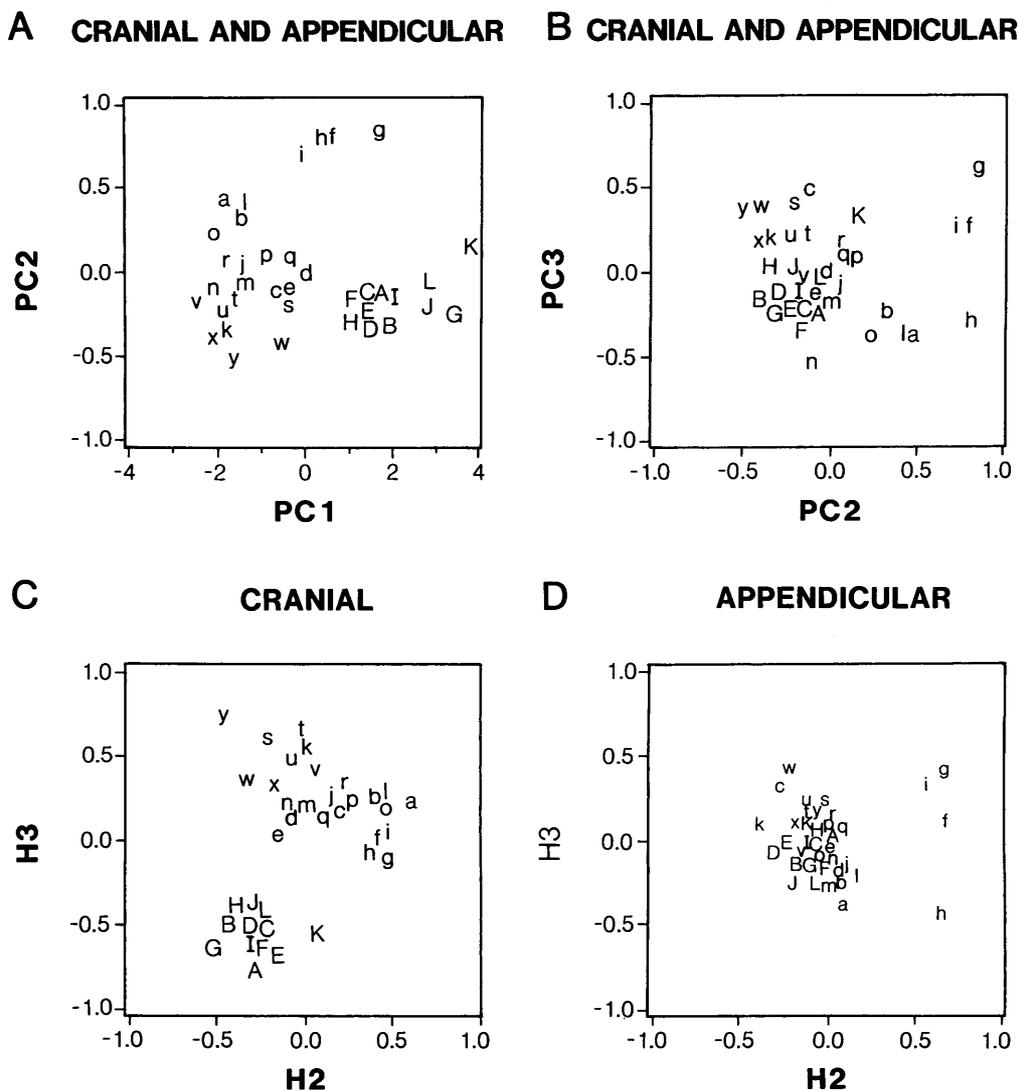


Fig. 1. The first three principal components of an analysis of the emballonurid data set with cranial and appendicular measurements (A and B). Separate analyses using sheared components were run on cranial measurements alone and on appendicular measurements alone (H2 and H3 in C and D). Species are indicated by letters, which are listed in Methods.

her mentors at the American Museum; for patiently wading through new methodology and giving excellent help as a member of her dissertation committee; for leaving characteristic, cryptic, and dependable notes on specimen tags of bats and other mammals in most of the major collections around the country, particularly at Field Museum; for being a colleague of encyclopedic knowledge

who unselfishly shares that knowledge; and for being a continual source of stimulation and friendship.

RESULTS

Morphological trends in the data, revealed by principal components analysis, revolve around general size, several wing measure-

ments, width-of-face measurements, and a tooth measurement. Eighty-seven percent of the variation in the family can be explained by the first component, which is related to a change in size. Size typically explains most of the variation in morphological studies on quantitative characters and is typically the first principal component. Component two explains 3.5 percent of the variation and is influenced primarily by the length of the first phalanx of digit III (shortest at positive end), postorbital width (widest at positive end), length of first phalanx of digit V (longest on positive side), and interorbital width (widest at positive end). Component three explains 1.9 percent of the total variation and is influenced by length of second phalanx of digits IV and V (longest at positive end) and length of M3 (longest at positive end).

