

# Size and Shape of the Skull of White-tailed Deer from the Eastern and Midwestern United States

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## ABSTRACT

We examined variation in the size and shape of 387 adult, female white-tailed deer (*Odocoileus virginianus*) skulls from the eastern and midwestern United States using a sheared principal components analysis. Within-group variation in size was significant, resulting in little separation of groups on this axis. Analysis of skull shape suggested greatest separation of those groups with more biogeographically divergent backgrounds, based upon the current geographic distance between some populations and the history of relocations of others. Established populations may have retained morphological characteristics of stock introduced into these areas.

**Key Words:** *Odocoileus*, crania, morphometry

## INTRODUCTION

The study of geographic variation is central to biogeography and the study of speciation. This information is also of importance to biologists interested in qualitative differences between or among populations and the reasons for such differences. The elucidation of geographic patterns of phenotypic and genetic variability allow the formation and testing of hypotheses regarding the underlying causes of variation and ultimately the speciation process.

It has been suggested that variations in the external environment have a greater influence on size than shape (Jolicouer and Mosiman 1960; Rees 1969a, 1970). Thus shape should be a better predictor of genetic affinities between groups. Humphries et al. (1981:291) defined shape as the "geometry of the organism after information about position, scale, and orientation has been removed".

Rees (1969a) believed that genetic affinities among groups might be a function of geographic distance if the following conditions were met:

- 1) long occupation of the range represented by the breeding groups under consideration,

- 2) no behavioral patterns that preclude random mating among neighboring animals,
- 3) no migration of animals,
- 4) gradual environmental change throughout the range under consideration so that the effect of selection would be a regular function of distance, and,
- 5) genetic continuum throughout the range represented by the breeding groups under consideration.

Rees (1969a:96) stated that "under these conditions the geographically close groups would have greater genetic affinities than would the more distant groups, so geographic distance could be used to predict relative genetic affinities." White-tailed deer provide an interesting test of the propensity of shape to reflect genetic affinities, given their broad geographic range, history of reintroductions, and low rates of interdemec gene flow. Our objectives were to examine size and shape variation in the skull of white-tailed deer and to explore whether shape could be used to predict hypothesized genetic affinities, based on current and past geographic relationships.

## METHODS

A total of 387 adult ( $\geq 2$  years of age), female white-tailed deer skulls from 16 localities within the eastern and midwestern United States were examined (Fig. 1). Museum specimens were examined when available; otherwise crania were solicited from hunters. Restricting analyses to adult females reduced the effects of age-related variation, and removed the effects of secondary-sexual variation.

Age of specimens was determined according to tooth eruption and wear (Severinghaus 1949). Cleaned and dried crania and rami were measured with a Helios dial micrometer (0.05 mm calibration) and a Dunlap measuring board (1.0 mm calibration). Twenty standard measurements taken from each skull are listed and described in Appendix A. Collection localities and museums housing specimens are presented in Appendix B.

Data were initially examined using descriptive statistics, frequency histograms, stem and leaf plots, and scatter plots; no outliers were detected, and assumptions of normality, linearity, homoscedasticity, and homogeneity of variance-covariance matrices (Box's *M*) were met. Specimens were grouped by collection locality. A principal components analysis was used to examine within-group, and subsequently among-group, variation and to examine relationships among variables. Principal components were factored from the covariance matrix of morphometric characters as suggested by Bookstein et al. (1985). The second and third components were sheared to remove the overall size effects, using a program designed by D. L. Swofford of the Smithsonian Institute. Shearing involves removing size using coefficients derived by regressing size on principal components centered by group; the residuals approximate a shape discriminating factor uncorrelated with size (Humphries et al. 1981).

According to Thorpe (1983) and others, interpreting ordinations using large samples can be misleading, given a large degree of character variation which might mask biogeographic patterns. Following Chernoff (1982) and Matthews (1987), 2 sets of 5 localities were chosen randomly, with the stipulation that no more than 2 localities from the same subspecies, or from within Illinois, be included within the same set. Each set

was then subjected to a sheared principal components analysis to explore whether localities could be distinguished in principal component space. The degree of overlap between groups was determined using a dot grid, where the number of dots in shared space / total number of dots in polygon of interest x 100 = % overlap.

