CRANIAL VARIATION AND ASYMMETRY IN SOUTHERN POPULATIONS OF THE PORCUPINE, *ERETHIZON DORSATUM*

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ABSTRACT.—Although *Erethizon dorsatum* is one of the most morphologically variable species of North American mammals, the few studies addressing this variation are mostly qualitative. Standard and paired (right- and left-sided) cranial and mandibular measurements for 112 specimens, primarily from New Mexico, Oklahoma, and Texas, were analyzed quantitatively. Based on dental characters, specimens were grouped by age into four classes (juvenile, subadult, young adult, and old adult). Sexual dimorphism is not pronounced in porcupines, although males average larger than females in all age categories except the juvenile category, where the opposite is true. For each character assessed, there was significant age-class variation, but only least rostral breadth exhibited an interactive effect between sex and age. Individual variation was considerable, in part because of continued growth in certain parts of the skull where fusion occurs either late in life or not at all. The pronounced asymmetry fits Van Valen's (1962) definition of fluctuating asymmetry, but whether the phenomenon is induced by environmental, genetic, developmental, or behavioral factors is speculative. Because determinant characters for currently recognized subspecies are found to be mostly age-dependent, and because populations from the three subspecies best represented in our sample are morphometrically indistinguishable, we propose that *E. d. couesi* be synonomized under *E. d. epixanthum*. Additional work probably will further reduce the number of recognized races of the North American porcupine. *Key words*: porcupine morphometrics; cranial asymmetry; cranial variation.

Little information on morphological variation in porcupines is available. Hibbard and Mooser (1963:246) declared the species ". . . probably one of the most variable rodents in North America," a sentiment earlier expressed by Hollister (1912), and also reflected in osteological studies of the postcranial skeleton (Gupta, 1965). The most comprehensive published treatments (Anderson and Rand, 1943; Sutton, 1972) are mostly qualitative, although some aspects of individual and age variation of the skull are addressed. Only Ahlberg (1969) provided an extensive review of morphometric traits; although the focus of this dissertation was a systematic review of the nominal subspecies, the work unfortunately has not been published.

Neglect of the porcupine by systematic workers is probably due in large part to limited sample sizes. Representative series are not easily collected from most localities, and many specimens appear to be opportunistic finds (weathered remains or skulls salvaged from animals killed along roadways, for example). Although their value as geographic vouchers usually warrants retention in systematic collections, such specimens are often of unknown sex and may be damaged or only partially intact. Anderson and Rand (1943), in whose study pelage was an important character, attributed their limited sample size to the awkwardness in handling such large and prickly animals. Only 24 of the 42 specimens tabulated by those authors were complete for the five measurements taken.

Cranial asymmetry in porcupines was alluded to by Anderson and Rand (1943) and briefly treated by Sutton (1972). More recently, Stangl *et al.* (1988) detailed a markedly asymmetrical adult porcupine skull with deciduous premolars. Their preliminary (and quite limited) survey of several specimens from the Midwestern State University Collection of Recent Mammals confirmed the pronounced cranial asymmetry in porcupines and served as the impetus for the present undertaking. In this paper, we evaluate cranial asymmetry, age and geographic variation, and secondary sexual variation in porcupines from the southern part of their distribution within the United States.

METHODS AND MATERIALS

For this study, we selected a geographic area (Fig. 1) —the southwestern United States— in which *Erethizon dorsatum* has not been well studied and from which sufficient specimens were available. Almost all (99 of 112) were from New Mexico, Oklahoma, and Texas (Fig. 1); limited samples from Arizona (N=2), Colorado (N=4), Idaho (N=1), South Dakota (N=1), Wisconsin (N=3), and Wyoming (N=2) were included for comparative study (Appendix 1). Holdings from the following insitutions (with acronyms) were examined: Midwestern State University (MWSU), Texas A&M University (TCWC), Texas Tech University (TTU), University of Texas-El Paso (UTEP), Oklahoma State University (OSU), University of Oklahoma (OU), and University of New Mexico (MSB).

We intended to take 21 cranial and mandibular measurments from each specimen, but because of the fragmentary or damaged nature of many, not all measurements were available. Standard (nonpaired) measurements included postpalatal length, least rostral breadth, least infraorbital breadth, and mastoid breadth. Both right-side and left-side measurements (Fig. 2) were taken for the following bilateral characters: lengths of auditory bullae, lengths of maxillary and mandibular toothrows (alveolar), lengths of maxillary and mandibular diastemas, greatest widths of individual nasals, and distance from anteriormost and posteriormost nasal junctions to posterior margins of left and right zygomatic arches. Development of the temporalis musculature as defined by cranial muscle scars (Fig. 3), and any asymmetry or directional deviation of these scars or of the sagittal crest, were recorded.

Measurements were taken with dial calipers to the nearest 0.1 mm for most characters and to the nearest 0.01 mm for some. When possible, specimens were classed by sex. Individuals also were categorized into four general age classed by dental development, using Taylor (1935) and Sutton (1972) as authorities. Class 0 Individuals (juveniles) possess less-than-complete sets of dentition, and probably are no older than nine months. Class 1 individuals (subadults) are characterized by eruption of all molars, but retention of the deciduous premolars, and range from nine months to about two years of age. In class 2 individuals (young adults), the permanent premolars are in place. Class 3 individuals (old adults) were distinguished by excessive wear of the rooted cheekteeth.

Two-way (sex, age) analyses of variance (ANOVAs) were conducted for each of the 21 measurements. Because only specimens of known sex could be used, analyses included only half of the 112 specimens examined. The two-way ANOVAs allowed us to inspect the data

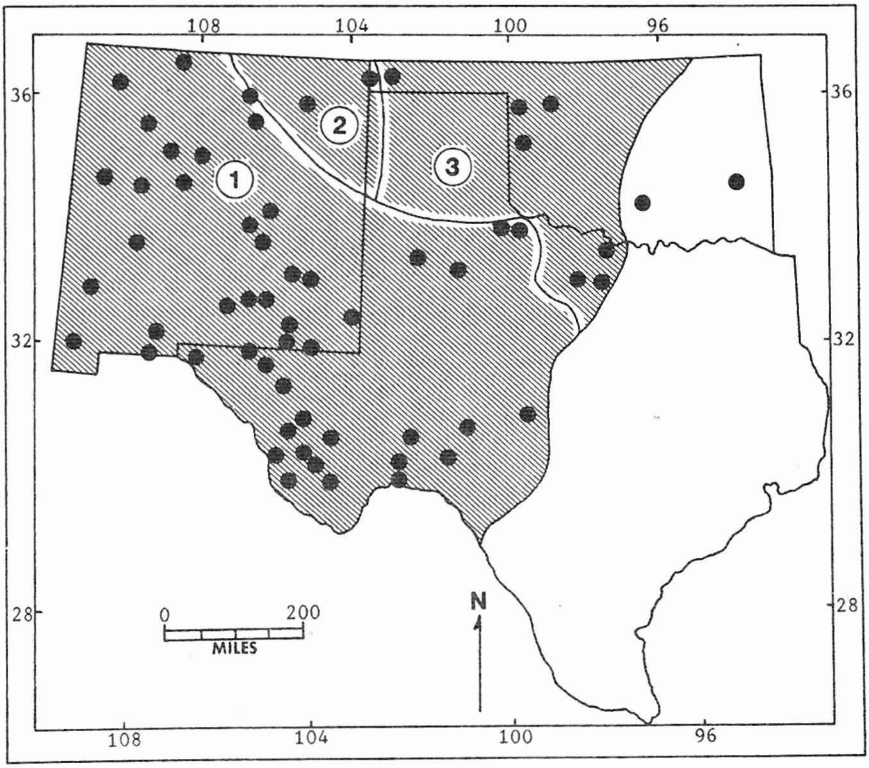

FIGURE 1. —Distribution of specimens examined of *Erethizon dorsatum* from states of New Mexico, Oklahoma, and Texas; superimposed general range of species follows Hall (1981). Included nominal subspecies are *E. d. couesi* (1); *E. d. epixanthum* (2); and *E. d. bruneri* (3). Closely situated localities may be represented by a single symbol.

for an interaction effect between age and sex, and to assess secondary sexual dimorphism across all age classes.

