INTRASPECIFIC VARIATION AND PHENETIC AFFINITIES OF *DERMANURA HARTII*, WITH REAPPLICATION OF THE SPECIFIC NAME *ENCHISTHENES HARTII*

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Abstract.—We examined most available specimens of the phyllostomid bat species *Dermanura hartii* (Chiroptera: Phyllostomidae) to assess its intraspecific variation and evaluate the phenetic affinities of the species. Twenty-two mensural characters were utilized and univariate and multivariate analyses were used for testing variation among populations and between sexes. Little variation was detected between sexes or among populations. A few geographically variable characters appear generally to conform to Bergmann's rule. Our findings support the monotypic status for this bat species. Cluster and ordination analyses of *D. hartii* with other *Dermanura* species and *Koopmania concolor* show *D. hartii* to be the most distinct phenetically of this assemblage. These data and other recently published evidence are consistent with inclusion of *D. hartii* in the monotypic genus *Enchisthenes*. Reapplication of the specific name *Enchisthenes hartii* is proposed, and the synonymy is provided.

Key words: *Enchisthenes, Dermanura,* intraspecific variation, geographic variation, taxonomy

The New World frugivorous bat *Dermanura hartii* is a widespread species, occurring from north-central México (and an extralimital record from Arizona) through Central and South America, and south to Bolivia (Fig. 1). Although it more commonly inhabits densely forested highlands, it has been found in localities near sea level. It is considered uncommon or rare in most of its range, although it has been found abundantly in a few localities in South America. It is unclear whether the distribution is continuous throughout its range, or whether the reported populations are in fact disjunct, as is suggested by the absence of specimens from Nicaragua, northern Colombia, and north-central Perú.

An intriguing aspect of this species is the possibility that very little variability exists among populations, notwithstanding the large size of its distribution. Baker and López (1968) found little difference between specimens from Trinidad and northeastern México, and suggested that little geographic variation occurs in the species. Should this prove to be the case after all specimens have been examined, this may be the most uniform small mammal species known, with such an extensive distribution. However, Goodwin (1940) mentioned that some individuals out of a large series of specimens collected from owl pellets in southern Ecuador were smaller and with slight cranial differences than a specimen from Honduras. Nonetheless, neither Goodwin nor any other authors have identified intraspecific variation deemed worthy of taxonomic distinction, and no subspecies have been described.

Since the species was described as *Artibeus hartii*, based on one specimen from Trinidad (Thomas, 1892), the generic assignment of the species has been unstable. Andersen (1906) erected the monotypic genus *Enchisthenes* for this taxon; other authors have regarded the species either as comprising the monotypic *Enchisthenes* (Hall and Kelson, 1959; Jones and Carter, 1976; Hall, 1981), or as included in the species-rich *Artibeus* (Goodwin, 1969; Honacki et al., 1982; Koopman, 1978, 1993). Owen (1987), in following Koopman's (1978) assignment of *hartii* to the genus *Artibeus*, allocated the species to *Dermanura*, which he considered to be the appropiate genus for the small *Artibeus*-type bats. Most recently, Van Den Bussche et al. (1993) stated that *Enchisthenes* could be best characterized as a genus, based upon their analysis of nuclear satellite DNA and mitochondrial cytochrome b sequence data. It is not clear whether they intended to resurrect use of the name *Enchisthenes hartii*; however, their analyses do not provide synapomorphic support for recognition of *Enchisthenes*, and they included no formal taxonomic proposal for recognition of generic status for the taxon. We therefore follow the us-

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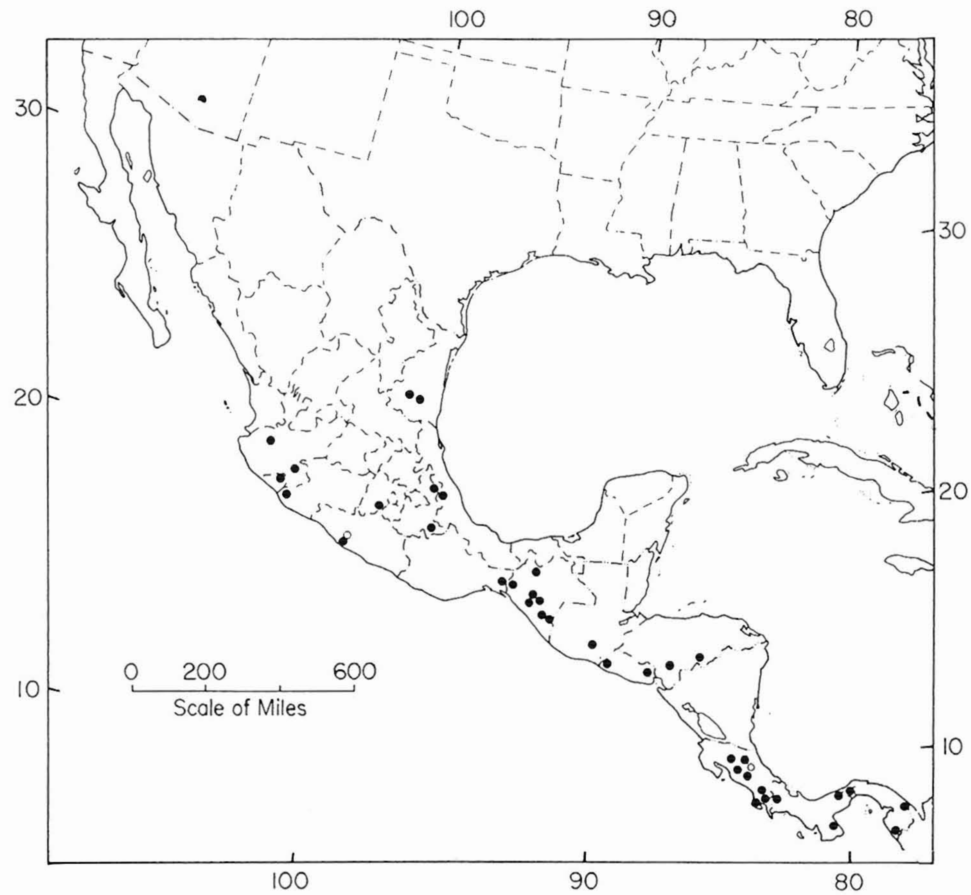


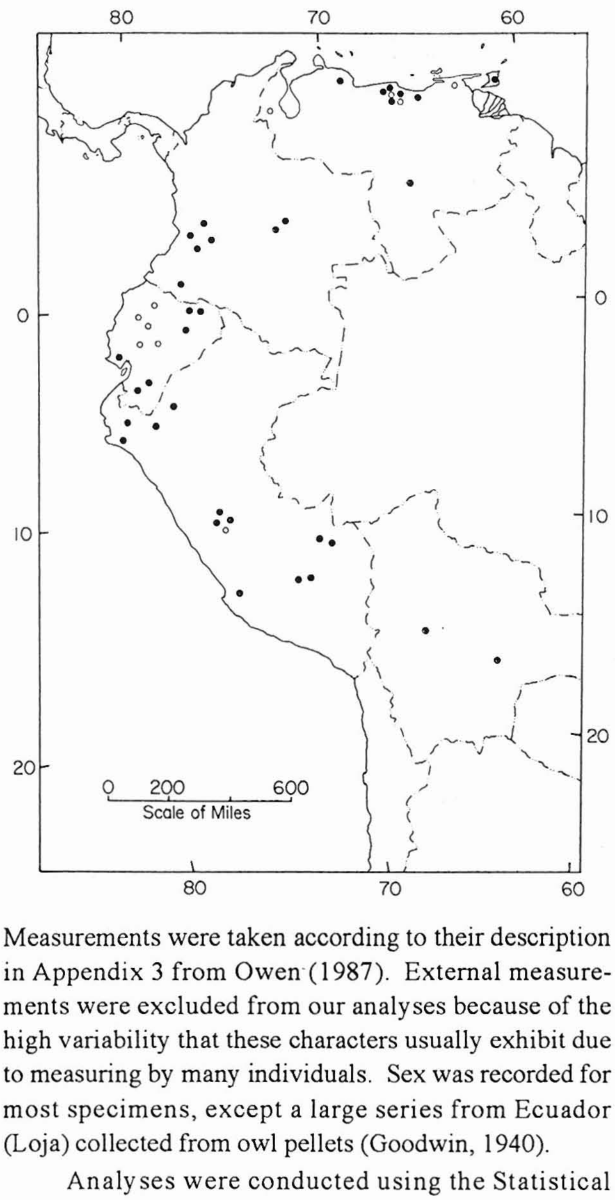
Fig. 1. Maps for North and Central America (A), and South America (B, opposite page), showing the localities of provenance of the specimens examined (filled circles) of *Dermanura hartii*. Open circles indicate localities from where specimens are known, but which were not examined.