## RESULTS

Factor loadings on the size, sheared PC-II, and sheared PC-III axes for the first random set of localities accounted for 52%, 12%, and 8% of the total variance, respectively (Table 1). Loadings on the size axis indicated that skeletal (i.e. non-dental cranial) characters were more important to the size component than were dental characters (length of the upper or lower molariform tooth rows). Loadings on the sheared PC-II axis contrasted the width of the nasals, and to a lesser degree width of the rostrum, with all of the length measurements (particularly length of the nasals and height of the mandible). Thus, specimens with shorter crania and mandibles had broader nasals and, to a lesser degree, broader rostra. Loadings on the sheared PC-III axis contrasted length of the incisive foramin with the width of the rostrum, postpalatal length, and width across the occipital condyles. Thus, specimens with longer incisive foramina were characterized by narrower rostra, shorter skulls posterior to the palate, and were narrower across the occipital condyles.

Ordination of individual component scores for the first random set of regions revealed much overlap between groups on the size and sheared PC-II axes (Fig. 2a). The Missouri and Tennessee samples were largely separated ( $\geq 80\%$  nonoverlap) on the combined sheared PC-II and sheared PC-III axes (Fig. 2b). The Tennessee sample exhibited varying degrees of nonoverlap with the remaining samples. The northwestern Illinois, southcentral Illinois, and Kansas samples were not distinctive. While the northwestern Illinois polygon essentially completely enclosed the Missouri specimens, the Kansas and southcentral Illinois samples overlaid the Missouri polygon by 72.7% and 57.7%, respectively.

Factor loadings on the size, sheared PC-II, and sheared PC-III axes for the second random set of localities accounted for 41%, 15%, and 9% of the total variance, respectively (Table 2). Loadings on the size axis indicated that skeletal characters were of greater importance to this axis than were dental characters. Loadings on the sheared PC-II axis contrasted the width of the nasals with all of the length measurements (particularly length of the nasals and diastema width). Thus, specimens with shorter skulls were characterized by broader nasals. Loadings on the sheared PC-III axis contrasted the length of the incisive foramin and to a lesser degree the length of the diastema with the length of the upper and lower molariform tooth rows, length of the skull posterior to the palate, height of the mandible, and 3 width measurements (width across M2M2, condylar width, and rostral width).

Ordination of individual principal component scores for the second random set of regions revealed a large degree of overlap between most groups on the size and sheared PC-II axes (Fig. 3a). The Minnesota polygon, however, coincided with only 42.6% of the South Carolina sample. Southern Illinois overlaid the Minnesota, westcentral Illinois, and Michigan samples by 42.9%, 55.7%, and 60.0%, respectively. The southern Illinois

polygon exhibited 93.6% congruence with the South Carolina sample. The westcentral Illinois, Minnesota, and Michigan polygons were not distinctive.

The South Carolina and Minnesota samples were clearly separated on the combined sheared PC-II and sheared PC-III axes (Fig. 6b). The southern Illinois polygon was shifted toward the lower right, and overlaid the Minnesota, westcentral Illinois, and Michigan samples by 34.7%, 46.9%, and 58.9%, respectively. Southern Illinois overlapped 41.2% of the South Carolina sample. The westcentral Illinois sample superimposed 86.4% and 89.0% of the Minnesota and Michigan polygons, respectively. The Michigan polygon overlapped 31.5% of the southern Illinois and 52.3% of the Minnesota samples.

## DISCUSSION

Sheared principal components analysis indicated that there was a relatively large size component to the observed variation in cranial characters. White-tailed deer exhibit a high degree of genetic and morphometric variation at the individual level (Long 1968; Smith et al. 1984), which might be expected in a large, herbivorous placental occupying a broad niche (Long 1969).

Our results suggested a length-width relationship, in that animals with longer skulls had narrower crania. McCain (1970) found a change in the proportion of skull length and width with age in the Key deer, *Odocoileus virginianus clavium*, and both McCain (1970) and Maffei et al. (1988) suggested several length-width ratios which they thought might be used to distinguish some subspecies.

We detected a large degree of separation between Tennessee and Missouri, its nearest geographic neighbor, on the sheared PC axes. This agrees with discriminant function (Levengood 1991) and UPGMA cluster analyses (Levengood 1991; Levengood et al. 1994) of the same samples. The distinctiveness of these 2 groups may reflect their genetic ancestry. The southwestern Tennessee herd was descended from introduced North Carolina, Oklahoma, and Texas stock (TN Wildl. Res. Agency 1991), while the Missouri herd was comprised of Michigan, Minnesota, and native stock (Robb 1959). Rees (1969b) found that mandible size had not decreased in a Tennessee population descended from northern (MI and WI) stock.