The placement of species on the first two components, shows species of *Taphozous*–*Saccolaimus* well separated from all other genera except *Diclidurus* because of their larger size (fig. 1A). *Diclidurus* is distinct from all other genera because of its wing configuration (unusually short first phalanx of digit III and long first phalanx of digit V), wide postorbital and interorbital breadths, and somewhat longer M3s. On PC3 *Diclidurus* is less cohesive because *Diclidurus isabella* has a short second phalanx of digit IV, and of digit V to a lesser degree, while the other three species in the genus have long ones (fig. 1B). All other emballonurid genera—*Emballonura*, *Coleura*, *Rhynchonycteris*, *Saccopteryx*, *Centronycteris*, *Peropteryx*, *Cormura*, and *Balantiopteryx*—are in one large indistinguishable group.

Using the shearing method to remove the effect of size gives somewhat different results. The main difference is that the *Taphozous*–*Saccolaimus* group forms a distinctive morphological entity based on cranial characters but not appendicular characters (fig. 1C). *Diclidurus* is highly distinctive based on features of the wing but much less so for cranial features (fig. 1D).

In examining the makeup of the multivariate analyses, we regressed each of the 38 characters against a composite quantity to represent size (see Methods). A sample of the characters that are heavily loaded on com-

ponents two and three can be seen as extremes from the regression line to a greater or lesser degree in the bivariate plots (fig. 2). The simple plots clarify and verify the multivariate picture so that it is easy to see what characters influence the principal components.

DISCUSSION

Morphological relationships within the emballonurids parallel the phylogenetic hypotheses of Robbins and Sarich (1988) in some cases, and run contrary to them in others. The most basic split discovered by Robbins and Sarich was *Taphozous* and *Saccolaimus* versus the rest of the emballonurids. Our data show that *Taphozous* and *Saccolaimus* are a distinctive group in size and cranial shape. This is a case where time has increased morphological distinction between groups. The next most distinctive group is the genus *Diclidurus*. Its skull morphology is similar to that of *Balantiopteryx*, and both occupy an extreme of H2 (fig. 1C). However, *Diclidurus* is distinct in wing morphology. The recognition of this genus as a separate subfamily is based largely on postcranial morphology, particularly the shape of the clavicle and the construction of the tibia, but also, because the cranium has a wide supra-orbital bone that overhangs the interorbital/postorbital region (Miller, 1907; Koopman, 1984b). Electrophoretic data indicate that *Diclidurus* belongs within the large group of New World genera. If Robbins and Sarich (1988) are correct, this is a case where morphological distinctiveness does not indicate phylogenetic distance.

Another finding of Robbins and Sarich (1988) was recognition of the *Emballonura*–*Coleura* group of Old World bats versus the New World genera. This differs from Barghoorn's (1977) placement of *Coleura* with the New World forms. However, his placement of *Coleura* was based on the loss of an incisor. Tooth reduction may occur in unrelated taxa, reducing the reliability of this character. Overall, we prefer the grouping of Robbins and Sarich (1988). Actually, the electrophoretic data indicate that *Emballonura* is paraphyletic, with *Coleura* included within. Our