age of the last revision of this taxon (Owen, 1987), and refer to the species as *Dermanura hartii*.

We have undertaken the study of this bat species for two reasons: first, these bats represent a widely distributed species for which no thorough study of intraspecific variation (either geographic or sexual) has been performed; and second, the phenetic affinities of the species need to be evaluated in relation to those species with which it most closely shares phylogenetic affinity, species of the genera *Koopmania* and *Dermanura* (Owen, 1987, 1991).

Material and Methods

We examined 412 museum specimens representing the entire known range of *Dermanura hartii*, and including most of the available specimens in North American collections (Canada, U.S.A., and México—see Appendix 1). Only 41 specimens that we are aware of from the literature were not examined (Appendix 2). Twenty-two skull characters were measured with a Fowler Ultra-Cal II caliper (to 0.1mm) for each adult specimen (i.e., specimens with all cranial sutures completely fused). The characters are: skull length (SKULL), postorbital width (POST), lacrimal width (LACR), zygomatic width (ZYGO), mastoid width (MAST), braincase width (BRAINB), braincase height (BRAINH), braincase length (BRAINL), palatal length (PALAT), maxillary toothrow length (MAXIL), palatal width at second molar (WMOL), upper first molar length (UM1L), upper first molar width (UM1W), dentary length (DENTL), condylocanine length (CONCAN), mandibular toothrow length (TOOTH), condylomolar length (CONMOL), temporal moment arm length (TEMMOM), masseter moment arm length (MASMOM), coronoid height (CORONH), dentary thickness (DENTH), and condyle length (CONDL). A binocular microscope was used to enhance measurement precision for the following characters: MAXIL, UM1L, UM1W, DENTL, CONCAN, TOOTH, CONMOL, TEMMOM, and MASMOM.



Measurements were taken according to their description in Appendix 3 from Owen (1987). External measurements were excluded from our analyses because of the high variability that these characters usually exhibit due to measuring by many individuals. Sex was recorded for most specimens, except a large series from Ecuador (Loja) collected from owl pellets (Goodwin, 1940).

Analyses were conducted using the Statistical Analysis System (SAS Institute, Inc., 1985), and the Numerical Taxonomy Programs (NT-SYS) (Rohlf, 1993). The measurements were transformed to their natural logarithms, to linearize the allometric component of the data, and thereby to legitimize linear operations on the data (Owen, 1988). Because sexual dimorphism is known for a number of stenodermatine species (Swanepoel and Genoways, 1979), the mean value of each character was calculated separately for each sex.

Geographic and Secondary Sexual Variation

Preliminary analyses of individual variation showed not differences in grouping the populations by either political boundaries or geographical regions. Because we were able to determine boundaries rather than physiographic provenance, analysis of intraspecific variation within *D. hartii* was performed using a UPGMA clustering of individuals and of populations by country, based on the matrix of average taxonomic distances computed from the log-transformed data matrix. This allowed us to ascertain the presence of any clear morphometric group, as well as its geographic identity. Also, the data were subjected to a principal components analysis (PCA) of the character variance-covariance matrix of the log-transformed data matrix by country. This procedure allows ordination of samples on a minimum number of axes accounting for a maximum amount of the data variance, in order to determine visually the groups that may occur within the overall sample. We generated a three-dimensional diagram from the first three principal components. Onto this we superimposed the minimum spanning tree generated from the average taxonomic distance matrix.

To examine the possibility of a morphometric pattern corresponding to the geographic distribution of the species, we conducted a two-way (country versus sex) multiple analysis of variance (MANOVA) of the five populations with largest samples, covering most of the distribution of this species. Each of the five samples represents a population collected from one locality, or very nearby localities, as follows: México (Chiapas), Costa Rica, Colombia (Meta), Venezuela (Distrito Federal), and Perú (Huánuco).

In addition, we conducted a univariate two-way ANOVA for each character separately, to examine the effects of sex and locality for each morphometric character and the interaction between those two primary effects. A Duncan's multiple range test was used to examine morphometric variation among localities. In order to view graphically the results from the ANOVA analyses, we plotted the mean values of those characters that have significant differences in the univariate two-way tests. Finally, in order to ascertain geographic patterns of secondary sexual variation, a one-way ANOVA was performed by sex for each one of the five largest populations.

Phenetic Affinities

We examined the phenetic affinities of this species to its congeners and to *Koopmania concolor*. Species and specimens examined for this are listed in Appendix 3; when possible, 10 males and 10 females were studied. For *D. hartii*, each of the five largest samples was in-

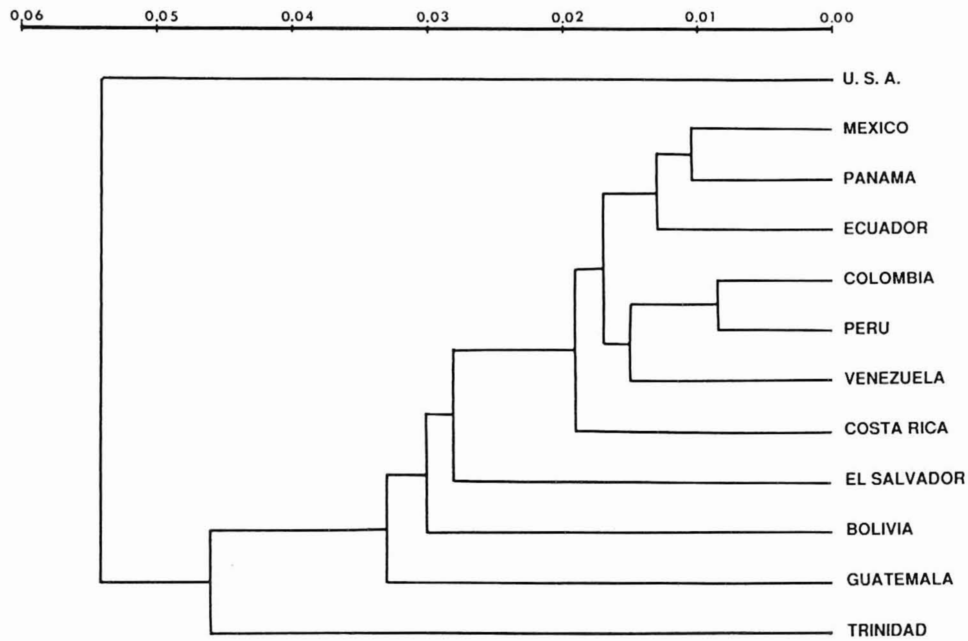


Fig. 2. Dendrogram showing the result of the cluster analysis of the populations of *Dermanura hartii* separated by country of provenance. Cophenetic correlation coefficient = 0.958.

cluded separately in the analyses, in order to evaluate interspecific affinities in the context of *D. hartii* intraspecific variation. The log-transformed character values were standardized to a mean of zero and standard deviation of one, to equalize influence among characters. For the cluster analysis, the unweighted pair-group method using arithmetic averages (UPGMA) was performed on the matrix of correlations among taxa. For the principal components analysis (PCA), the matrix of pair-wise character correlations was calculated, and eigenvectors were extracted from this matrix. The standardized characters were projected onto the first three eigenvectors to visualize intertaxon relationships in a reduced component space. Finally, a minimum spanning tree (MST) was calculated from the intertaxon correlation matrix, and superimposed onto the three-dimensional diagram from the PCA.