The lack of differentiation between samples from Kansas and the 2 Illinois localities agrees with Rees (1969b), who found that mandibles from both northeastern and southeastern Kansas grouped with northcentral samples. In another study (Levengood et al. 1994) the Kansas sample clustered with large specimens from more northerly localities. The existing Kansas deer herd is the result of expansions of remnant populations following near-extirpation during the late 19th and early 20th centuries (K. Sexson, KS Dept. Wildlife and Parks, pers. commun.).

Our results indicated greater discrimination between Missouri and both the Kansas and southcentral Illinois samples, as compared to northwestern Illinois. This contrasts the findings of Levengood et al. (1994), however, the phenetic distance between the Kansas, northwestern Illinois, and southcentral Illinois samples in their study was small. Rees

(1969b) found that archeological and contemporary Missouri samples grouped with the northcentral region, based on a series of dental characters. The present Missouri herd is a result of the expansion of several remnant populations and restocking of unoccupied ranges using animals from these expanding populations, as well as deer from Michigan and Minnesota (Robb 1959). It is plausible that our Missouri sample represents an intergradation between northern and southern forms, since Minnesota x Missouri hybrids were used to stock some areas (Robb 1959). Levenson (1991) found the Missouri sample to be intermediate between large (northern) and small (southern) morphotypes.

In the present study the range of variation in the northwestern Illinois sample encompassed nearly all of that observed in the Missouri and southcentral Illinois samples. Deer from Illinois and Missouri share a common background, since animals from Michigan were used in restocking programs in both states (Pietsch 1954; Robb 1959). While the southcentral Illinois and southeastern Missouri sampling localities were geographically close, these herds are separated by the Mississippi River which may provide an impediment to genetic exchange in a species characterized by low rates of interdemographic gene flow.

The Minnesota and South Carolina samples exhibited nearly complete separation on the shape axes. Deer inhabiting the Minnesota sampling area were descended from the original herd occupying this region (J. Mooty, MN DNR, pers. commun.). Similarly, the Savannah River Plant herd (SC) is descended from remnants of native herds which persisted along the Savannah River corridor (Hillestad 1984).

The low congruence between the Minnesota and Michigan samples on the combined major shape axes may be the result of a combination of isolation by distance and obstruction of gene flow. Rees (1970) theorized that dissimilarities in skull shape between deer from Upper and Lower Michigan (separated by the Strait of Macinac) reflected their genetic isolation.

The greater congruence between the westcentral Illinois and Michigan and Minnesota samples, as compared with southern Illinois, may reflect the history of the Illinois deer herd. White-tailed deer were virtually eliminated from Illinois by the early 20th century, the last reported sightings coming from southern Illinois around 1910 (Pietsch 1954; Calhoun and Loomis 1974). The reintroduction of deer into Illinois began in the 1930s, with some animals provided by Michigan and Wisconsin (Pietsch 1954). Remnant populations probably persisted in more inaccessible portions of southern Illinois (Pietsch 1954; Calhoun and Loomis 1974), however, the degree to which these genotypes were conserved remains unknown.

Our analysis of shape revealed greatest separation between groups with more divergent backgrounds, based upon geographic distance, impediments to genetic exchange, and history of relocations. While Gavin and May (1988) demonstrated an association between genetic and geographic distance in a study of white-tailed deer from the Pacific northwest and New York, Ellsworth et al. (1994a) concluded that distance was not an important factor in mtDNA differentiation in populations from the southeastern United States. Leberg et al. (1994) failed to detect a clear relationship between genetic and geographic

distance in deer from the eastern United States. These authors did, however, find an association between reintroduction history and both genetic and geographic distances.

Ellsworth et al. (1994b) concluded that relocated deer contributed little to the genetic make-up of populations from the southeastern United States. The authors postulated that in certain instances, local gene pools might have been impacted through the introduction of animals from other herds. Leberg et al. (1994) concluded that gene flow between native and introduced herds has not been sufficient to completely eliminate characteristics of source populations. This is not inconsistent with Ellsworth et al. (1994a), who concluded that the behavioral characteristics of this species which restricted gene flow between populations were sufficient to maintain phylogeographic patterns.

