GERALD SCOTT BALES

A MULTIVARIATE MORPHOMETRIC STUDY OF LIVING AND FOSSIL RHINOCEROS SKULLS

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A MULTIVARIATE MORPHOMETRIC STUDY OF LIVING AND FOSSIL RHINOCEROS SKULLS

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure Number	Description	Page

ABSTRACT

The Rhinocerotoidea is a Superfamily of perissodactyl mammals whose evolutionary history extends from the Eocene epoch to the Present. This history is represented by a collection of fossils which is qualitatively and quantitatively one of the best among vertebrates. Such a fossil record allows study of larger scale aspects of morphological evolution in vertebrates, particularly in large mammalian herbivores. Rhinocerotoid diversity comprises fifty-five genera in three families with four extant genera. This study is a multivariate morphometric investigation of within-group and among-groups variation in the skulls and mandibles of the living and fossil genera. The living genera are biological analogues by which the fossil genera may be more confidently interpreted. Osteo-dental landmarks provided 19 linear measurements for skulls and 11 linear measurements for mandibles. Adult skulls (83 living; 101 fossil) and adult mandibles (80 living; 117 fossil) were analysed for four living and fourteen fossil genera. Measurements and sample sizes were maximized under the constraints required by complete data. Some measurements were estimated by a multiple regression technique. Each genus was analyzed by the principal components method (PC, within-group analyses) where specimens are ordinated along axes of maximum variation. Living genera were analysed first: geographic, taxonomic, and sex dimorphic correlations with morphometric differences were identified. These results were included as part of the total information used to analyse the variation within fossil genera. In several fossil genera, subgeneric groups were identified using geographic, taxonomic, temporal\stratigraphic, and analogue variation data. Overall PC results indicate that variational patterns in fossil genera are similar to those in living analogues. The PC subgroups were analyzed by canonical variates (CV, among-groups analyses) where PC means are ordinated along orthogonal, variance maximizing axes. Determination of these axes relies on an estimate of average within-group variation provided by pooling of the PC subgroups. The CV ordination was analysed with respect to morphometric affinites, and correlations with taxonomy, qualitative characters, diet, horn type, and temporal patterns. Results show that morphometric affinites are most uniquely correlated with horn type, least correlated with diet. Temporal patterns show that general morphological trends occur at the genus level. Evolutionary changes at the subgeneric level indicate more irregular pathways. In general, morphology and size change simultaneously.

CHAPTER 1.

INTRODUCTION

OVERVIEW

The perissodactyl superfamily Rhinocerotoidea is one of the many mammalian groups which evolved in the Cenozoic Era. Like other mammalian radiations, rhinocerotoids evolved from a few, small, primitive forms to a variety of more specialized, often larger, forms resulting in a large diversity of taxa most of which have become extinct. Among vertebrates, the Rhinocerotoidea has one of the largest fossil records and is thus amenable to studies of morphological (skeletal) evolution within a long-lived, higher taxon. This abundance of fossils increases the probability that all groups (primitive, derived, and transitional) are included and that the range of normal variation within groups or populations is represented. A further important advantage of the rhinoceros superfamily is the persistence to the present of five species that can serve as analogues of the fossil taxa. Morphological variation in analogue taxa, correlated with ecogeographical, physiological, behavioral, and other biological factors, provides the most appropriate measure for interpreting intraspecific, intrageneric, and intergeneric morphological variation in extinct taxa.

This study is a multivariate morphometric analysis of skull and mandible morphology both within and among 15 fossil and 4 living rhinocerotoid genera. Genera are the initial focus of analysis because generic-level taxonomies are more complete, accurate, and stable than are species-level assignments. Multiple measurements of osteological features from representative samples of skulls and mandibles provide the data for analysis. Within-group analyses seek to: (a) compare living and fossil generic variation, (b) dissect the variation in each genus using geographic, temporal/stratigraphic, taxonomic, and variational data relevant to subgeneric level variation, and (c) provide a standard of within-group variation for use in comparative studies of among-groups variation and relationships. Among-groups analyses seek to be both descriptive and explanatory by observing the patterns and correlates of morphology with respect to morphometric affinities, taxonomy, phylogenetic character states, horn types, diet, and temporal sequences.

The Rhinocerotoidea has been less studied relative to the size of its fossil record than a comparable group, the Equoidea (horses). The latter group has played a prominent role in discussions of vertebrate evolution. This study of rhinocerotoid skull morphology will contribute to those discussions by providing further insights into the evolution of vertebrates in general and of large mammalian herbivores in particular.

RESEARCH QUESTIONS

Within-group Studies

(1) What is the pattern of variation in living taxa across genera and species?

(2) How does morphological variation in fossil rhinoceros genera compare to that of living genera and species?

(3) Is fossil generic variation reducible to subgeneric groups based on factors known to be correlated with species-level variation (e.g., time/stratigraphy, ecogeography, diet, or other biological factors)?

(4) Is variation in fossil subgeneric groups consistent with species-level variation in living analogues and with previous species-level taxonomic assignments?