Results

Geographic and Secondary Sexual Variation

The phenogram based on the cluster analysis (Fig. 2) provides a summary of the phenetic relationships among the populations of *Dermanura hartii* divided by country. The results show no distinctive geographic groupings, and samples from as far apart as México, Panamá, and Ecuador are phenetically quite similar.

The principal components analysis of the specimens by country also did not show any clear groupings (Fig. 3). The first three components together accounted for more than 80 percent of the phenetic variation (41.7, 27.2, and 12.3 percent, respectively). There is no apparent separation of any geographic group, nor is there any consistent relationship among geographically-close

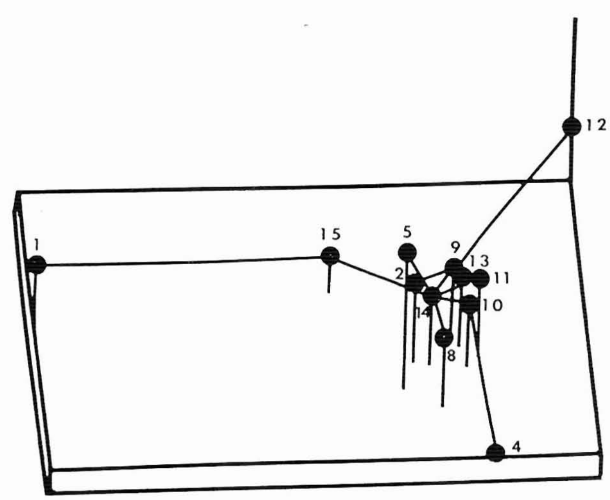


Fig. 3. 3-dimensional plot of principal components analysis from character correlation matrix for *D. hartii* populations by country. For character loadings see Table 1. Minimun spanning tree calculated from taxon correlation matrix. Country codes are as follows: 1, U. S. A.; 2, México; 4, Guatemala; 5, El Salvador; 8, Costa Rica; 9, Panamá; 10, Colombia; 11, Venezuela; 12, Trinidad; 13, Ecuador; 14, Perú; 15, Bolivia.

Table 1. Character loadings and percent variance for the three principal components from principal component analysis based on the character variance-covariance matrix. Value in bold-face is the highest loading for that character on any component.

	COMPONENTS				
VARIABLE	1	2	3	4	5
SKULL	0.0000	0.0043	-0.0033	0.0032	**-0.0046**
POST	0.0100	0.0036	-0.0033	-0.0087	**0.0107**
LACR	0.0096	0.0087	-0.0041	**-0.0147**	0.0040
ZYGO	0.0046	**-0.0077**	-0.0072	-0.0029	0.0025
MAST	0.0063	0.0019	**-0.0117**	-0.0035	-0.0005
BRAINB	**0.0073**	-0.0056	-0.0059	0.0006	0.0028
BRAINH	0.0013	0.0000	**-0.0031**	0.0018	0.0024
BRAINL	0.0026	0.0037	-0.0023	-0.0003	**-0.0070**
PALAT	**-0.0050**	0.0023	-0.0019	-0.0019	-0.0047
MAXIL	**-0.0106**	0.0003	0.0079	0.0054	0.0009
WMOL	0.0108	-0.0060	-0.0059	0.0046	**0.0115**
UM1L	**-0.0560**	-0.0145	-0.0043	-0.0015	-0.0003
UM1W	-0.0019	**-0.0164**	-0.0122	-0.0046	-0.0073
DENTL	0.0027	0.0021	**-0.0080**	0.0004	0.0005
CONCAN	-0.0019	**0.0042**	-0.0036	0.0009	0.0007
TOOTH	**-0.0076**	0.0024	0.0070	0.0036	0.0013
CONMOL	0.0114	0.0061	**-0.0233**	-0.0037	-0.0050
TEMMOM	**0.0224**	-0.0013	-0.0024	0.0111	0.0014
MASMOM	0.0230	**-0.0401**	0.0012	0.0118	-0.0028
CORONH	0.0119	0.0005	0.0054	-0.0062	**-0.0176**
DENTH	0.0109	**0.0312**	0.0054	0.0104	-0.0033
CONDL	0.0185	-0.0141	**0.0186**	-0.0176	0.0009
PERCENT VARIANCE	41.68	27.19	12.25	8.64	5.93

populations. The single specimen from Arizona is closest to the isolated specimens from Bolivia, and most of the large samples are phenetically quite similar.

Of the 22 characters evaluated, six loaded most heavily on component 1 (Table 1). The two with positive values are related to cranial and mandibular form components, whereas the four with negative loadings are related to maxillary and mandibular toothrow dimensions. Six characters showed highest loadings for component 2; four of these were negative. These are general skull breadth and mandibular characters. Four characters had highest loadings (three negative) for component 3. The remaining five character loadings were associated with components 4 (one) and 5 (four). Components 1 through 5 accounted for 41.7, 27.2, 12.3, 8.6 and 5.9 percent of the variation, respectively.

From these analyses, there appear to be no discernable patterns of variation among the geographically-defined populations, and as such no major separation of populations that could indicate taxonomic distinctness. This was tested through a two-way MANOVA (Wilk's Lambda). Results showed overall multivariate significant differences, both among the five large samples examined, and due to the sex-country interaction effect (Table 2). The differences are primarily due to highly significant differences on dentary thickness (DENTH). This character is the only one showing significant differences for the three studied effects in the two-way test. Other characters with significant differences on the two-way tests are: among countries, ZYGO and BRAINH; between sexes, CONMOL and MASMOM; and country-sex interaction effect, PALAT and UM1W. One-way univariate tests (ANOVA) showed very few significant differences: six for locality comparisons and one for comparisons between sexes (DENTH) (Table 2). Duncan's multiple range tests among countries do not show consistent patterns of variation, and for 14 of the 22 characters (64 percent), they show a homogeneous group of the five populations examined.

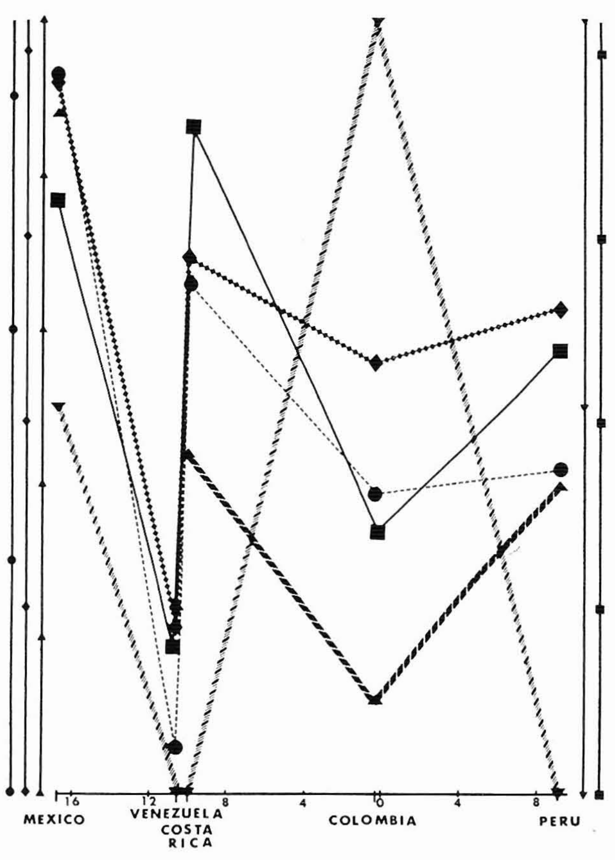
The graphic generated from plotting the characters that are significantly different among countries, or due to the interaction effect (Fig. 4), does not indicate a strong pattern to this variation. In general, it seems that populations to the north of the Isthmus of Panamá are more similar in size to those from Perú, whereas those populations in northern South America are slightly smaller.