The introduced populations in our study may have retained morphological characteristics of stock reintroduced into the areas sampled. The degree to which these characteristics were conserved may be dependent upon the number of animals representing native stock inhabiting these areas and the success of reintroduced animals in establishing founder populations. Such information has ramifications for biogeographic studies and species reintroductions.

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Table 1. Sheared principal component loadings for 20 cranial characters from 146 specimens of *Odocoileus virginianus* from five regions (first random set) of the eastern and midwestern United States.

Character	Size	Sheared PC-II	Sheared PC-III
Greatest length skull	0.19	-0.15	-0.07
Condlobasal length	0.18	-0.15	-0.07
Nasal length	0.25	-0.29	-0.07
Least nasal width	0.45	0.78	0.09
Least interorbital width	0.22	-0.02	-0.07
Zygomatic width	0.17	0.00	-0.10
Palatal length	0.20	-0.17	-0.04
Palatal width	0.24	-0.12	-0.13
Length UPM2M3	0.07	-0.18	0.00
Length LPM2M3	0.05	-0.17	0.06
Width across M2M2	0.15	0.00	-0.09
Diastema length	0.33	-0.16	-0.12
Cranial breadth	0.16	0.02	-0.07
Cranial height	0.14	-0.02	-0.00
Incisive foramine	0.33	-0.19	0.89
Postpalatal length	0.14	-0.15	-0.19
Condylar width	0.14	-0.09	-0.15
Rostral breadth	0.30	0.15	-0.21
Mandible length	0.18	-0.14	-0.10
Mandible height	0.22	-0.16	-0.13
% of variance	52.0	12.0	8.0

Table 2. Sheared principal component loadings for 20 cranial characters from 175 specimens of *Odocoileus virginianus* from five regions (second random set) of the eastern and midwestern United States.

Character	Size	Sheared PC-II	Sheared PC-III
Greatest length skull	0.15	-0.19	-0.06
Condylbasal length	0.15	-0.21	-0.07
Nasal length	0.20	-0.38	-0.12
Least nasal width	0.62	0.63	0.02
Least interorbital width	0.22	-0.01	-0.08
Zygomatic width	0.16	-0.02	-0.06
Palatal length	0.18	-0.24	-0.02
Palatal width	0.25	-0.03	-0.03
Length UPM2M3	0.02	-0.13	-0.16
Length LPM2M3	0.02	-0.12	-0.24
Width across M2M2	0.14	-0.04	-0.15
Diastema length	0.26	-0.30	0.16
Cranial breadth	0.10	-0.02	-0.10
Cranial height	0.12	0.01	-0.12
Incisive foramin	0.32	-0.18	0.79
Postpalatal length	0.11	-0.09	-0.17
Condylar width	0.07	-0.23	-0.25
Rostral breadth	0.29	0.09	-0.23
Mandible length	0.15	-0.19	-0.07
Mandible height	0.18	-0.12	-0.18
% of variance	41.0	15.0	9.0

Figure 1. Map depicting collection localities for *Odocoileus virginianus* skulls examined in this study.