Because the effect of age-sex interaction was found to be unimportant (and sexes were distributed about evenly with respect to age), we pooled sexes (including specimens of unknown sex) for one-way ANOVAs to evaluate age variation based on the complete sample. On the basis of results of the one-way ANOVAs for age variation, we pooled age classes 2 and 3 (young and old adults) for one-way ANOVAs to evaluate secondary sexual dimorphism among adult porcupines. All ANOVAs were run using PROC GLM of SAS version 5 (SAS Institute Inc., 1985).

Finally, we evaluated geographic variation using principal components analysis (PCA). For this analysis, only adult age classes (2 and 3) were used. Each character was standardized to a mean of zero and variance to one, so that all characters would be equally important. Eigenvectors were extracted from the character correlation matrix. The standardized character values for each individual were projected onto the first three eigenvectors. These three-dimensional coordinates for each specimen then were visualized in a diagram in order to inspect for concordance of morphometric and geographic patterns. These analyses were conducted using NTSYS-pc, version 1.50 (Rohlf, 1988).

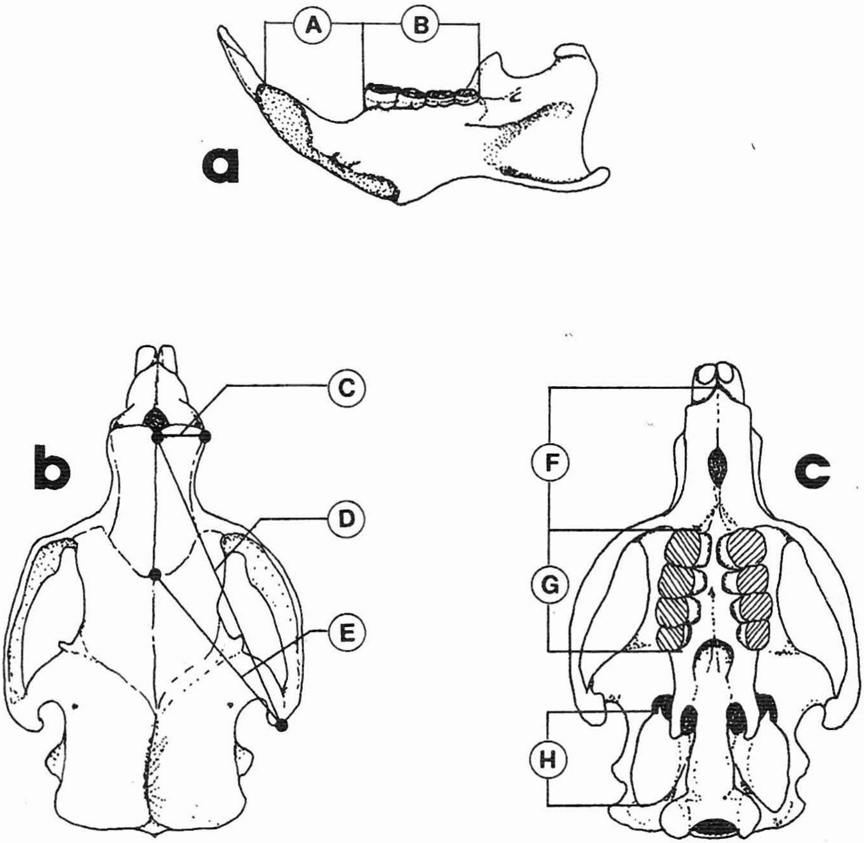

FIGURE 2. —Paired mandibular (a) and cranial (b-c) measurements of *Erethizon dorsatum* utilized in this study. See text for explanation of specific measurements.

RESULTS

Older porcupines (age classes 2 and 3) are more common in collections than young animals, but they are less often represented by complete (known sex and intact skulls) data. Sample sizes of *Erethizon dorsatum* for each known age class and of known sex are, therefore, relatively small. However, comparisons of these groupings (Appendix 2) suggest that juveniles (age class 0) are consistently smaller for all characters; that subadults (age class 1) mostly have achieved adult (age classes 2 and 3) size; and that females of all age categories tend to be more variable than males. The negligible interactive effect between age and sex (Appendix 2; least rostral breadth the only exception) permitted pooling of both sexed and unsexed specimens to examine age variation in more detail (Appendix 2), and the minimal distinction between young and old adults

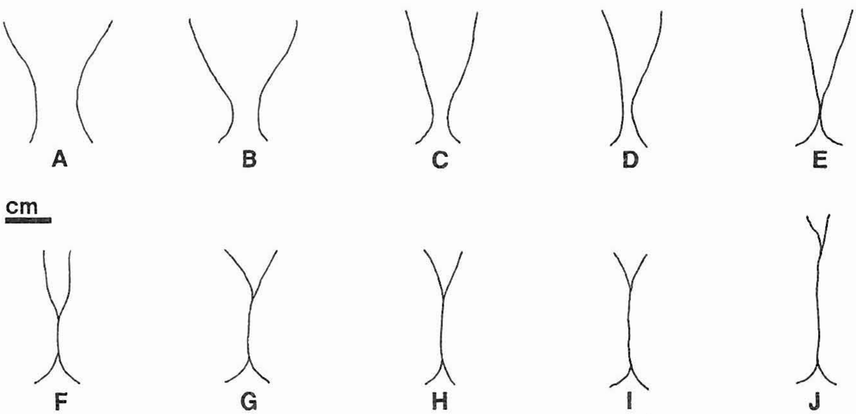

FIGURE 3. —Dorsal view of medial margins of temporalis muscle scars, illustrating stages of muscle migration and formation of sagittal crests among age classes of *Erethizon dorsatum* age classes 0, a-b; 1, c-d; 2, e-i; 3, j.

observed therein allowed combining adults irrespective of age, to characterize sexual dimorphism (Table 1).

We found juvenile female porcupines to average larger than their male counterparts, although this may reflect a limited sample size. As subadults, males average larger for most characters. Adult males average larger than females, but the difference between sexes was significant in only two instances (Table 1). Comparison of Table 1 with Appendix 2 suggests that larger samples of adult porcupines might increase the number of characters found to be significantly different between sexes.

Every porcupine in our study for which at least two of the eight paired measurements were available exhibited measureable asymmetry for from one to all of those characters, with the exception of a single unsexed subadult, which was symmetrical for each of the four available paired characters. Means for most of these characters did not vary significantly, indicating expression of fluctuating asymmetry.

The first three components of the principal component analysis explain 51.7, 15.8, and 8.0 percent of the matrix variance. With about three-fourths of the total variance represented (Fig. 4), no morphometric patterning or segregation can be seen that coincides with taxonomic relationships. Additonal analyses, for which no figures are shown, indicated similar lack of patterning based on sex and age class (between the two older adult classes).