Table 2. F-values and significance values for two-way MANOVA and one-way ANOVA of five largest populations of Dermanura hartii, *calculated from the log-transformed data. Duncan's multiple range groups are shown below the means for each character. Significance values are as follows: *, 0.05 ≥ P > 0.01; **0.01 ≥ P > 0.001; ***0.001 ≥ P.*

	TWO-WAY TESTS				ONE-WAY TESTS BY COUNTRY						ONE WAY TESTS BY SEX		
	F-values				F-value	Means					F-value	Means	
Variable	Ctry	Sex	Ctry & Sex	Total	Ctry	Mexico	Costa Rica	Venezuela	Colombia	Perú	Sex	Male	Female
N						22	19	44	31	32		65	83
SKULL	1.92	1.76	0.73	1.37	1.88	20.68	20.68	20.45	20.54	20.62	1.85	20.62	20.53
POST	0.18	0.90	0.95	0.60	0.12	5.73	5.75	5.74	5.76	5.75	1.13	5.77	5.73
LACR	0.83	0.12	0.54	0.62	1.30	6.02	6.01	5.91	5.98	5.90	0.01	5.95	5.95
ZYGO	2.53*	0.12	0.11	1.19	3.41*	12.51	12.42	12.22	12.33	12.34	0.04	12.35	12.33
MAST	1.02	2.20	0.53	0.93	1.26	10.76	10.84	10.68	10.71	10.74	0.15	10.74	10.72
BRAINB	2.22	0.03	0.37	1.15	2.49*	9.60	9.60	9.45	9.57	9.55	0.05	9.53	9.54
BRAINH	4.92**	0.04	1.81	2.99	4.44**	8.88	8.79	8.59	8.73	8.76	0.04	8.74	8.72
BRAINL	2.26	0.85	0.69	1.40	2.63*	12.36	12.30	12.09	12.05	12.14	0.21	12.71	12.14
PALAT	1.60	2.46	3.42**	2.50*	1.04	9.57	9.46	9.41	9.38	9.45	1.87	9.48	9.41
MAXIL	0.23	1.69	0.70	0.60	0.34	6.88	6.83	6.85	6.85	6.88	2.85	6.89	6.84
WMOL	0.88	2.20	0.15	0.70	1.65	4.96	4.87	4.97	4.93	5.03	0.59	4.97	4.95
UM1L	0.37	0.53	1.19	0.75	0.67	1.62	1.60	1.61	1.61	1.59	1.20	1.61	1.60
UM1W	0.26	1.63	3.19*	1.71	0.21	2.30	2.29	2.29	2.31	2.29	0.54	2.29	2.30
DENTL	0.36	2.98	2.31	1.52	0.16	13.25	13.27	13.21	13.23	13.24	1.26	13.27	13.21
CONCAN	0.20	2.73	1.09	0.88	0.47	12.87	12.82	12.78	12.81	12.84	2.21	12.86	12.78
TOOTH	1.16	0.51	0.79	0.92	0.67	7.21	7.18	7.18	7.19	7.12	1.69	7.20	7.15
CONMOL	1.67	4.74*	0.96	1.70	1.94	5.57	5.61	5.47	5.53	5.52	3.01	5.56	5.50
TEMMOM	0.85	3.69	1.00	1.23	1.44	4.33	4.28	4.26	4.33	4.37	2.02	4.34	4.29
MASMOM	1.11	9.82**	0.46	1.79	1.22	2.32	2.24	2.25	2.30	2.31	7.87***	2.33	2.25
CORONH	0.92	2.12	0.90	1.04	1.35	4.93	4.97	4.88	4.98	4.97	2.26	4.97	4.91
DENTH	6.01***	7.34**	1.99*	4.37***	6.46***	2.16	2.18	2.04	2.07	2.12	2.86	2.12	2.08
CONDL	1.82	0.02	1.25	1.37	3.32*	2.24	2.19	2.16	2.09	2.18	0.37	2.16	2.17
WILK'S LAMBDA	1.486**	1.468	1.348*										

Table 3. F-values and significance levels for one-way univariate analysis (ANOVA) of sexes within country. Wilk's Lambda cannot be calculated for samples from Mexico and Costa Rica, due to insufficient degrees of freedom. Significance levels are designated by asterisks: *, *0.05* ≥ P > *0.01;* **, *0.01* ≥ P *0.001;* ***, *0.001* ≥ P.

VARIABLES	MEXICO	COSTA RICA	VENEZUELA	COLOMBIA	PERU
N	26	22	53	41	38
SKULL	3.48	0.28	0.16	2.07	0.41
POST	1.30	0.28	0.02	3.09	0.20
LACR	0.00	0.01	0.18	0.60	1.64
ZYGO	0.50	0.02	0.00	0.13	0.01
MAST	1.08	0.06	0.00	3.66	0.25
BRAINB	0.00	0.42	0.01	0.98	0.03
BRAINH	3.33	0.12	0.02	0.29	3.27
BRAINL	0.70	0.08	1.31	0.04	1.17
PALAT	0.91	2.74	3.61	9.77**	1.45
MAXIL	1.35	1.36	0.17	1.77	0.06
WMOL	0.33	0.06	0.90	0.09	1.24
UM1L	0.50	3.88	0.23	1.49	0.09
UM1W	0.67	0.04	1.19	0.69	14.52***
DENTL	12.18**	0.02	0.22	3.15	0.18
CONCAN	7.77*	0.05	0.01	2.40	0.84
TOOTH	0.02	0.00	0.44	3.16	0.14
CONMOL	3.48	0.09	0.21	2.98	2.04
TEMMOM	0.13	1.51	2.56	2.68	0.62
MASMOM	4.30	0.01	4.84*	2.40	1.06
CORONH	3.56	0.23	1.06	1.14	0.78
DENTH	10.27**	0.20	1.33	0.71	1.85
CONDL	3.08	0.00	0.97	0.68	1.08
WILK'S LAMBDA	—	—	0.91	0.58	2.40



The results of the one-way ANOVA by sex within country (Table 3) only showed six significant values out of 110 tested (5.45 percent), confirming that *D. hartii* does not exhibit sexual dimorphism in most of its distribution. Each of the three characters exhibiting a sex-by-country interaction effect in the two-way ANOVAs (PALAT, UM1W, and DENTH) was found to show significant sexual dimorphism in only one population (Colombia, Perú, and México, respectively).