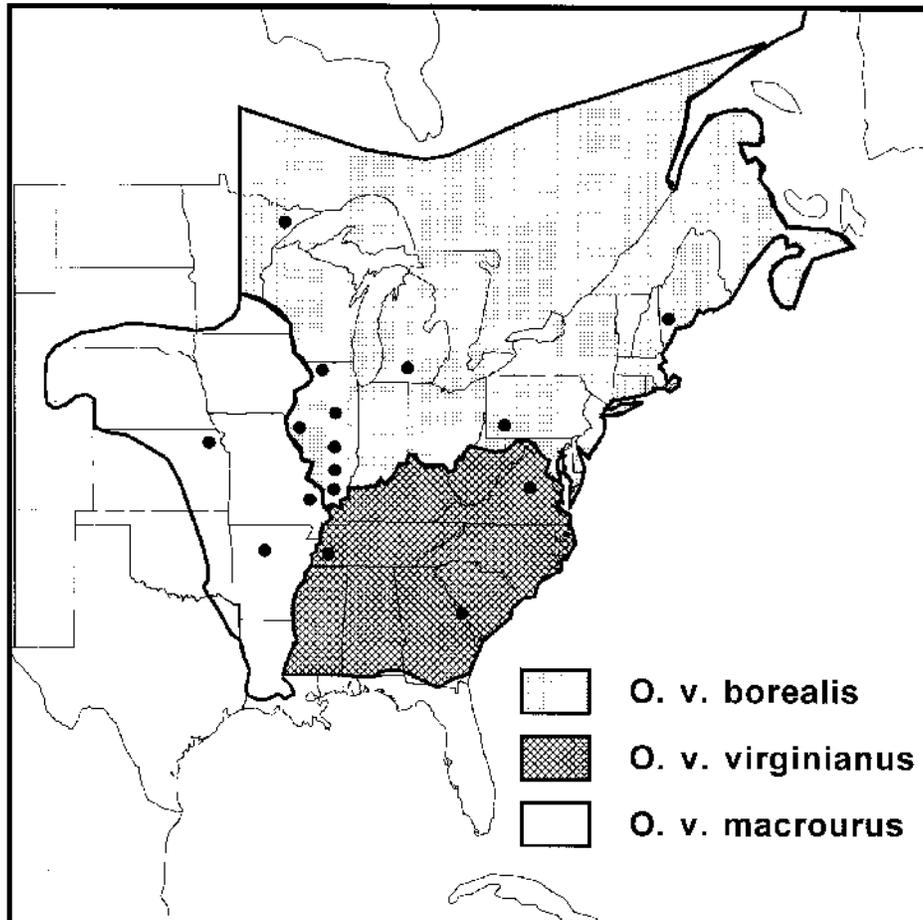


Figure 2. Results of a sheared principal components analysis of the first random set of localities: a, axes I (size) and II, and b, axes II and III. Polygons enclose individual scores for a given region.