DISCUSSION

Age Variation

Juveniles.—Porcupines are born in a precocial state, already possessing incisors, deciduous premolars and the first molars (Taylor, 1935; Jackson,

TABLE 1.— Sexual dimorphism of cranial characters in adult porcupines (age classes 2 and 3).

Sex (N)	Mean ± SE	Range	CV
	Greatest length of left bulla		
M (14)	21.59 ± 0.33	19.50-23.55	5.67
F (16)	20.81 ± 0.46	18.70-24.82	9.13
	Greatest length of right bulla		
M (14)	21.79 ± 0.40	19.85-24.35	6.83
F (16)	20.92 ± 0.42	19.07-24.10	8.56
	Length of left maxillary toothrow		
M (13)	26.28 ± 0.32	24.35-28.00	4.44
F (16)	25.71 ± 0.42	22.30-27.60	5.40
	Length of right maxillary toothrow		
M (14)	26.21 ± 0.30	24.55-27.80	4.28
F (16)	25.64 ± 0.40	22.30-27.60	4.96
	Length of left mandibular toothrow		
M (14)	30.16 ± 0.36	28.85-32.55	4.44
F (16)	29.74 ± 0.56	26.90-33.00	5.56
	Length of right mandibular toothrow		
M (14)	30.18 ± 0.37	28.80-32.85	4.57
F (15)	29.78 ± 0.62	27.20-33.85	6.07
	Length of left maxillary diastema		
M (12)	30.58 ± 0.85	26.55-35.20	9.61
F (14)	28.24 ± 1.30	21.65-35.40	17.17
	Length of right maxillary diastema		
M (12)	30.56 ± 0.84	26.55-35.10	9.55
F (15)	28.11 ± 1.21	21.94-36.35	16.63
	Length of left mandibular diastema		
M (13)	18.03 ± 0.72	13.50-21.40	14.36
F (16)	16.86 ± 0.71	12.87-22.50	16.01
	Length of right mandibular diastema		
M (13)	18.02 ± 0.78	12.75-22.10	15.62
F (14)	16.93 ± 0.81	12.87-22.45	17.03
	Greatest width of left nasal		
M (11)	11.64 ± 0.43	9.05-13.80	12.34
F (16)	11.50 ± 0.34	8.00-13.60	12.26
	Greatest width of right nasal		
M (11)	11.39 ± 0.48	8.95-13.90	13.84
F (16)	11.43 ± 0.34	8.00-13.60	12.20

TABLE 1. Continued

	Greatest distance between anterior nasal junction and left zygomatic arch		
M (11)	73.22 ± 0.87	70.30-77.65	3.94
F (14)	70.19 ± 1.21	61.00-78.62	6.49
	Greatest distance between anterior nasal junction and right zygomatic arch *		
M (10)	73.55 ± 0.96	69.90-77.80	4.13
F (15)	69.47 ± 1.23	60.50-77.25	7.04
	Greatest distance between posterior nasal junction and left zygomatic arch		
M (12)	48.11 ± 0.61	44.30-51.30	4.42
F (12)	47.42 ± 1.06	39.85-51.90	8.11
	Greatest distance between posterior nasal junction and right zygomatic arch		
M (11)	47.81 ± 0.76	43.25-51.50	5.27
F (13)	46.84 ± 1.09	38.80-52.45	8.89
	Greatest post-palatal length *		
M (12)	42.02 ± 0.74	37.45-46.85	6.13
F (15)	39.05 ± 0.93	32.80-46.10	8.94
	Least rostral breadth		
M (11)	21.38 ± 0.64	18.30-26.05	9.95
F (16)	21.10 ± 0.54	18.10-25.40	10.12
	Least infraorbital breadth		
M (13)	30.40 ± 1.96	22.30-37.10	14.18
F (14)	28.55 ± 0.69	25.20-33.45	9.10
	Greatest zygomatic width		
M (11)	70.93 ± 0.54	68.95-74.10	2.54
F (13)	68.16 ± 2.02	59.10-78.40	7.86
	Greatest mastoid breadth		
M (13)	45.60 ± 0.86	40.60-50.70	6.78
F (14)	43.96 ± 1.21	39.80-52.40	9.52

One-way analysis of variance: * $P < 0.05$.

1961; Sutton, 1972; Woods, 1973). Juvenile females average larger than juvenile males, a trend reversed in the older three age classes (Appendix 2). The rostrum is proportionally short, and narrowed anteriorly. The skull roof is smooth, because scars defining the extent of the temporalis muscles are situated more laterally in the young animals (Fig. 3) than in those in older age groups.

Subadults.—Porcupines grow rapidly, and by the time the third molars have erupted, skull roof sutures have disappeared and the animals nearly have reached adult body size. Sutton (1972) noted that most skull growth during this stage is directed anteriorly (the rostrum appears quite short

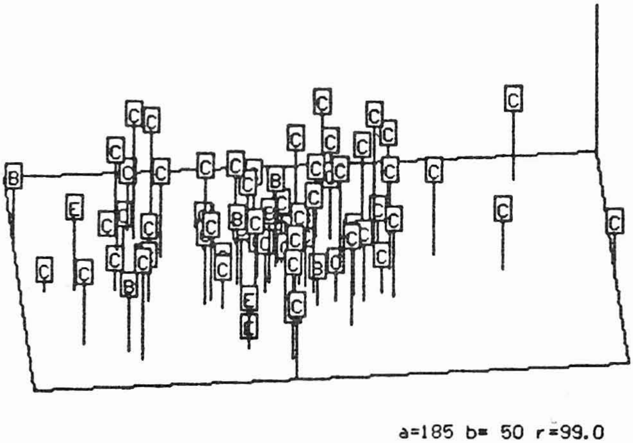

FIGURE 4. —Representation of adult (age classes 2 and 3) specimens of *Erethizon dorsatum* in space of first three principal components. Specimen symbols indicate subspecific designations (Hall, 1981): B, *bruneri;* C, *couesi*; D, *dorsatum*; E, *epixanthum*. Note lack of clusters corresponding to subspecific identities.

and slender in subadults when compared to older animals), except for widening of the zygomatic arches. Zygomatic breadth in subadults is significantly less than in adults, and the measurements reflecting rostral growth (rostral breadth, paired nasal-zygoma measurements) are significantly larger for adults (Appendix 2).

Migration of the developing temporalis medially up the skull roof becomes obvious, and for the first time instances where the two muscle masses meet posteriorly are found. The beginnings of a sagittal crest may be evident in advanced cases of muscle development.

Adults.—Adult porcupines are defined by the replacement of deciduous premolars by permanent teeth. Nevertheless, certain regions of the skull continue to grow through life or at least until late in life, and the resultant individual variation can be dramatic (Anderson and Rand, 1943). This is supported by the statistical distinction between young and old adults for six of the 21 characters (Appendix 2), and by extremely large coefficients of variation in old adults of those characters judged to grow through life. Sutton (1972) observed that nasal sutures begin to close posteriorly, but are seldom completely fused. Old adults average larger than young adults for all characters except the toothrow measurements, and are significantly larger for measurements that reflect an increase in rostral length (maxillary diastema and anterior nasal junction to posterior ends of zygomatic arches (Appendix 2). Width of the nasals continues to increase posteriorly in older adults (and significantly so for the left nasal), accounting for the wide range in measurements of nasal widths, large coefficients of variation, and a broad and distally stout rostrum when viewed dorsally. Sutton (1972) and Anderson and Rand (1943) correctly attributed much individual cranial variation in adults to this continued widening of the rostrum and lengthening of the skull.