Fig. 4. Plot of the mean values of those characters showing significant differences among five populations of *Dermanura hartii* tested using a two-way MANOVA. The symbols, characters, significant effects, and value ranges (mm) in the graphic are as follows:

Symbol	Character	Significant effect	First value	Increments
circle	ZYGO	ctry	12.20	0.10
diamond	BRAINH	ctry	8.50	0.10
apex-up triangle	PALAT	ctry&sex	9.35	0.05
apex-down triangle	UMIW	ctry&sex	2.29	0.01
square	DENTH	ctry, sex, ctry&sex	2.00	0.05

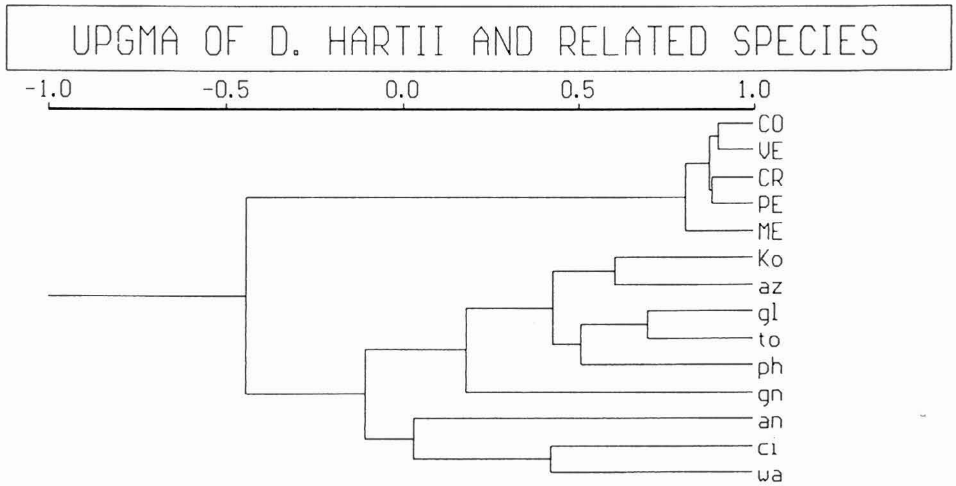


Fig. 5. UPGMA phenogram for correlation matrix among five populations of *D. hartii*, and recognized species of *Dermanura* and *Koopmania*. Acronyms for *D. hartii* populations are: CO, Colombia; CR, Costa Rica; ME, México; PE, Perú; VE, Venezuela. Acronyms for the *Dermanura* species are: an, *anderseni*; az, *azteca*; ci, *cinerea*; gl, *glauca*; gn, *gnoma*; ph, *phaeotis*; to, *tolteca*; wa, *watsoni*; Ko is *Koopmania concolor*. Cophenetic correlation coefficient = 0.905.

Phenetic Affinities

Cluster analysis of *D. hartii* populations, other *Dermanura* species, and *Koopmania concolor* (Fig. 5) confirms that *D. hartii* exhibits very little interpopulational variation, and also shows *D. hartii* to be the most phenetically distinct member of the *Dermanura-Koopmania* clade (*sensu* Owen, 1987). *Koopmania*, although shown by Owen (1991) to be phylogenetically distinct from *Dermanura*, is phenetically within the range of *Dermanura* species exclusive of *D. hartii*. This finding agrees with that of Owen's (1988) phenetic assessment of all stenodermatine species.

Principal components analysis also indicates that populations of *D. hartii* are quite similar, and quite dissimilar to the other species evaluated (Fig. 6). The minimum spanning tree superimposed on the three-dimensional diagram also emphasizes the distinctness of *D. hartii* from the other species. Principal component 1 accounts for 73.7 percent of the data variance,

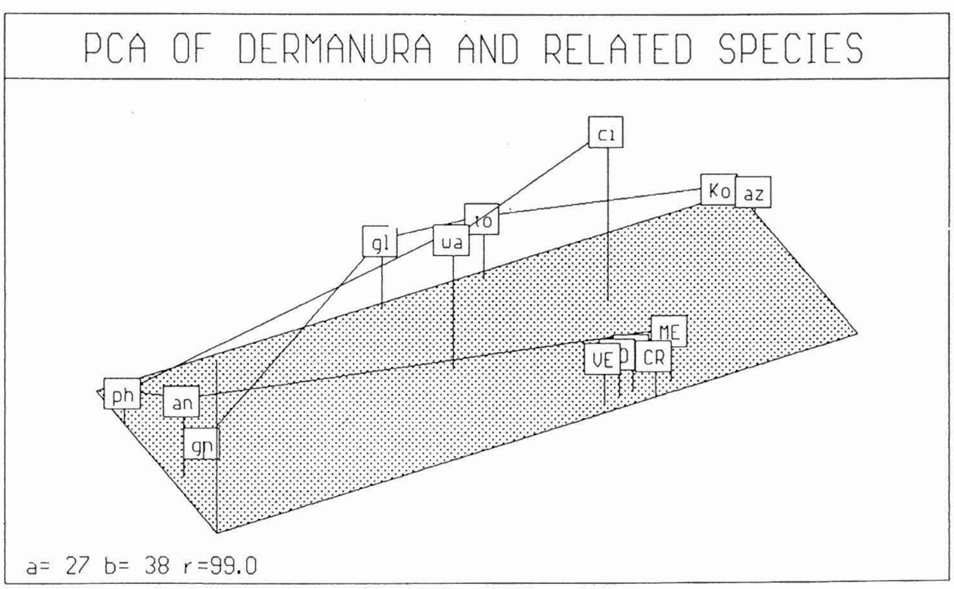


Fig. 6. 3-dimensional plot of principal components analysis from character correlation matrix for *D. hartii* populations, *Dermanura* and *Koopmania* species as in Fig. 5. For character loadings see Table 3. Minimun Spanning Tree calculated from taxon correlation matrix.

and components 2 and 3 account for 14.4 and 4.9 percent, respectively (Table 4). Component 1 is a general size component, with 38 of the 44 characters loading most heavily on this component, all positively. The remaining components relate to various aspects of shape, with six characters loading most heavily on component 2 (four positively, two negatively).

Discussion

Dermanura hartii is a species that does not show sexual dimorphism, contrary to what has been found for several other species of the tribe Stenodermatini (Swanepoel and Genoways, 1979; Tamsitt and Valdivieso, 1986). When summarizing the data from the preceding authors, it is found that 22 of the 31 phyllostomid species (71 percent) showed sexual dimorphism. Within those 22 species, the only one related to the *Dermanura* group was *D. watsoni*, and neither *Artibeus* (*sensu stricto*) nor *Koopmania* was included.

Most earlier studies on *Dermanura hartii* were limited to cursory examination of a few specimens. In fact, only Baker and López (1968) had noted the similarity of specimens separated by a large distance (Mexican and Trinidadian specimens). Our study shows that no population or group of populations is taxonomically distinct, and we concur with the historic perception that the species is monotypic. This is all the more noteworthy, given the apparent distributional discontinuities in certain areas of Central and South America. Although these could be a sampling artifact, we consider this to be unlikely, as considerable collecting has been done in both of those regions (e.g., Aellen, 1970; Davis, 1975; Jones and Owen, 1986; Patton et al., 1982).

An interesting pattern was found from the review of the mean values for the character measurements of the five studied populations (Table 2, Fig. 4). Those populations at the northern (México and Costa Rica) and southern (Perú) extremes of the distributional range are slightly (not significantly) larger than those in the more central areas (Venezuela and Colombia). This could be interpreted as this species conforming to Bergmann's (1847) rule regarding the inverse relationship of variation of body size in homeotherms with ambient temperature, with a size increase due to increasing (N or S) latitude (Bogdanowicz, 1990).

A similar pattern was found for populations of *Carollia castanea*, with populations from México and Bolivia being slightly larger than those from near the equator (McLellan, 1984). Although one explanation of this pattern was conformance to Bergmann's rule, other *Carollia* species mostly showed a north-south cline.