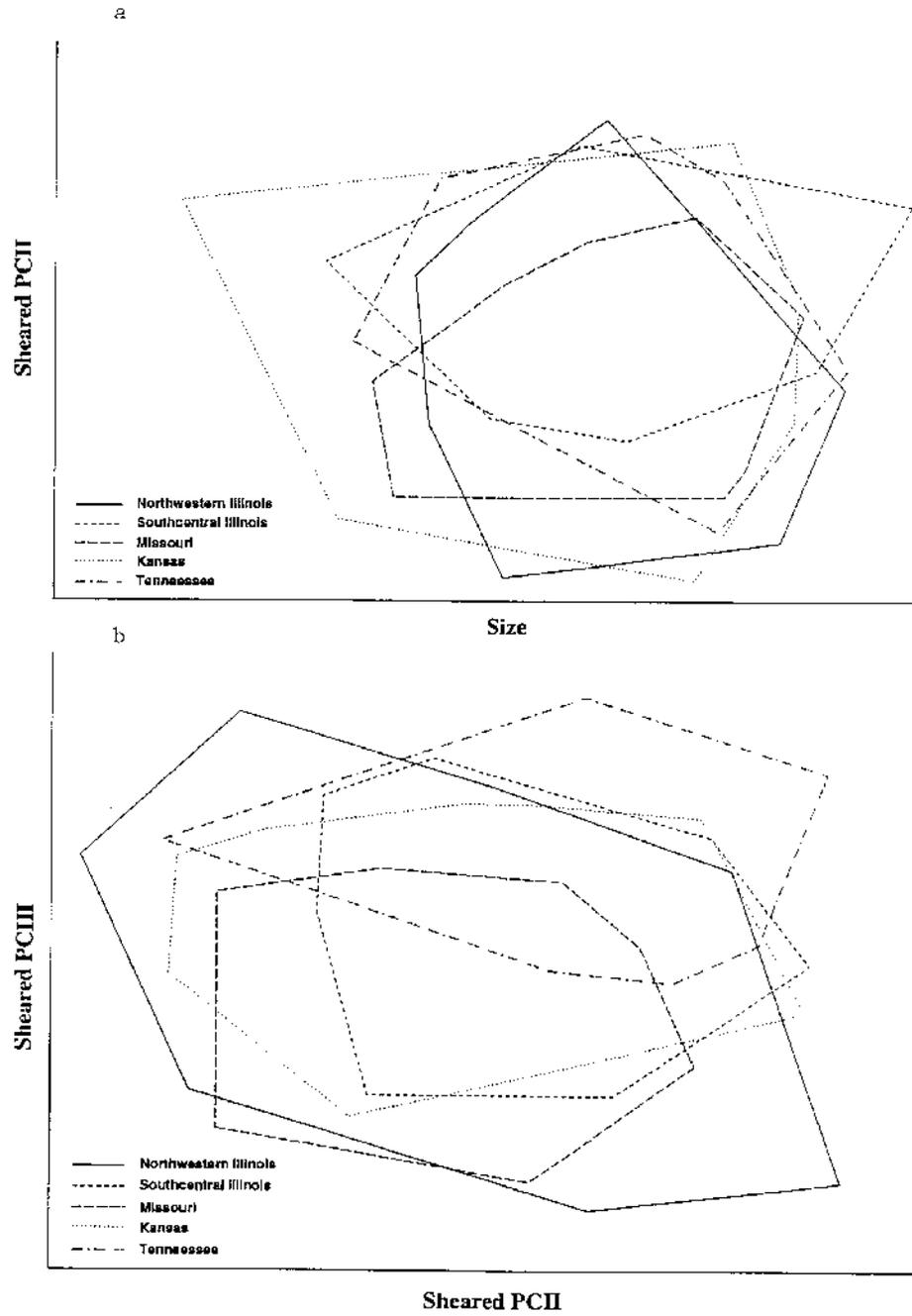
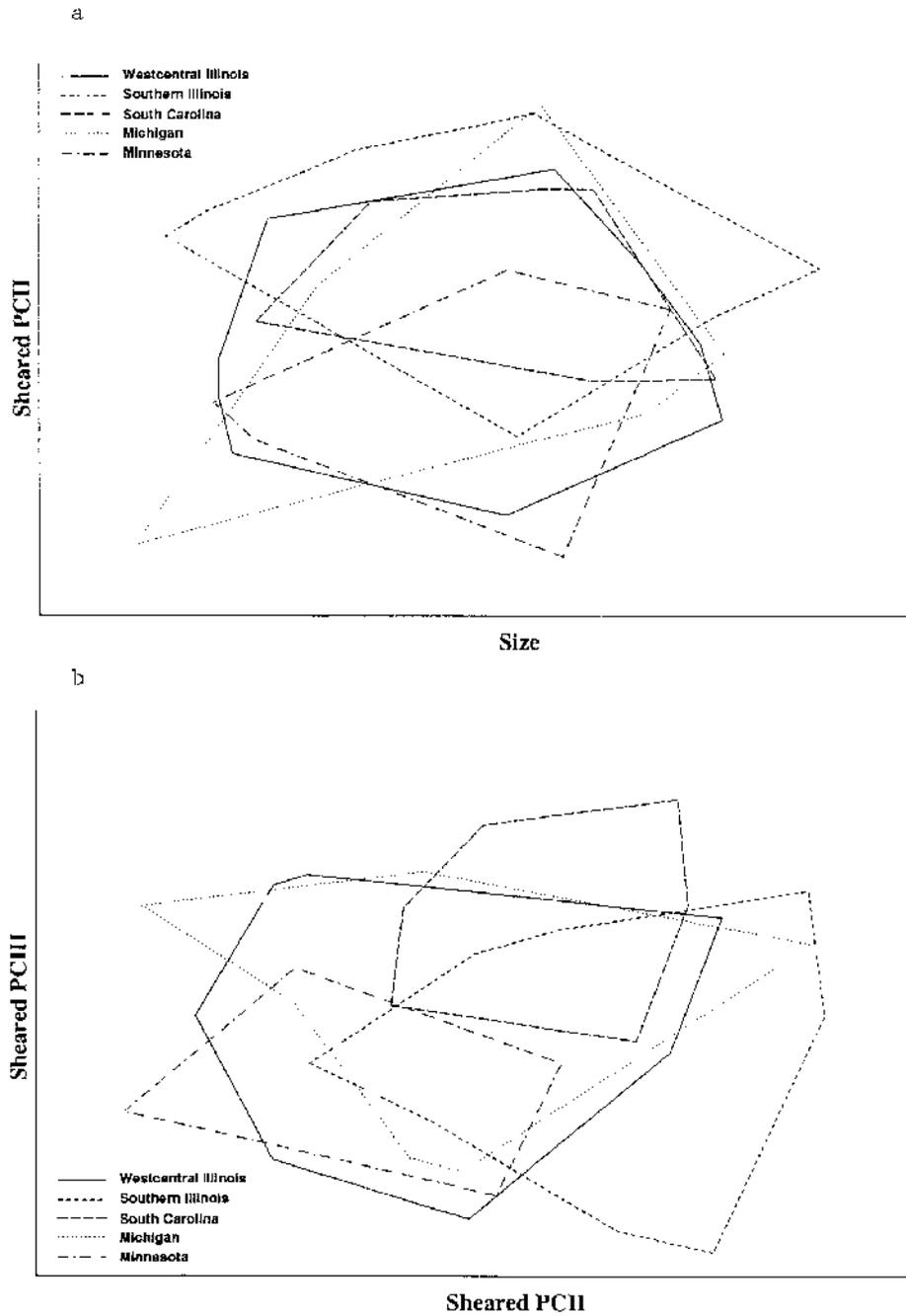