The cheekteeth of porcupines are brachyodont, and wider at the midsection than at either the alveolar margin or at the occlusal surface of an unworn tooth. The shorter toothrows of juveniles easily attributed to the lack of a complete dental battery. Old adults (age class 3 individuals) are defined somewhat arbitrarily as exhibiting excessive toothwear. Adjacent cheekteeth appear always to remain in contact, regardless of age. When compared to younger adults, the toothrows of old individuals average shorter as the occlusal surface becomes worn below the widest (midsection) portion of these teeth. The fact that adjacent premolars and molars remain in contact rather than exhibiting gaps at this stage of wear indicates that the teeth continue to gather together, perhaps in response to masticatory mechanics. This phenomenon must characterize many other brachyodont taxa, and currently is being described for camelids (W. W. Dalquest, personal communication).

Vertical migration of the temporalis proceeds, in most adults, to the point where the two masses meet posteriorly and continue anteriorly, initiating the formation of sagittal crests as sites for muscle attachment.

Sexual Dimorphism

With an admittedly small reference series, Anderson and Rand (1943) described females as being less variable than males, and less pronounced in degree of development of cranial characters. We have found no basis for such a conclusion. In fact, adult females in our study exhibited higher coefficients of variation than males for all but three measurements (Table 1).

One aging trend in porcupines is the advancement medially of the marginal muscle scars of the temporalis, and the formation of a sagittal crest if the two lateral muscle masses meet along the frontal suture. If males exhibit a more rapid or pronounced migration and development of temporalis muscle mass than do females, there also is considerable overlap between the sexes. Pattern and rate of advancement of the temporalis muscle scars exhibit considerable individual variation (Fig. 3). Both sexes may be marked by sagittal crests, but in at least one extremely old adult (sex unknown), margins of muscle scars were less advanced than in most subadults.

Asymmetry

Van Valen (1962) provided a useful introduction into the phenomenon of character asymmetry in animals. The most prevalent types of asymmetry (Van Valen, 1962; Leamy, 1984) are directional (means of the sides differ) and fluctuating (random differences between sides, but with nearly equal means). While fluctuating asymmetry probably typifies all bilateral characters, it seldom is developed to the degree that it is readily visible. Most examples of directional asymmetry are of soft anatomical features, and for cranial characters only the distorted skulls of cetaceans (see Yurick and Gaskin, 1987, 1988) seem consistently to provide good examples in mammals.

Even for an animal so large that asymmetry may be readily visible, cranial asymmetry in *Erethizon dorsatum* is pronounced. Certain asymmetrical aspects of the skull already have been qualitatively described by inspection (deviation from midline of the sagittal crest—Stangl et al., 1988; differential development of zygomatic arches—Sutton, 1972). Asymmetry of the sagittal crest is well illustrated in the figures of Hall (1981:851—drawing) and Jackson (1961:271—photograph).

Sampling error, resulting from a small sample, led Stangl et al. (1988) to suggest directional asymmetry of the sagittal crest. Deviation may occur randomly to the left or right, and less commonly may assume a sigmoid configuration. However, Sutton (1972) noted that the left zygomatic arch extended further posteriorly than did the right. This is the only supported instance of directional asymmetry in porcupines, but in our study was restricted to males (posterior nasal junction to posterior end of zygomatic arch, $P = 0.01855$).

Factors Influencing Variability

Several studies have indicated that environmental stress (for example, less than optimum habitat or forage) is correlated with a higher degree of fluctuating asymmetry in a variety of species (for example, muskrats—Pankakoski et al., 1987; humans—Bailit et al., 1970; and three species of fishes—Valentine et al., 1973). Such a coincidence would be difficult to test with porcupines from our study area. We found negligible differentiation between western (New Mexico and Trans-Pecos Texas) populations, where favored habitat is extensive and uniform, and eastern populations, which are from the southeastern periphery of the range of the species (and, therefore, presumably marginal habitat), and where they are less common than farther west. Only directional asymmetry for a single character (mandibular toothrow, $P = 0.038$) in western porcupines was noted. Suitable habitat in Oklahoma and eastern Texas is mostly restricted to canyons and waterways, but individuals may wander widely, and are often found in unexpected circumstances. In fact, recent evidence (Caire et al., 1990; Stangl et al., 1989) reveals a southeastern expansion of the range. The influence of environmental factors on porcupine asymmetry clearly cannot be resolved here.

The genetic basis for fluctuating asymmetry in house mice (Bader, 1965; Howe and Parsons, 1967; Leamy, 1984; has been examined for a variety of characters, and with conflicting results. However, nothing is known of genetic variability in porcupines (Woods, 1973). Nevertheless, bone is a living, dynamic tissue that may respond to environmental pressures placed upon it. Masticatory musculature of porcupines is strongly developed and compared to other hystricognathus rodents, the temporalis is particularly massive (Woods, 1972). Unequal development of the muscle could clearly account for distortion over time of a skull, as has been remarked on in the case of a gopher (Vaughan, 1961). Even in juvenile animals, muscle scars of the powerful temporalis may be remarkably asymmetrical (Fig. 3), and the sagittal crests of older animals often are deviated to one side—see figures in Hall (1981), Jackson (1961), and Stangl et al. (1988), probably in response to unequal muscle development. Deviation of the sagittal crest tends to become more common and pronounced with age. About half of the young adults exhibited noticeable deviation of the crest, whereas nearly all of the oldest age class individuals did so.

The well-developed masseter inserts along the rostrum and zygomatic arch, and together with the temporalis may affect skull morphology in a complex fashion. A comparative assessment of complementary muscle masses used in mastication would be enlightening.

Although there may be a developmental basis for differential development of jaw musculature, preferential use of one side while chewing might also lead to unequal muscle development (left- or right-jawed). The grinding movement in porcupines has been described by Maynard Smith and Savage (1959) as mostly fore and aft, although soft foods might be crushed by lateral movement of the jaws. Woods (1972) speculated that chewing must be mostly on one side or the other. Such behavior might be expected to result in heavier wear of cheekteeth on the favored side, although the preferred browsing habits indicated by the brachyodont dentition of porcupines would not be expected to rapidly wear teeth. Differences in crown height of cheekteeth on left and right sides of individual specimens appeared negligible, with the exception of an old, unsexed specimen, in which heavily worn dentition demonstrated noticeably greater wear on the left side. However, such factors in cleaned skulls as loose or missing teeth, and differential erosion or chipping of alveolar margins did not allow a sufficient sample size with consistently repeatable measurements to further evaluate this possible causative factor.

Geographic Variation and Systematic Implications

The range of *Erethizon dorsatum* is vast, encompassing much of North America (Hall, 1981), and recent evidence (Caire et al., 1989; Stangl et al., 1989) indicates a southeastern expansion. Descriptions of six nominal races are based on geographically distant localities (Nebraska, *E. d.*

bruneri; Arizona, *E. d. couesi*; eastern Canada, *E. d. dorsatum*; California, *E. d. epixanthum*; Alaska, *E. d. myops*; and British Columbia, *E. d. nigrescens*), and from times (1916, 1897, 1758, 1835, 1900, and 1903, respectively) when little comparative material and specimens from intervening parts of the range were available. Additionally, not all descriptions were based upon complete or adult specimens. The holotype of *E. d. couesi* was described as "not quite adult . . . skull Grade B" by Poole and Schantz (1942). Grade B skulls were defined by those authors as "sufficiently defective to lack some essential characters."