Table 4. Loadings of 44 characters (male and female values for 22 morphometric characters) onto first three principal components from character correlation matrix for Dermanura *species (including* D. hartii) *and* Koopmania concolor. *Components 1, 2, and 3 account for 73.7, 14.4, and 4.9 percent of the variance, respectively. Value in bold-face is the highest loading for that character on any component.*

	COMPONENTS		
CHARACTER	1	2	3
MZYGO	**0.919**	-0.049	-0.292
MMAST	**0.980**	-0.052	-0.165
MBRAINB	**0.939**	-0.111	-0.277
MBRAINH	**0.930**	0.150	-0.021
MBRAINL	**0.927**	0.101	0.165
MPALAT	**0.883**	-0.240	0.190
MMAXIL	0.534	**-0.766**	0.317
MWMOL	0.285	**0.842**	-0.421
MUMIL	**0.802**	0.421	0.356
MUMIW	**0.739**	0.463	0.195
MDENTL	**0.966**	-0.206	0.047
MCONCAN	**0.971**	-0.170	0.079
MTOOTH	**0.930**	-0.218	0.010
MCONMOL	**0.900**	-0.246	0.171
MTEMMOM	**0.923**	0.218	0.049
MMASMOM	0.640	**0.683**	0.176
MCORONH	**0.893**	0.370	0.130
MDENTH	**0.899**	-0.328	0.143
MCONDL	**0.921**	-0.019	0.023
MSKULL	**0.978**	-0.136	-0.019
MPOST	**0.784**	-0.532	-0.261
MLACR	**0.828**	-0.355	-0.295
FZYGO	**0.931**	-0.042	-0.238
FMAST	**0.966**	0.060	-0.197
FBRAINB	**0.912**	-0.115	-0.356
FBRAINH	**0.959**	0.161	-0.156
FBRAINL	**0.906**	0.086	0.235
FPALAT	**0.909**	-0.140	0.248
FMAXIL	0.534	**-0.746**	0.344
FWMOL	0.253	**0.887**	-0.372
FUMIL	**0.796**	0.500	0.261
FUMIW	**0.801**	0.417	-0.005
FDENTL	**0.979**	-0.115	0.059
FCONCAN	**0.986**	-0.066	0.080
FTOOTH	**0.937**	-0.220	-0.053
FCONMOL	**0.919**	0.021	0.251
FTEMMOM	**0.875**	0.378	-0.034
FMASMOM	0.627	**0.720**	0.213
FCORONH	**0.808**	0.471	0.080
FDENTH	**0.920**	-0.189	0.065
FCONDL	**0.896**	0.106	-0.095
FSKULL	**0.990**	-0.058	0.007
FPOST	**0.733**	-0.509	-0.429
FLACR	**0.824**	-0.264	-0.401

Therefore, it was hypothesized that competition was the most important factor driving body size in these populations.

Differences in cranial and mandibular measurements between the five largest populations of *D. hartii* can be viewed from a functional standpoint as well. In fact, the most variable character, dentary thickness, is one of those mentioned by Freeman (1981) as relating to possible functional differences on molossid bats. She suggested that a thickening of the dentary, along with some other changes, could be related to a diet consisting of hard-shelled foods, which could suggest geographic variation in food preferences. As very little is known of *D. hartii* food habits (Gardner, 1977), further study is needed to address this possibility.

Phenetic analyses showed a clear separation of *D. hartii* from all other *Dermanura* species as well as from *Koopmania concolor*. We agree with the statement of Van Den Bussche et al. (1993) that "*Enchisthenes* is best recognized as a genus with unique karyology (Baker et al., 1979), allozymes (Koop and Baker, 1983), morphology (Owen, 1987, 1991), and rDNA restriction-site data (Van Den Bussche, 1992), as well as the molecular data described herein" (Van Den Bussche et al., 1993:955). The appropriate name for the one included species is therefore *Enchisthenes hartii* (Thomas, 1892). No subspecies are recognized, and the present study documents that this species exhibits remarkably little geographic variation. The synonymy for this species is as follows:

***Enchisthenes hartii** (Thomas, 1892)*

Artibeus hartii Thomas, 1892:409. Type locality Botanic Gardens, Trinidad; restricted to Botanic Gardens, Port-of-Spain, Trinidad by Thomas (1893).

Enchisthenes hartii Andersen, 1906:419. Generic description and name combination; type species *Artibeus hartii* Thomas, 1892, by monotypy.

Dermanura hartii Owen, 1987:47. Name combination.

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Appendix I

Localities of the specimens of Enchisthenes hartii *examined (number of specimens by locality is given in parentheses). Coordinates for most of the localities were compiled from the bibliography. Museum acronyms are listed in acknowledgments.*

U.S.A.

Arizona
Pima Co., Tucson (UA 11995)

MEXICO

Chiapas
15 mi ESE Tonalá, 16° 45' N, 93° 07' W, 100ft (LACM 13528)
38 km N Huixtla, 15° 29' N, 92° 29' W, 460m (LACM 13529-13533, 13535)
38 km S[sic] Huixtla (UA 8217)
6.4 km N, 3.6 km W Unión Juárez, 15° 07' N, 92° 07W, 1740m (ENCB 17418-17420)
Mpio. Angel Albino Corzo, "El Triunfo", 7 km SSW Finca Prusia, 15° 20'N, 92° 29'W, 1100m (IBUNAM 19246, 20255-20259, 20847-20850)
4 mi SE Rayón, 17° 10' N, 92° 55' W, 5500ft (MSU 15391)
Finca San Salvador, 15 km SE San Clemente, 16° 28' N, 93° 30'W, 1000m (KU 102600)
Puente Mosquito, carretera Artiaga a Tapachula (UA 16227)
1 km W Rancho San Miguel, 24 km W (by road) Cintalapa, 16° 46' N, 93° 43' W, 610m (UA 15465)

Colima
San Antonio, 3900ft (LACM 55911)

Guerrero
Mpio. Atoyac, Retrocesos, 1550 m (MZFC 464)

Jalisco
10 mi SE Talpa de Allende, 20° 23' N, 104° 51'W, 5350 ft (KU 97039)
2 km N Ciudad Guzmán, 19° 41' N, 103° 29' W, 5400 ft (FMNH 83309, 83317-83319, 83328)

México
Malinaltenango, 1400 m (UAMI 5528)

Michoacán
4 km SE Aquila, 200 m (IBUNAM)

Oaxaca
Juchitán, Zanatepec, 4000 ft (AMNH 206872)

Puebla
Mpio. Hueytamalco, El Guayabal, Rancho Las Margaritas (IBUNAM 16224, 16227)
Rancho Las Margaritas, 9 km NW Hueytamalco, 600 m (UAMI 1318)
3 km N Cuautempan, 1690 m (UAMI 4674)
Mazacoatlán, 1200 m (UAMI 4675)

Tamaulipas
Aserradero del Infiernillo Cave, 11 km W Gómez Farías, 23° 04' N, 99° 13' W, 4400 ft (AMNH 166057)
Rancho del Cielo, 23° 04' N, 99° 12' W (TTU 5581)

Veracruz
2 mi (by road) N Teocelo, 1000 m (UMMZ 113689)

GUATEMALA

Sacatepequez
3 mi NE Antiqua, 14° 34' N, 90° 44' W, 5900 ft (CM 73904-73906)

EL SALVADOR

Ahuachapan
Bosque El Imposible, Cerro Campana, 1200 m (ROM 94169)

Morazán
Finca Bustamante, Cerro Cacahuatique, 13° 45' N, 88° 12' W, 1663 m (ROM 85896, TCWC 37503)

HONDURAS

Distrito Central
La Flor Archaga, 2 km N Río Choluteca, 14° 18' N, 87° 18' W, 420 m (AMNH 126239)