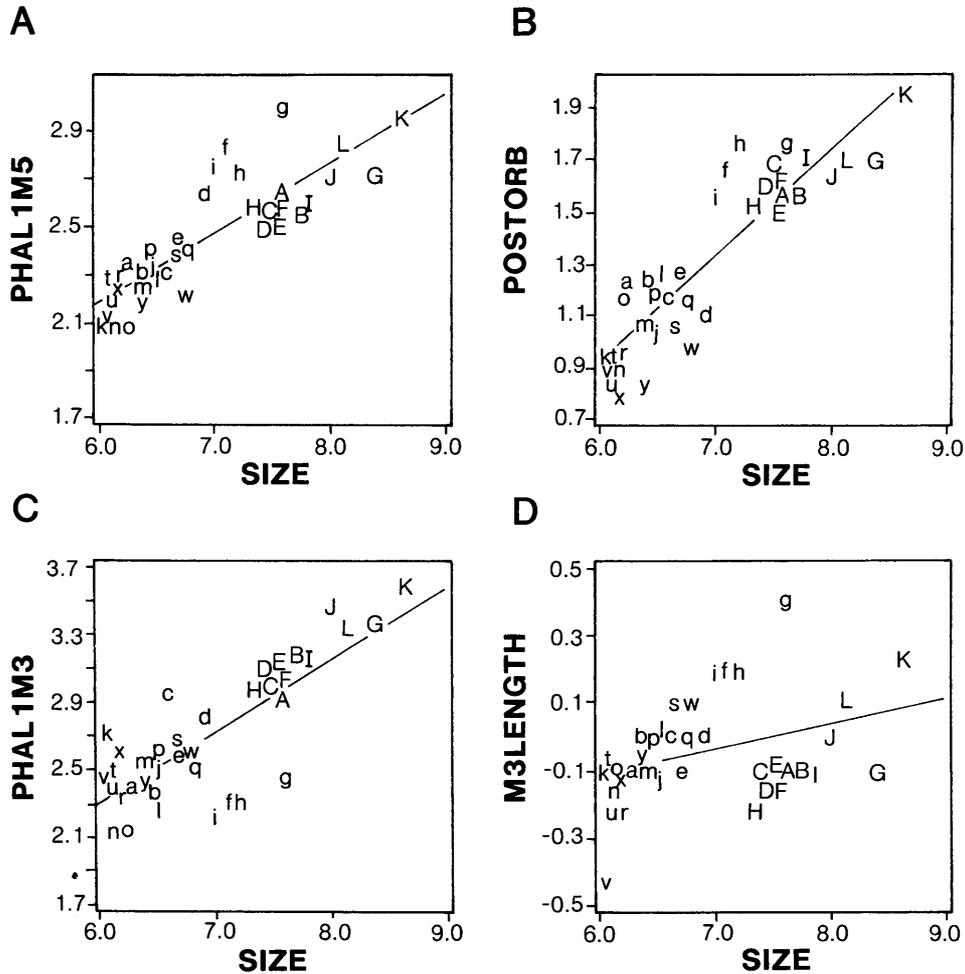


Fig. 2. Bivariate plots for variables (natural logs) first phalanx of digit III (A), postorbital breadth (B), first phalanx of digit V (C), and length of M3 (D) against SIZE (see Methods for explanation of SIZE). Lines plotted in each scattergram are linear regression lines; the relevant statistics for the lines are (A) $a = 0.43$, $b = 0.29$, $P < 0.0001$; (B) $a = -1.52$, $b = 0.40$, $P < 0.0001$; (C) $a = -0.36$, $b = 0.44$, $P < 0.0001$; and (D) $a = -0.56$, $b = 0.07$, $P < 0.03$. Species are indicated by letters, which are listed in Methods.

morphological data indicate a close similarity between *Emballonura* and *Coleura*. There is, however, no great distinction between these two genera and the New World forms.

Miller (1907: 85) stated under principal subdivisions in the family that "the genera of Emballonuridae as a whole form a very homogeneous group, but the South American *Diclidurus* is so different from the others that it must be regarded as forming a distinct sub-family." Simpson (1945: 55) lumped many of the New World genera (*Cormura*, *Perop-*

teryx, *Peronymus*, *Centronycteris*, and *Balantiopteryx*) under the name *Saccopteryx* and stated in a footnote that "As in many other cases, but to an exaggerated degree, I here unite a number of units almost universally called genera by modern mammalogists. They are however, manifestly and closely allied, cover less morphologic range than do many genera, and include so few species that generic separation has no practical value. This seems an obvious case, one of many, in which subgeneric rank has everything to be said for