Even today, little is known of geographic variation in the species (Jones et al., 1988). Sutton (1972) remarked that male porcupines tended to have larger frontal bulges over the orbits, and that this trend was particularly well developed in *E. d. epixanthum*. However, the only published attempt to detail geographic variation and the status of porcupine subspecies was that of Anderson and Rand (1943), who synonomized the two existing nominal species (*dorsatum* and *epixanthum*) under *Erethizon dorsatum*, and then proceeded to characterize the five subspecies thought to occur in Canada. With an admittedly small sample (71 skulls and 63 skins), their diagnoses of what they considered valid taxa were based on pelage color, skull contour (sagittal and occipital crests, bulging or swelling of frontals, depression of frontal-parietal region), nasal shape, and premaxillary ridge. They concluded that these characters were not clinal (although noted that few intermediate samples were available), and that some populations were noticeably more variable than others.

Ahlberg (1969), in a quantitative evaluation of specimens from through-out the range of *Erethizon dorsatum*, concluded by recognizing only two subspecies: *E. d. dorsatum* (including *picinum*) and *E. d. epixanthum* (including *bruneri, couesi, nigrescens,* and *myops*). Under this classification, all specimens from our study region would represent the subspecies *E. d. epixanthum*.

Three nominal subspecies of the porcupine were mapped by Hall (1981) as occurring in our study area—*Erethizon dorsatum couesi* to the west and southwest, *E. d. bruneri* in Oklahoma, eastern Colorado, and the Texas Panhandle, and *E. d. epixanthum* in northeastern New Mexico and central Colorado (Fig. 1). The results of our principal components analysis (Fig. 4) reveal no suggestion of morphometric pattern coinciding with subspecific designations in any of the first three components. We agree with Ahlberg (1969) that the presently recognized subspecies *E. d. bruneri* and *E. d. couesi* are not morhpometrically distinct from *E. d. epixanthum* (*sensu* Hall, 1981). Based on this, and the wide degree of apparently nongeographic variability in pelage characters as well as mensural characters, we conclude that populations presently recognized as *E. d. bruneri* and *E. d. couesi* should be synonomized under *E. d.*

epixanthum. We suspect that the remainder of Ahlberg's (1969) taxonomic conclusions also will be supported by future work.

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APPENDIX 1.—Following is a listing of localities for specimens of *Erethizon dorsatum* examined for this study. Counties within each state are ordered alphabetically. Localities within counties are not presented in any particular order. Acronyms for repositories are given in the Methods and Materials section.

ARIZONA.—No specific locality, 1 (MWSU). *Apache Co.*: no specific locality, 1 (MWSU). COLORADO.—*Baca Co.*: 14 mi. N Springfield, 1 (TCWC). *Duray Co.*: 15 mi. S Ridgeway, 2 (MWSU). *Park Co.*: 2.5 mi. W Fairplay, 1 (TCWC). IDAHO.—*Bannock Co.*: Pocatello, 1 (TCWC). NEW MEXICO.—No specific locality, 2 (1 MSB, 1 OSU). *Bernalillo Co.*: University of New Mexico campus, Albuquerque, 1 (MSB); no specific locality, 1 (MSB). *Chaves Co.*: Bitterlake National Wildlife Refuge, 2 (MSB); no specific locality, 1 (MSB). *Colfax Co.*: no specific locality, 1. *Dona Ana Co.*: 23 mi. E El Paso, 1 (UTEP); no specific locality, 1 (UTEP). *Eddy Co.*: Dark Canyon, 1 (MSB); Rocky Arroyo, 2 (UTEP). *Grant Co.*: Upper Black Hawk Canyon, T. 18 S, R. 16 W, sec. 21, 1 (UTEP). *Hidalgo Co.*: Doubtful Canyon, 8 mi. N, 2 mi. W Steins, 1 (MSB); E San Luis Pass, 1 (MSB). *Lea Co.*: Hobbs, 1 (MWSU). *Lincoln Co.*: 8 mi. SSW Corona, 1 (MWSU). *McKinley Co.*: 3 mi. E, 2 mi. S Estrella, 1 (MSB). *Otero Co.*: 29 mi. E Cloudcroft, 1 (TTU); T. 20 S, R. 12 E, sec. 17, 1 (UTEP); Hwy. 506 at McGregor Boundary, 1 (UTEP). *Rio Arriba Co.*: Sargeant Ranch, Chama, 1 (MSB); 10.5 mi. E Chama, 1 (MSB). *San Juan Co.*: T. 32 N, R. 6 W, sec. 15, 1 (MSB); T. 31 N, R. 7 W, sec. 20, 1 (MSB); no specific locality, 3 (MSB). *Santa Fe Co.*: no specific locality, 1 (MSB). *Socorro Co.*: 2 mi. E Baldy Crossing, Magdalena Mtns., 1 (MSB). *Taos Co.*: 4 mi. NE Tres Ritos, 1 (MSB). *Torrance Co.*: 10 mi. E Clines Corner on I-40, 1 (OSU); 25 mi. W Clines Corner, 1 (MWSU); 7 mi. W Morarity, 1 (MSB); 2 mi. S, 3 mi. W Monzano, 1 (MSB); New Canyon, Monzano Mtns., 1 (MSB); 4 mi. NE Corona, 1 (MSB). *Valencia Co.*: Mirabal Spring, Mount Taylor, 1 (MSB). OKLAHOMA.—No specific locality, 1 (OSU). *Cimarron Co.*: T. 5 N, R. 2 E, sec. 10, 1 (OU); 6 mi. N Kenton, 1 (OSU); 4 mi. N Kenton, 1, (OSU); 1.1 mi. E Kenton, 1 (MWSU); SE Kenton, 1; (OU); 10 mi. N Boise City, 1 (OSU); no specific locality, 1 (OSU). *Ellis Co.* Fargo, 1 (OU). *Garvin Co.*: 3 mi. W Hennipen, 1 (OSU). *Latimer Co.*: near Wilburton, 1 (OSU). *Major Co.*: 1.3 mi. W Cheater, 1 (OSU). *Roger Mills Co.*: 5.2 mi. W Cheyenne, 1 (OSU). SOUTH DAKOTA.—*Stanley Co.*: 4 mi. S, 11.5 mi. E Ft. Pierre, 1 (TTU). TEXAS.—No specific locality, 1 (TTU). *Archer Co.*: 15 mi. N Archer City, 1 (MWSU). *Baylor Co.*: 5 mi. S Seymour, 1 (MWSU). *Brewster Co.*: 2.5 mi. W Marathon, 1 (TTU); 3 mi. W Alpine, 1 (TCWC); 2.7 mi. S Alpine, 1 (UTEP). *Childress Co.*: 12 mi. N Childress, 1 (MWSU). *Culberson Co.*: Guadalupe Mountains National Park, 6 (3 TTU, 2 UTEP, 1 TCWC). *Dickens Co.*: 10 mi. S, 14 mi. E Dickens, 1 (TTU). *El Paso Co.*: UTEP campus, El Paso, 2 (UTEP); Hueco Tanks, 1 (UTEP); 7.5 mi. N Hueco Tanks, 1 (UTEP); vicinity Hueco Tanks, 1 (UTEP); near jct. Transmit Rd. and entrance to Tom Mays Park, 1 (UTEP); Transmit Rd., near I-10, 1 (UTEP); Transmit Rd., 2.2 mi. E I-10, 1 (UTEP). *Hardeman Co.*: Quanah, 1 (MWSU). *Jeff Davis Co.*: 36 mi. N Fort Davis, 1 (TCWC); 9 mi. NE Fort Davis, 1 (TTU); 9 km. N, 9.5 km. E Fort Davis, 1 (TTU); Madera Canyon Campgrounds, 1 (TTU); 2 mi. NW Fort Davis, 1 (UTEP); 8 mi. NW Alpine, 1 (TTU); 1 mi. ESE Mt. Livermore, 1 (UTEP); McDonald Observatory, 1 (MWSU); Davis Mountains State Park, 1 (TTU); no specific locality, 1 (TTU). *Kimble Co.*: 7 mi. E Junction, 1 (MWSU). *Lubbock Co.*: Lubbock, 2 (TTU); 10 mi. W Lubbock, 1 (TTU). *Mason Co.*: no specific locality, 1 (TCWC). *Pecos Co..*: 11.4 mi. N, 19.8 mi. E Marathon, 1 (TTU). *Presidio Co.*: 80 mi. SW Marfa, 1 (TCWC); Clay Miller Ranch, Sierra Vieja, 1 (TTU); Bandera Mesa, 1 (MWSU); 5 mi. NE Bandera Mesa, 1 (MWSU). *Sutton Co.*: 21 mi. SE Sonora, 1 (MWSU). *Val Verde Co.*: 12 mi. N Comstock, 2 (1 MWSU, 1 TCWC). *Wichita Co.*: 9 mi. W Iowa Park, 1 (MWSU); Wichita Falls, 1 (MWSU). WISCONSIN.—*Oconto Co.*: 5 mi. E Mountain Bear Paw Scout Camp, 3 (TTU). WYOMING.—*Johnson Co.*: 12 mi. S, 9.5 mi. W Buffalo, 1 (TTU); 12 mi. W Lake Village, Yellowstone National Park, 1 (MWSU).