El Paraíso
Chichicaste, 14° 07' N, 86° 16' W, 480 m (TCWC 21834)

COSTA RICA

Alajuela
2.5 mi SSE Cariblanco (TTU 34315)

Guanacaste
1 mi by air SE Tilaran (LACM 42418)

Puntarenas
Finca Helechales, 14 km NE Potrero Grande, 1100 m (LACM 26794)
4 km S San Vito de Java (=Finca Las Cruces, 2 km S San Vito, 1300 m (LACM 28750, 28751, 28768)
Monteverde, 1500 m (KU 134897)
2 km SW Rincón de Osa, 15 m (MSB 26805)
2.1 mi S, 1.1 mi E San Vito, Las Cruces Tropical Botanical Garden (TTU 34316, 34317)

San José
Fila la Máquina, ca. 7.5 km E Canaán, 9° 26' N, 83° 35' W, 2600 m (LSUMZ 12882-12893)

PANAMA

Canal Zone
Quarry Heights, near Panamá, 8° 57' N, 79° 34' W (USNM 317623)
Barro Colorado Island, WMW 15, 9° 09' N, 79° 51' W (USNM 539813)

Chiriqui
El Volcán, 14.5 km NW Finca Santa Clara, 8° 51' 30" N, 82° 44' 45" W, 1200-1500 m (USNM 537601)

Darién
4 mi W top of Cerro Malí, 4800 ft (KU 99365)
Tacarcuna Village Camp., 8° 05' N, 77° 17' W, 594 m (USNM 310213-310230, 339030-339032)
Cerro Mali, 8° 07' N, 77° 14' W, 4700 ft (USNM 338046-338049)
Cerro Tacarcuna, 8° 10' N, 77° 18' W, 4100 ft (USNM 338050, 338051, 338053-338058)
Cerro Mali, 8° 07' N, 77° 14' W, 4100 ft (USNM 338052)

Los Santos
Cerro Hoya, Los Santos, 7° 18' N, 80° 42'W, 2600 ft (USNM 323537-323542)

TRINIDAD

St. George
Blanchisseuse (TTU 5371)
Maracas Valley (TTU 5243)

VENEZUELA

Aragua
Rancho Grande Biological Station (USNM 370782)
13 km NW Maracay, Rancho Grande Biological Station, 10° 21' N, 67° 40' W, 1050 m (USNM 517491)
14 km NW El Portachuelo, 10° 21' N, 67° 40' W, 1130 m (USNM 517492-517498)

Carabobo
35 km NW Puerto Cabello (USNM 372387)
La Copa, 4 km NW Montalban, 1537 m (USNM 455926-455928)

Distrito Federal
Los Venados, 4 km NNW Caracas, 10° 32' N, 66° 54' W, 1400-1739 m (USNM 370726, 370729, 370730, 370733, 370734, 370736-370738, 370744)
9.4 km N Caracas (USNM 370745, 370747, 370751-370757, 370761-370763, 370766, 370767, 370769-370773, 372384, 372385, 372388, 387555, 387556)
5 km N Caracas (USNM 370727, 370731, 370732, 370735, 370740-370743, 387557, 387558)
Pico El Avila, 5 km NNE-6 km NNW Caracas, 10° 33' N, 66° 52' W, 1982-2250 m (USNM 370748, 370750, 370758, 370759, 370764, 370765, 370768, 372386)
3 km S, 46 km W Caracas (USNM 387560, 387561)

Falcon
Hacienda Socopito, 80 km NW Carora, 10° 30' N, 70° 44' W, 450-480 m (USNM 441474)
56 km S, 99 km E Coro, near Riecito (USNM 455921)

Guárico
57 km S, 49 km E Caracas (USNM 387564, 387565)

Miranda
27 km N Altagracia de Orituco (TCWC 41356-41358)
Petare, 10 km E Caracas, 825m (CM 6035)
24 km N Altagracia (TTU 48131)
25 km N Altagracia de Orituco, 2200 ft (TCWC 49001)
8 km S Caracas (USNM 387562)

Monagas
1 km N, 3 km W Caracas (USNM 409217, 409218)

Territorio Federal de Amazonas
Río Manapiare, San Juan, 163 km ESE Pto. Ayacucho, 155 m (USNM 409220)

Zulia
3 km S, 19 km W Machiques (=Novito, 19 km WSW Machiques), 10° 02' N, 72° 43' W, 1135 m (USNM 441472)

COLOMBIA

Cauca
Calibio, 6000 ft (FMNH 113560, 113572)
Alta Micay (Betania), 1000 ft (FMNH 113604)
Mechenguito (ROM 63208)

Meta
Villavicencio, 4° 09' N, 72° 59' W, 500 m (ROM 53652-53657)
Restrepo, 15° 73' N, 73° 33' W, 1000 m (ROM 53647-53651, 62564, 62568-62571, 62573, 62575, 62578, 62582, 62583, 62585)
Restrepo, Upin Salt Mine (TTU 9098, 9111, 9113-9116, 9412, 9414, 9415, 9417, 9418, 9434, 9469, 9486, 9487, 9489, 9490, 9496)
El Bosque Estate (ROM 75091)

Nariño
Llorente (FMNH 113520)
Patia (ROM 62533)

Valle
2 km S Pance, approx. 20 km S Cali, 3° 20' N, 76° 38' W, 1650 m (TU 3860, 3861, 5627-5638; USNM 483909-483938)
Río Zabaletas, 29 km SE Buenaventura, 3° 53' N, 77° 04' W (USNM 483939-483942)
Guayuyaco (ROM 49218)

ECUADOR

Guayas
3 mi E San José, Río de Jiler, Santa Elena Canton, ca. 2° 35' S, 78° 15' W (LACM 33097)

Loja
Casanja Valley, approx. 2900 ft (AMNH 257493-257412, 257414-257416)

Morona Santiago
0.5 km W Macas, 2° 19' S, 78° 07' W (TTU 40073)

Napo
Santa Cecilia, 00° 03' S, 75° 58' W, 340 m (KU 139574)

Napo Pataza
Limon Cocha, 00° 25' S, 79° 37' W (MSU 10689)

Pastaza
Mera (USNM 548252-548261)

Zamora-Chinchipe
3 km NE Cumbaratza, 3000 ft (USNM 513470)

PERU

Amazonas
43 km (by road) NE Chiriaco (LSUMZ 21534)
12 trail km E La Peca (LSUMZ 21462-21464, 21466)
Cordillera Colón, E La Peca (LSUMZ 21467)
5 km N, 5 km E Pomacochas, 5.8° S, 77.9° W, 6000 ft (MVZ 135599)

Ayacucho
Huanhuachayo, 12° 44' S, 73° 47' W, 1660 m (AMNH 233791)

Cuzco
40 km (by road) E Quincemil, ca. 700 ft (LSUMZ 19208)
Quincemil, Hacienda Cadena (FMNH 93608-93613)
Cordillera Vilcabamba, summit, 12° 36' S, 73° 29' W, 3540 m (AMNH 233599, 233603)
Cordillera Vilcabamba, west side, 12° 38' S, 73° 36' W, 2065-2260 m (AMNH 233753)

Huánuco
Cerros del Sira, 9° 25' S, 74° 43' W, 1880-1960 m (AMNH 233798)
Leoncio Prado Prov., 1 km S Tingo María (CM 98711)
Leoncio Prado Prov., 9 km S, 2 km E Tingo María, 9° 22' S, 75° 58' W (CM 98713-98724; TCWC 48807-48818; TTU 46226-46238)

Lambayeque
Las Juntas, ca. 14 km N, 25 km E Olmos (LSUMZ 27251, 27252)