(5) Are size and shape differences among demes and between sexes consistent with those in living analogues?

(6) What evolutionary size-shape changes occurred within fossil genera?

Among-groups Studies

(1) What are the morphometric affinites of specimens and group means observed in the canonical variates space?

(2) What are the morphometric relationships of the generic-subgeneric groups with respect to recent taxonomies and taxonomic characters?

(4) Are there morphological relationships based on anatomical/functional/behavioral groupings such as mode of herbivory or horn arrangement?

(5) What are the patterns of size and shape evolution relative to hypothesized intrageneric and intergeneric phylogenies?

BACKGROUND

The following is a brief discussion of the rhinocerotoid superfamily and its component familiss. Detailed discussions of genera are given in Chapter 3 as prefaces to the within-group studies of each genus.

Superfamily Rhinocerotoidea

The Rhinocerotoidea is a large, diverse superfamily of perissodactyl mammals comprised of three monophyletic families:

Amynodontidae, Hyracodontidae, and Rhinocerotidae (Figure 1). Four genera have survived to the Recent and comprise the living African and Asian rhinocerotids. In North America, rhinocerotoids populated much of the western interior (Intermontane and Great Plains regions) from the early Eocene through the Miocene as documented by relatively numerous fossils. During much of this time, various species were believed to have been ecologically dominant by virtue of their large body-sizes and relative abundances. Understanding the pattern of rhinoceros evolution in North America is complicated by migrations to and from Europe and Asia via continental land bridges (Figure 2). During most of the Cenozoic, an above sea-level connection between Alaska and Siberia (Bering Land Bridge) provided an ice-free route for bidirectional movement of respective biotas. Rhinocerotoids which may have used this route were *Hyrachyus* (from Asia), *Forstercooperia* (to Asia[?]), and *Trigonias* (from Asia). Several routes of migration were open between Europe and North America (McKenna, 1972, 1975) and may have been used by *Menoceras* (and possibly *Trigonias*).

FIGURE 1. Most current phylogentic classification of the genera of Rhinocerotoidea (after Prothero et al., 1986). Genera used in this study indicated by asterisks (*). *Hyrachyus* is the primitive ancestor.