APPENDIX 2. —Variation by age and sex in cranial measurements (in mm) of *Erethizon dorsatum* from New Mexico, Oklahoma, and Texas. Two-way (sex X age class) ANOVAs show all characters to exhibit significant age-class variation ($P < 0.001$ for all characters except right and left mandibular diastemas, where $P < 0.05$), and one character (least rostral breadth) to exhibit an interactive effect ($P < 0.05$). For each character, the third group ("all") reports a one-way ANOVA (age) for all specimens, including those of unknown sex. For all characters, the one-way ANOVA was significant at $P < 0.001$.

Sex and age class(N)	Mean ± SE	Range	CV	Duncan's Test[2]
	Greatest length of left bulla			
Male				
3 (3)	22.33 ± 0.93	20.55-23.55	7.24	
2 (11)	21.39 ± 0.33	19.50-22.55	5.16	
1 (4)	21.26 ± 0.41	20.35-22.10	3.88	
0 (4)	16.26 ± 0.67	15.10-18.18	8.22	
Female				
3 (6)	21.23 ± 1.07	18.80-24.82	12.32	
2 (10)	20.57 ± 0.45	18.70-23.00	6.96	
1 (6)	20.22 ± 0.94	16.45-22.95	11.43	
0 (10)	18.33 ± 0.52	14.90-20.60	8.97	
All				
3 (17)	21.93 ± 0.51	18.80-24.82	9.51	
2 (50)	21.53 ± 0.24	18.68-25.65	7.79	
1 (18)	20.77 ± 0.38	16.45-22.95	7.81	
0 (16)	17.68 ± 0.43	14.90-20.60	9.68	
	Greatest length of right bulla			
Male				
3 (3)	22.35 ± 1.14	20.40-24.35	8.84	
2 (11)	21.64 ± 0.42	19.85-23.80	6.50	
1 (4)	21.13 ±0.48	20.05-22.15	4.58	
0 (4)	16.31 ± 0.74	15.00-18.43	9.09	
Female				
3 (6)	21.28 ± 0.92	19.20-24.10	10.59	
2 (10)	20.70 ± 0.49	19.07-23.75	7.46	
1 (6)	20.24 ± 1.01	16.45-22.85	12.19	
0 (9)	18.59 ± 0.43	16.85-20.60	6.94	
All				
3 (19)	22.24 ± 0.46	19.20-24.75	9.00	
2 (50)	21.57 ± 0.25	18.25-25.65	8.03	
1 (18)	20.74 ± 0.42	16.45-23.20	8.51	
0 (15)	17.86 ± 0.41	15.00-20.60	8.78	
	Length of left maxillary toothrow *			
Male				
3 (3)	25.85 ± 0.53	25.05-26.85	3.55	
2 (10)	26.41 ± 0.39	24.35-28.00	4.71	
1 (4)	24.67 ± 0.64	22.75-25.40	5.21	
0 (3)	19.95 ± 0.45	19.15-20.70	3.89	

APPENDIX 2. Continued

Female			
3 (6)	25.63 ± 0.74	22.30-27.35	7.11
2 (10)	25.76 ± 0.37	24.60-27.60	4.53
1 (7)	24.60 ± 0.55	22.90-26.80	5.96
0 (11)	21.09 ± 0.53	18.35-23.85	8.36
All			
3 (19)	25.13 ± 0.35	22.30-27.35	6.12
2 (52)	25.94 ± 0.15	23.55-28.00	4.25
1 (21)	24.23 ± 0.31	21.50-26.80	5.95
0 (16)	20.94 ± 0.40	18.35-23.85	7.66
	Length of right maxillary toothrow *		
Male			
3 (3)	25.72 ± 0.66	24.55-26.85	4.47
2 (11)	26.35 ± 0.34	24.60-27.80	4.29
1 (4)	24.67 ± 0.64	22.75-25.40	5.21
0 (4)	20.46 ± 0.60	19.15-22.00	5.89
Female			
3 (6)	25.47 ± 0.69	22.30-27.35	6.66
2 (10)	25.74 ± 0.33	24.60-27.60	4.00
1 (7)	24.52 ± 0.52	22.90-26.80	5.59
0 (11)	21.09 ± 0.54	18.35-23.85	8.50
All			
3 (20)	25.21 ± 0.36	22.30-27.85	6.32
2 (53)	25.94 ± 0.15	23.55-27.80	4.09
1 (21)	24.20 ± 0.31	21.50-26.80	5.88
0 (17)	20.99 ± 0.39	18.35-23.85	7.58
	Length of left mandibular toothrow		
Male			
3 (3)	28.98 ± 0.09	28.85-29.15	0.53
2 (11)	30.48 ± 0.40	28.85-32.55	4.39
1 (3)	28.85 ± 0.84	27.20-29.90	5.01
0 (4)	22.99 ± 1.55	20.00-26.50	13.52
Female			
3 (6)	29.73 ± 0.80	26.90-33.00	6.63
2 (10)	29.74 ± 0.49	27.45-32.65	5.20
1 (7)	28.91 ± 0.50	27.20-30.20	4.24
0 (11)	23.48 ± 0.95	17.95-27.75	13.48
All			
3 (17)	29.39 ± 0.41	26.35-33.00	5.72
2 (39)	29.96 ± 0.20	27.45-32.65	4.21
1 (18)	28.33 ± 0.42	24.10-30.70	6.25
0 (16)	23.26 ± 0.71	17.95-27.75	12.57