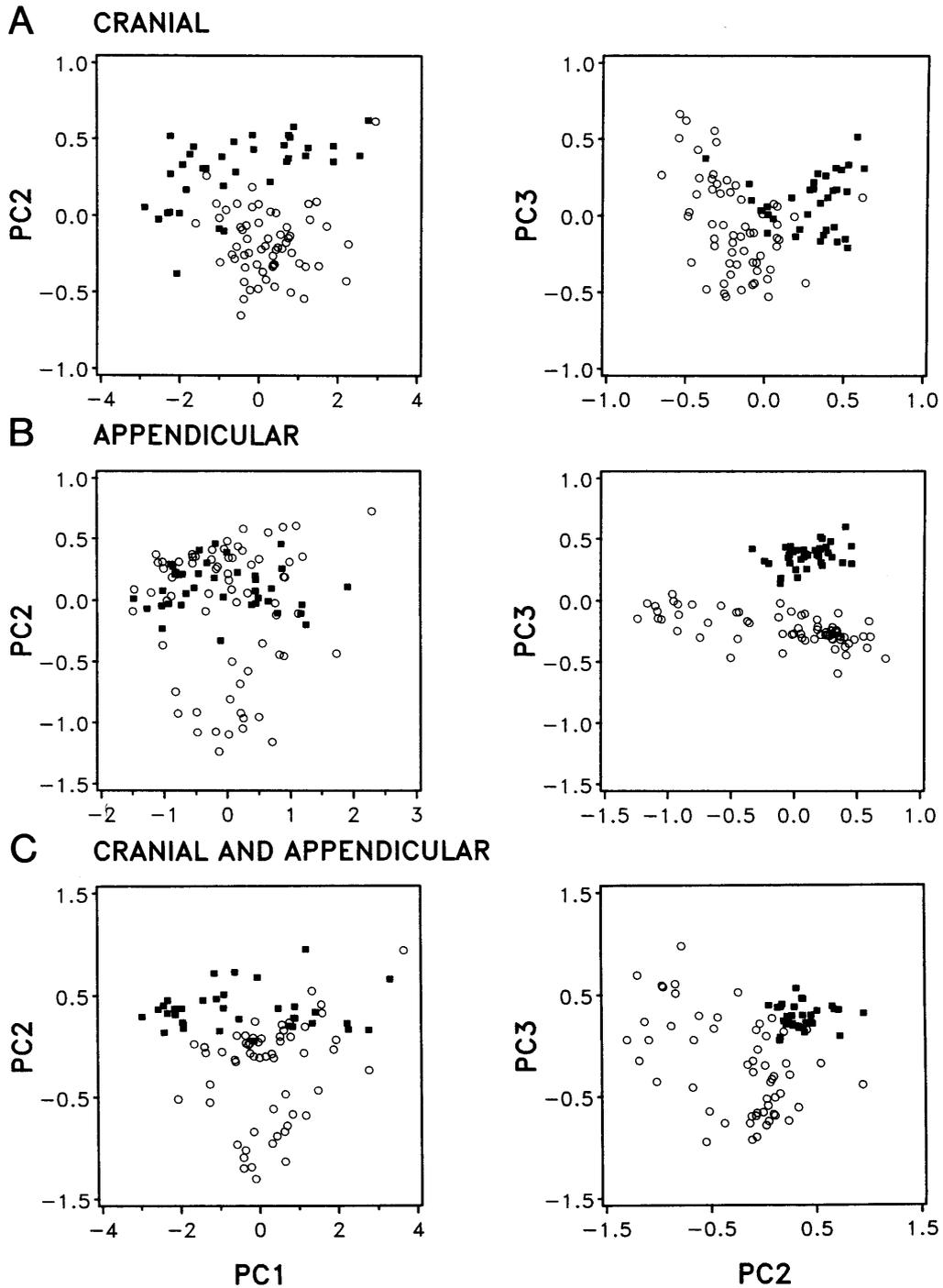


Fig. 3. Principal components analyses of the two-family data set, run on cranial measurements alone (A), appendicular measurements alone (B), and cranial and appendicular measurements together (C). Emballonurids are solid squares and molossids are open circles. Emballonurids are as variable as molossids in size (PC1, first column), but are much less variable in shape (PC2 and PC3).

it, both as better representing the real situation and as practically more convenient to everyone but the *Saccopteryx* specialist.”

We investigated these qualitative claims of homogeneity by using the same 38 characters measured previously by Freeman (1981) for the family Molossidae and comparing entire families with one another. Both families are insectivorous, both occur worldwide, and for both we had over 75 percent of the total species in the family represented in our analysis. However, emballonurids are thought to be primitive and are placed in Koopman's infraorder Yinochiroptera, whereas the molossids are derived and are in the Yangochiroptera (Koopman, 1984a).

One way to compare size and shape diversity in two families is to compare the amount of variation that is and is not explained by the first principal component. In emballonurids, the total variation of characters is 3.51, of which 3.09 (88%) is explained by the first principal component. This leaves only 0.418 (12%) for the “shape” components. In molossids, the total variation is 1.95, with the first component explaining 1.182 (61%), and the remaining 0.769 (39%) on the “shape” axes. The conclusion that can be drawn is that the emballonurids are not as variable in shape as are the molossids, and this lack of variation can be seen in a variety of graphical representations.

We have run the two-family data set for variation in cranial measurements alone, appendicular measurements alone, and cranial and appendicular measurements together (fig. 3). The size component (PC1) in the cranial run shows that although there are more smaller-sized species of emballonurids than molossids, variation in size across the families is similar. Sizes among the two families from the appendicular measurement run show a similar degree of variation.

However, it is in the shape components, here represented by PC2 and PC3, that emballonurids show much less variation (fig. 3). Although molossids are more variable than emballonurids in shape in each of the three runs, the most dramatic difference in variation can be seen in the graph of the two shape components in the run with all 38 characters (fig. 3C; PC2 versus PC3). Based on these

data, we conclude that emballonurids when compared to molossids morphometrically *are* a homogeneous group. This homogeneity may help explain why the emballonurids have been difficult to classify above the species level.

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