Madre de Dios
Aguas Calientes, Río Alto Madre de Dios, 1 km below Shintuya, 460 m (MVZ 166569)
ridge above Hacienda Amazonia, 950 m (FMNH 1257997, 125800, 125802, 125804, 125805)
ridge above Hacienda Amazonia, 780 m (FMNH 125784-125786, 125790, 125791, 125796)

Piura
15 km E Canchaque (LSUMZ 19207)

BOLIVIA

La Paz
1 mi W Puerto Linares, Tomonoco, 15° 29' S, 67° 31' W, 350 m (TTU 34880)

Cochabamba
approx. 25km (by road) W Comarapa, 17° 51' S, 64° 40' W, 2800 m (UMMZ 155846)

Appendix 2

Localities of specimens of Enchisthenes hartii *not examined (number of specimens is given in parentheses, followed by authors of record).*

MEXICO

Chiapas
Mpio. Angel Albino Corzo; Reserva "El Triunfo" (4)— León P. and Romo V., 1991

Guerrero
28 km (by road) N Tecpan de Galeana, 350 m (1)— Ramírez-Pulido and López-Forment, 1979

COSTA RICA

Cartago
Río Pacuare, Pacuare, ca. 40 m (1)— Gardner et al., 1970

Heredia
Vara Blanca, 10° 10' N, 84° 09' W, ca. 1800 m (5)— Gardner et al., 1970

Puntarenas
4.5 mi W San Vito de Java (1)— Armstrong, 1969

VENEZUELA

Distrito Federal
Boca de Tigre Valley, 5 km NW Caracas, 1394 m (1)— Handley, 1976
Hda. Carapiche, near El Limón, 48 km W Caracas, 380 m (4)— Handley, 1976

Falcón
Boca de Yaracuy, 28 km WNW Pto. Cabello, 2 m (1)— Handley, 1976

Guárico
Hda. Elvira, 10 km NE Altagracia, 630 m (3)— Handley, 1976

Miranda
San Andrés, 16 km SSE Caracas, 1144 m (3)— Handley, 1976

Monagas
San Agustín, 3-5 km NW Caripe, 1160-1180 m (4)— Handley, 1976

ECUADOR

Bolívar
Barraganete, 3 km SW Echeandía, 1° 26' S, 79° 17' W, 430 m (3)— Albuja V., 1982

Carchi
Maldonado, Cantón Tulcáan, 00° 55' N, 78° 07' W, 1500 m (1)— Albuja V., 1982

Pastaza
Puyo, 1° 30' S, 78° 00' W, 100 m (4)— Albuja V., 1982
Río Pucuno, 00° 42' S, 77° 08' W, 600 m (1)— Albuja V., 1982

Pichincha
Gualea, Cantón Quito, NW Nanegalito, 00° 07' S, 78° 50' W, 1300 m (2)— Albuja V., 1982

PERU

Junín
3.2 km N Vitoc, Río Tulumayo, ca. 850 m (1)— Gardner, 1976

Appendix 3

Localities of specimens used for phenetic analysis, other than Enchisthenes hartii.

Dermanura anderseni

BOLIVIA

Beni: Río Cureraba, Beni Reserve (USNM 564322); Río Mattos, Beni Reserve, near Totaizal (USNM 564323).

La Paz: 1 mi W Puerto Linares (TTU 34842).

COLOMBIA

Antioquia: 24 km S, 22 km W Zaragoza, at Buenos Aires, 450m (USNM 499499, 499500); 26 km S, 22 km W Zaragoza, at Aljibes, 630m (USNM 499501, 459502); 25 km S, 22 km W Zaragoza, at La Tirana, 520m (USNM 499503).

ECUADOR

Pastaza: Taculin, below Puyo (USNM 548279); Arajuno (USNM 548280).

PERU

Madre de Dios: Tambopata Explorer's Inn, 260m (USNM 562241).

Pasco: Prov. Oxapampa; San Juan, 900ft (USNM 364420-364423); 59 km W Pucallpa (USNM 461255).

Dermanura azteca

MEXICO

Nuevo León: Cueva de San Josecito, 2400m (DP 6107-6109, 6112-6119, 6126, 6170-6175, 6257); 1.3 km S, 0.8 km W San Josecito, 2400m (DP 6258).

Dermanura cinerea

TRINIDAD

St. George: Blanchisseusse (TTU 26578); Las Cuevas (TTU 5682, 8967, 8970, 26584-26595, 26856, 26858-26860).

Dermanura glauca

VENEZUELA

Carabobo: 4 km NW Montalban, La Copa, 1810m (USNM 440794, 440802-440818, 440820-440822).

Dermanura gnoma

VENEZUELA

T. F. Amazonas: 108 km SE Esmeralda (USNM 405490, 405491); Tamatama (USNM 405492); Río Orinoco (USNM 409127); San Juan (USNM 409129-409133); 12 km SSE Puerto Ayacucho (USNM 409134, 409135); 14 km SE Puerto Ayacucho (USNM 409138); 18 km SE Puerto Ayacucho (USNM 409148); 30 km S Ayacucho (USNM 409150); Morocoy, 65 km SSW Puerto Ayacucho (USNM 409139, 409141-409145).

Dermanura phaeotis

MEXICO

Michoacán: 18 km SE Caleta de Campos (ENCB 8498-8516, 8518).

Dermanura tolteca

MEXICO

Chiapas: 15.1 km N, 8 km W Ocozocuautla, 750m (ENCB 12958); 11.3 km N, 8 km W Ocozocuautla, 960m (ENCB 12959-12968); 9 km N, 8 km E Ocozocuautla, 800m (ENCB 12969, 12970); 5.6 km N, 5.1 km W Ocozocuautla, 820m (ENCB 12971); 5.5 km S, 17.6 km W Ocozocuautla, 600m (ENCB 14938, 14939); Cañón del Sumidero, 9.3 km N, 3 km W Tuxtla Gutiérrez, 300m (ENCB 15525, 15526, 15530, 15531).

Dermanura watsoni

MEXICO

Chiapas: Mpio. Ocosingo: Arroyo José, Est. Chajul de SEDUE, Reserva Montes Azules (IBUNAM 22852, 24447); Arroyo San Pablo, Reserva Montes Azules (IBUNAM 23714, 24451); Ejido Loma Bonita, Río Chajul (IBUNAM 24449); Est. Chajul de SEDUE, Reserva Montes Azules (IBUNAM 22320); Ejido Loma Bonita, Arroyo Puerto Rico (IBUNAM 24453); Ruinas de Palenque, 140m (ENCB 1621, 1624, 1629, 1630); 10 km N, 1.5 km E Raudales, 150m (ENCB 2073, 2074).

Veracruz: Río Basura, 3 km N Sontecomapan (ENCB 2585, 2588, 2589).

NICARAGUA

Zelaya: 3 km NW Rama (TTU 12934, 12948).

COSTA RICA

Alajuela: Cariblanco (TTU 12980).

Heredia: 7.3 mi SE Puerto Viejo (TTU 12977-12979, 13040-13043).

San José: 13.3 mi SW San Isidro (TTU 12981, 12982).

Koopmania concolor

VENEZUELA

Bolívar: 22.5 km NE Icabaru (USNM 440889); 85 km SSE El Dorado (USNM 387366, 387371, 387376).

T. F. Amazonas: Tamatama, 135m, Río Orinoco (USNM 408884, 545347-545349); Río Orinoco (USNM 408885); Casiquiare Canal, Capibara (USNM 408888); San Juan (USNM 408894, 408897, 408898); Río Manapiare, San Juan (USNM 408895, 408896, 408899); 25 km SSE Puerto Ayacucho (USNM 408900); 9 km SE Puerto Ayacucho (USNM 408901); 65 km SSW Puerto Ayacucho (USNM 408902); Belen (USNM 405202).