APPENDIX 2. Continued

	Length of right mandibular toothrow *		
Male			
3 (3)	28.97 ± 0.10	28.80-29.15	0.61
2 (11)	30.51 ± 0.42	28.90-32.85	4.52
1 (3)	28.87 ± 0.84	27.20-29.90	5.05
0 (3)	21.88 ± 1.55	20.00-24.95	12.24
Female			
3 (6)	29.88 ± 0.90	27.20-33.85	7.35
2 (9)	29.71 ± 0.55	27.45-32.65	5.51
1 (6)	28.93 ± 0.46	27.10-30.05	3.93
0 (11)	23.66 ± 0.98	17.95-28.15	13.79
All			
3 (16)	29.46 ± 0.45	26.40-33.85	6.16
2 (38)	29.95 ± 0.21	27.45-32.85	4.34
1 (18)	28.33 ± 0.41	24.10-30.70	6.21
0 (16)	23.19 ± 0.75	17.95-28.15	12.92
	Length of left maxillary diastema **		
Male			
3 (3)	33.62 ± 1.32	31.00-35.20	6.79
2 (9)	29.57 ± 0.82	26.55-33.40	8.27
1 (4)	27.90 ± 1.12	26.15-31.15	8.03
0 (4)	16.29 ± 0.82	14.55-18.20	10.84
Female			
3 (6)	29.46 ± 2.19	22.85-35.40	18.15
2 (8)	27.32 ± 1.62	21.65-36.35	16.77
1 (6)	24.42 ± 0.64	23.50-27.60	6.18
0 (11)	18.63 ± 0.91	12.50-23.30	16.16
All			
3 (19)	30.49 ± 0.99	22.85-35.45	14.13
2 (45)	28.08 ± 0.51	21.65-36.40	12.11
1 (18)	25.66 ± 0.64	20.40-31.15	10.53
0 (17)	18.09 ± 0.65	12.50-23.30	14.86
	Length of right maxillary diastema **		
Male			
3 (3)	33.57 ± 1.29	31.00-35.10	6.68
2 (9)	29.55 ± 0.81	26.55-33.40	8.22
1 (4)	27.90 ± 1.12	26.15-31.15	8.03
0 (4)	16.22 ± 0.77	14.55-17.95	9.46
Female			
3 (6)	29.43 ± 2.19	22.85-35.70	18.22
2 (9)	27.23 ± 1.42	21.94-36.35	15.62
1 (6)	25.46 ± 0.61	23.50-27.60	5.88
0 (11)	18.67 ± 0.92	12.50-23.60	16.27

APPENDIX 2. Continued

All			
3 (19)	30.50 ± 0.98	22.85-35.70	14.06
2 (45)	27.94 ± 0.50	21.94-36.40	12.01
1 (18)	26.66 ± 0.64	20.10-31.15	10.61
0 (17)	18.14 ± 0.66	12.50-23.60	15.04
	Length of left mandibular diastema		
Male			
3 (3)	21.13 ± 0.22	20.70-21.40	1.79
2 (10)	17.10 ± 0.69	13.50-21.20	12.72
1 (3)	17.08 ± 0.74	16.00-18.50	7.51
0 (4)	9.78 ± 0.53	8.75-11.10	10.89
Female			
3 (6)	18.23 ± 1.34	14.85-22.50	17.95
2 (10)	16.03 ± 0.65	12.87-19.65	12.73
1 (6)	14.90 ± 0.94	12.90-19.30	15.43
0 (11)	11.14 ± 0.53	7.95-13.80	15.86
All			
3 (17)	19.21 ± 0.60	14.85-22.50	12.91
2 (37)	16.97 ± 0.34	12.87-22.25	12.19
1 (18)	14.92 ± 0.43	12.90-19.30	12.36
0 (17)	10.86 ± 0.39	7.95-13.80	14.78
	Length of right mandibular diastema		
Male			
3 (3)	21.42 ± 0.39	20.75-22.10	3.15
2 (10)	17.00 ± 0.74	12.75-21.20	13.74
1 (3)	17.08 ± 0.74	16.00-18.50	7.51
0 (3)	9.33 ± 0.42	8.75-10.15	7.81
Female			
3 (6)	18.27 ± 1.31	14.90-22.45	17.55
2 (8)	15.93 ± 0.82	12.87-19.65	14.60
1 (6)	15.17 ± 0.90	12.90-19.30	14.57
0 (11)	11.15 ± 0.53	7.95-13.80	15.80
All			
3 (16	19.17 ± 0.63	14.90-22.45	13.15
2 (35)	16.98 ± 0.37	12.75-22.25	12.77
1 (17)	15.15 ± 0.44	12.90-19.30	11.88
0 (16)	10.85 ± 0.41	7.95-13.80	15.24
	Greatest width of left nasal		
Male			
3 (3)	12.57 ± 0.67	11.50-13.80	9.22
2 (8)	11.29 ± 0.51	9.05-13.70	12.69
1 (4)	10.81 ± 0.46	9.45-11.45	8.49
0 (4)	7.83 ± 0.44	7.00- 9.03	11.11

APPENDIX 2. Continued

Female			
3 (6)	11.91 ± 0.48	10.10-13.60	9.93
2 (10)	11.24 ± 0.48	8.00-13.25	13.62
1 (6)	10.81 ± 0.33	9.85-11.95	7.55
0 (11)	8.50 ± 0.32	6.80-10.15	12.50
All			
3 (18)	12.20 ± 0.31	9.62-13.85	10.76
2 (40)	11.33 ± 0.22	8.00-13.90	12.01
1 (19)	10.63 ± 0.18	9.45-11.95	7.22
0 (17)	8.41 ± 0.26	6.80-10.15	12.52
	Greatest width of right nasal		
Male			
3 (2)	12.70 ± 1.20	11.50-13.90	13.36
2 (9)	11.09 ± 0.50	8.95-13.70	13.42
1 (4)	11.05 ± 0.38	9.95-11.55	6.85
0 (4)	7.85 ± 0.48	7.00- 9.20	12.30
Female			
3 (6)	11.88 ± 0.49	10.05-13.60	10.13
2 (10)	11.19 ± 0.47	8.00-13.25	13.40
1 (7)	10.79 ± 0.32	9.90-11.65	7.32
0 (11)	8.43 ± 0.33	6.80-10.15	12.80
All			
3 (17)	12.08 ± 0.38	8.62-13.90	12.97
2 (41)	11.29 ± 0.22	8.00-13.90	12.24
1 (10)	10.71 ± 0.17	9.45-11.65	6.87
0 (17)	8.38 ± 0.26	6.80-10.15	12.85
	Greatest distance between anterior nasal junction and left zygomatic arch **		
Male			
3 (3)	76.68 ± 0.50	76.00-77.65	1.12
2 (8)	71.92 ± 0.76	70.30-76.05	2.98
1 (3)	69.62 ± 2.72	66.25-75.00	6.77
0 (4)	49.81 ± 2.62	43.30-55.27	10.51
Female			
3 (6)	70.99 ± 2.05	64.90-78.62	7.07
2 (8)	68.59 ± 1.57	61.00-76.00	6.37
1 (6)	65.45 ± 2.09	60.20-75.30	7.69
0 (10)	53.03 ± 1.64	43.00-60.55	9.78
All			
3 (16)	72.52 ± 1.02	64.90-78.62	5.62
2 (38)	70.60 ± 0.60	61.00-78.10	5.20
1 (17)	66.20 ± 1.19	55.90-75.30	7.41
0 (16)	55.63 ± 1.28	43.00-60.55	9.74