Figure 3. Results of a sheared principal components analysis of the second random set of localities: a, axes I (size) and II, and b, axes II and III. Polygons enclose individual scores for a given region.



**APPENDIX A**  
**Description of cranial measurements**

- Greatest length of skull - from anterior edge of premaxillae to posterior point of skull
- Condylbasal length - from anterior edge of premaxillae to posteriormost edge of occipital condyles
- Nasal length - greatest antero-posterior length of nasals
- Least nasal length - narrowest width across nasals
- Rostral breadth - greatest breadth of rostrum measured through a line extending ventrally from the posteriormost edge of the premaxillary-maxillary suture
- Least interorbital width - narrowest width between the orbits
- Cranial breadth - greatest width of the braincase measured across the squamosals
- Cranial height - greatest height of the braincase measured vertically from the basisphenoid to the juncture of the front-parietal sutures
- Upper PM2-M3 - length upper molariform tooth row, measured at the tartar line
- Lower PM2-M3 - length lower molariform tooth row, measured at the tartar line
- Width across M2-M2 - distance between the lateral edges of M2 at the posterior lateral margin of tooth
- Diastema length - posterior margin alveolus of the canine to anterior margin alveolus of first premolar
- Zygomatic width - greatest width across zygomatic arches
- Palatal length - anterior edge of premaxillae to staphylion
- Palatal width - least width of palate
- Incisive foramen - greatest length anterior palatal foramen
- Postpalatal length - anterior rim foramen magnum to staphylion
- Condylar width - distance between lateral borders of occipital condyles
- Mandible length - greatest length of ramus
- Mandible height - vertical distance from base of mandible to tip of coronoid process

**APPENDIX B**  
**Specimens Examined**

Collection localities, number of specimens, and acronyms of museums housing specimens.

ILLINOIS: Adams Co., 16 (CWRL); Adams or Pike Co., 30 (CWRL); Alexander Co., Horseshoe Lake Conservation Area, 14 (CWRL), Horseshoe Lake Conservation Area or Crab Orchard National Wildlife Refuge (Williamson Co.), 4 (CWRL); Carroll Co., 11 (CWRL), Carroll or JoDaviess Co., 4 (CWRL); Carroll, Jo Daviess, or Whiteside Co., 37 (CWRL); Jefferson Co., 8 (CWRL); Jo Daviess Co., 10 (CWRL); Pike Co., 25 (CWRL); Washington Co., 12 (CWRL); Williamson Co., Crab Orchard NWR, 56 (CWRL). KANSAS: Douglas Co., 1 (KU); Douglas, Jefferson, or Leavenworth Co., 24 (CWRL); Johnson Co., 1 (KU); Leavenworth Co., 3 (KU). MICHIGAN: Clinton, Ingham, or Shawassee Co., 24 (CWRL); Livingston Co., George Reserve, 6 (UMMZ). MINNESOTA: Cook, Itasca, Lake, St. Louis C., 34 (CWRL). MISSOURI: Cape Girardeau Co., 27 (CWRL). SOUTH CAROLINA: Aiken/Barnwell Cos., Savannah River Plant, 17 (CWRL). TENNESSEE: Carroll/Henderson Cos., Natchez Trace WMA, 1 (MSUMZ); Fayette/Hardeman Cos., Ames Plantation, 2 (MSUMZ); Hardeman Co., 3 (MSUMZ); Haywood Co., 1 (MSUMZ), Hatchie NWR, 11 (MSUMZ); Henderson Co., 1 (MSUMZ); Shelby Co., Shelby Forest WMA, 4 (MSUMZ).