APPENDIX 2. Continued

	Greatest distance between anterior nasal junction and right zygomatic arch **		
Male			
3 (3)	76.63 ± 0.82	75.05-77.80	1.86
2 (7)	72.23 ± 0.96	69.90-76.50	3.51
1 (4)	69.35 ± 2.85	65.90-75.00	7.11
0 (4)	49.63 ± 2.78	42.50-55.27	11.21
Female			
3 (6)	70.76 ± 1.87	65.50-77.25	6.47
2 (9)	68.62 ± 1.72	60.50-75.70	7.53
1 (6)	67.06 ± 2.08	60.10-75.00	7.60
0 (11)	53.82 ± 1.79	42.65-63.07	11.03
All			
3 (16)	72.49 ± 0.97	65.50-77.80	5.34
2 (39)	70.13 ± 0.63	60.50-78.15	5.58
1 (18)	66.08 ± 1.21	55.40-75.00	7.76
0 (17)	53.13 ± 1.40	42.50-63.07	10.84
	Greatest distance between posterior nasal junction and left zygomatic arch		
Male			
3 (3)	50.12 ± 1.13	47.85-51.30	3.92
2 (9)	47.45 ± 0.60	44.30-50.00	3.80
1 (4)	43.71 ± 2.14	40.50-49.65	9.77
0 (4)	36.66 ± 1.80	32.70-41.45	9.85
Female			
3 (4)	48.89 ± 2.15	42.65-51.90	8.81
2 (8)	46.69 ± 1.30	39.85-51.55	7.86
1 (6)	44.65 ± 1.34	40.55-48.50	7.37
0 (10)	37.86 ± 0.79	32.45-41.40	6.62
All			
3 (14)	49.59 ± 1.03	41.05-53.75	7.74
2 (44)	47.50 ± 0.43	39.85-53.60	6.05
1 (19)	44.19 ± 0.79	39.45-50.75	7.79
0 (16)	38.05 ± 0.74	32.45-42.60	7.83
	Greatest distance between posterior nasal junction and right zygomatic arch		
Male			
3 (3)	49.80 ± 1.12	47.70-51.50	3.88
2 (8)	47.06 ± 0.84	43.25-50.05	5.05
1 (4)	43.66 ± 2.16	40.50-49.65	9.89
0 (4)	36.43 ± 1.64	32.60-40.60	9.00
Female			
3 (4)	48.98 ± 2.08	43.25-52.45	8.49
2 (9)	45.89 ± 1.34	38.80-51.10	8.78
1 (6)	45.28 ± 1.24	40.60-48.55	6.69
0 (11)	38.26 ± 0.86	33.05-42.70	7.47

APPENDIX 2. Continued

All			
3 (15)	49.35 ± 0.88	43.25-52.95	6.90
2 (45)	47.23 ± 0.46	38.80-54.20	6.59
1 (18)	44.26 ± 0.84	39.25-50.90	8.04
0 (17)	38.25 ± 0.76	32.60-42.75	8.14
	Greatest post-palatal length **		
Male			
3 (3)	44.02 ± 0.82	43.20-45.65	3.21
2 (9)	41.36 ± 0.86	37.45-46.85	6.23
1 (4)	40.90 ± 1.04	39.15-43.90	5.09
0 (3)	27.65 ± 2.25	24.15-31.85	14.10
Female			
3 (6)	39.00 ± 0.93	35.90-41.60	5.82
2 (9)	39.09 ± 1.42	32.80-46.10	10.89
1 (6)	37.97 ± 1.45	34.95-44.65	9.35
0 (7)	30.92 ± 0.95	28.55-34.40	7.55
All			
3 (19)	40.81 ± 0.64	35.90-45.65	6.88
2 (47)	39.94 ± 0.55	29.85-50.20	9.44
1 (18)	38.14 ± 0.86	28.30-44.65	9.56
0 (11)	30.13 ± 0.87	24.15-34.40	9.61
	Least rostral breadth		
Male			
3 (3)	22.42 ± 0.74	21.40-23.85	5.70
2 (8)	20.99 ± 0.82	18.30-26.05	11.03
1 (4)	21.75 ± 0.47	20.80-23.05	4.35
0 (4)	13.21 ± 1.55	9.10-16.55	23.47
Female			
3 (6)	21.98 ± 1.01	18.75-25.40	11.20
2 (10)	20.58 ± 0.58	18.10-23.25	8.98
1 (6)	20.25 ± 0.74	17.15-22.25	8.95
0 (11)	17.00 ± 0.53	13.75-19.30	10.35
All			
3 (19)	22.34 ± 0.52	18.60-26.45	10.14
2 (43)	21.22 ± 0.28	18.10-26.60	8.78
1 (19)	20.17 ± 0.35	17.15-23.05	7.56
0 (17)	16.23 ± 0.65	9.10-19.70	16.51
	Least infraorbital breadth		
Male			
3 (3)	30.47 ± 2.33	27.30-35.00	13.22
2 (10)	30.38 ± 1.46	22.30-37.10	15.15
1 (4)	28.66 ± 1.14	26.10-31.65	7.96
0 (4)	22.69 ± 1.17	20.65-25.60	10.30

APPENDIX 2. Continued

Female			
3 (5)	28.70 ± 1.31	25.60-32.30	10.24
2 (9)	28.46 ± 0.86	25.20-33.45	9.03
1 (6)	29.04 ± 0.73	25.90-30.85	6.14
0 (11)	23.69 ± 0.53	21.20-27.80	7.38
All			
3 (19)	30.33 ± 0.65	25.60-37.80	9.33
2 (46)	29.89 ± 0.46	22.30-37.10	10.35
1 (19)	27.99 ± 0.49	23.70-31.65	7.67
0 (17)	23.69 ± 0.51	20.65-28.00	8.81
		Greatest zygomatic width *	
Male			
3 (3)	69.93 ± 0.89	68.95-71.70	2.19
2 (8)	71.30 ± 0.65	69.10-74.10	2.58
1 (4)	67.90 ± 1.61	64.80-72.35	4.74
0 (4)	49.86 ± 3.59	42.80-58.80	14.41
Female			
3 (6)	69.70 ± 2.52	61.00-78.40	8.85
2 (7)	66.84 ± 1.75	59.10-73.10	6.91
1 (6)	64.67 ± 1.89	57.85-69.80	7.14
0 (10)	54.50 ± 1.53	44.70-60.75	8.90
All			
3 (16)	70.40 ± 1.01	61.00-78.40	5.73
2 (40)	68.48 ± 0.58	59.10-74.65	5.35
1 (20)	64.50 ± 0.93	57.40-72.35	6.43
0 (16)	53.95 ± 1.46	42.80-62.50	10.86
		Greatest mastoid breadth	
Male			
3 (3)	46.95 ± 1.88	44.90-50.70	6.93
2 (10)	45.19 ± 0.98	40.60-48.75	6.85
1 (4)	43.80 ± 0.74	42.35-45.45	3.40
0 (4)	36.53 ± 1.99	32.45-41.50	10.88
Female			
3 (6)	43.32 ± 2.15	39.50-52.40	11.64
2 (8)	42.94 ± 1.11	37.80-47.40	7.31
1 (6)	42.58 ± 1.22	39.65-47.70	7.02
0 (7)	39.59 ± 1.12	34.75-43.30	7.46
All			
3 (19)	45.72 ± 1.07	39.50-57.95	10.22
2 (46)	43.60 ± 0.40	37.80-48.75	6.22
1 (16)	42.47 ± 0.57	39.55-47.70	5.41
0 (13)	38.88 ± 1.02	32.45-44.72	9.43

1—From the two-way (sex X age) ANOVA, probability ranges are given for significant differences between sexes: * = 0.05 > P > 0.01; ** = 0.01 > P > 0.001.

2—Results are given for Duncan's multiple range test for age class. Those age classes grouped together are not significantly different ($\alpha = 0.05$).