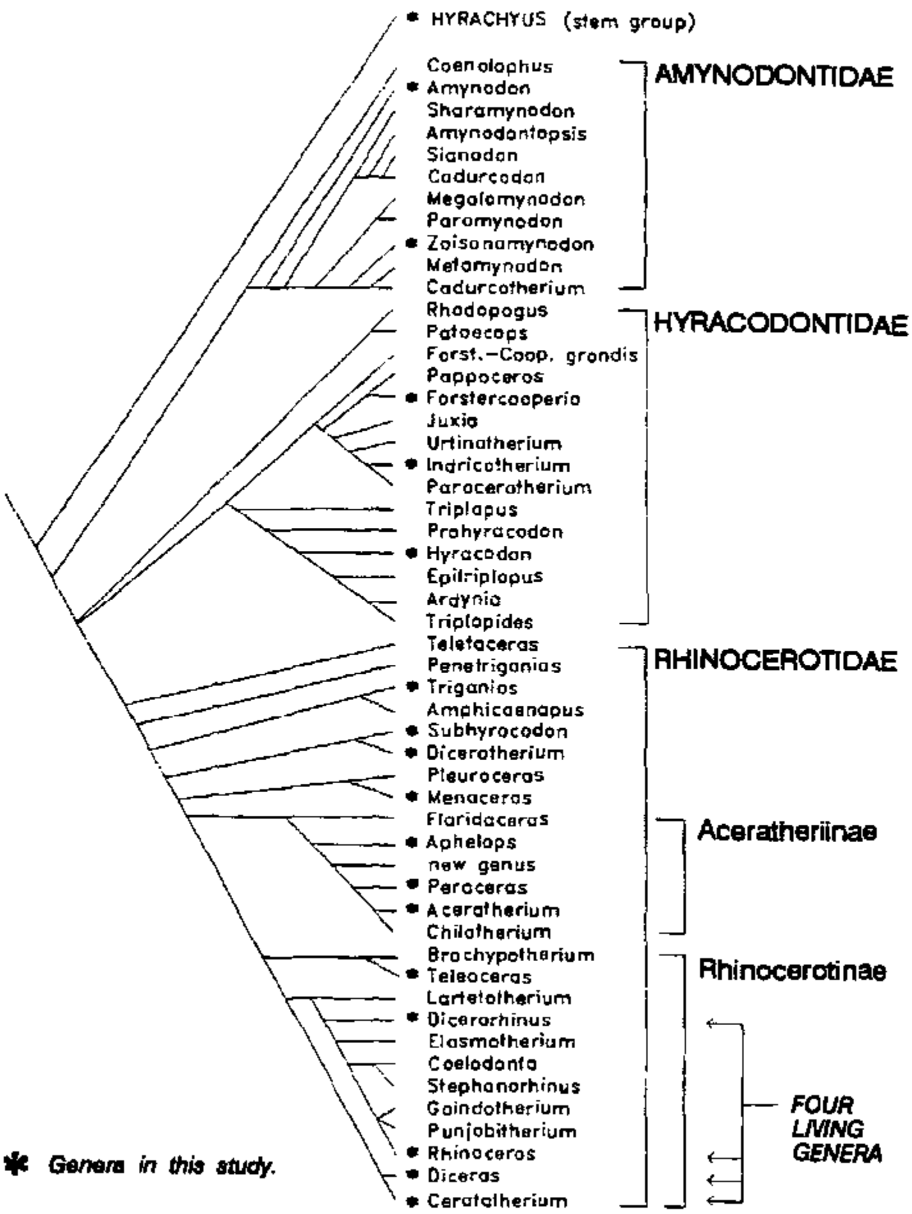
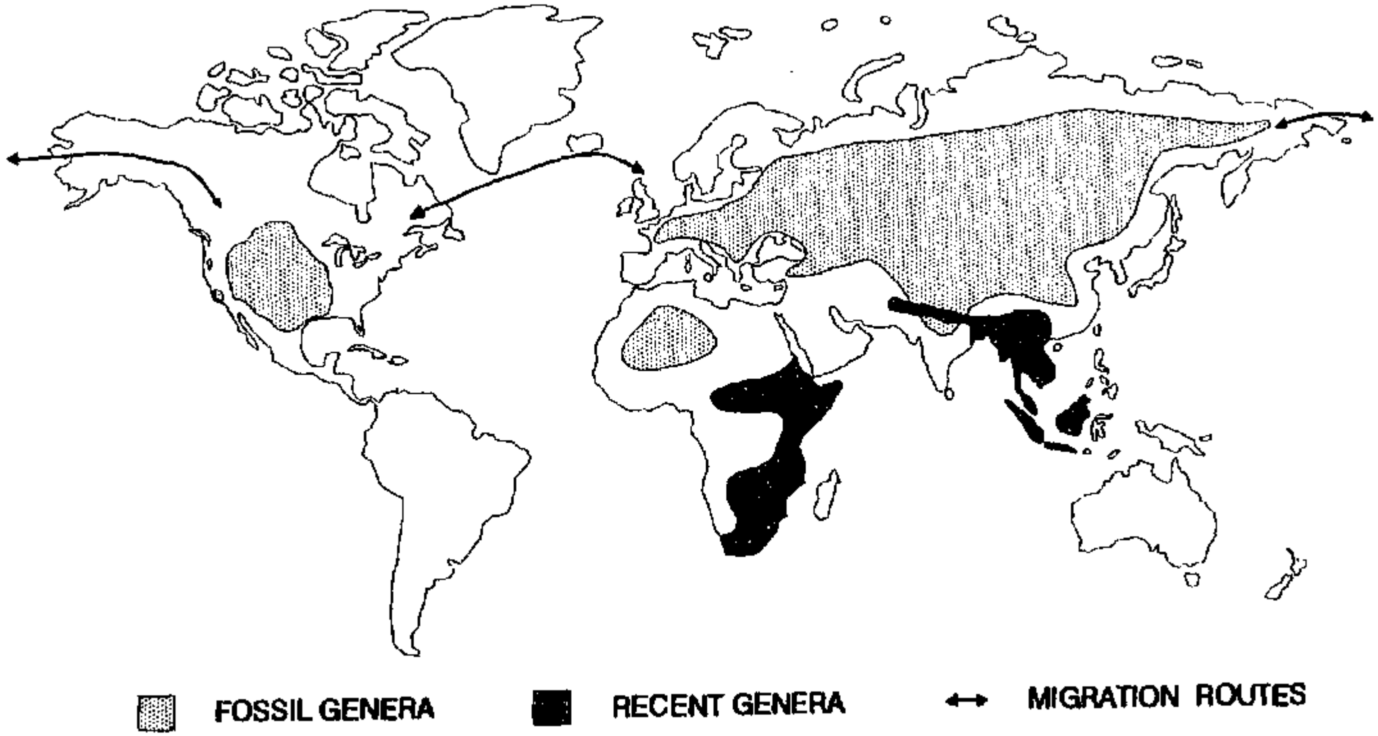

* HYRACHYUS (stem group)
Coenolophus
* Amynodon
Sharamynodon
Amynodontopsis
Sianodon
Cadurcodon
Megalamynodon
Paramynodon
* Zaisanamynodon
Metamynodon
Cadurcotherium
AMYNODONTIDAE
Rhodopagus
Pataecops
Forst.-Coop. grandis
Pappoceras
* Forstercooperia
Juxia
Urtinotherium
* Indricotherium
Paraceratherium
Triplopus
Prohyracodon
* Hyracodon
Epitriplopus
Ardynia
Triplopides
HYRACODONTIDAE
Teletaceras
Penetrigonias
* Trigonias
Amphicaenopus
* Subhyracodon
* Diceratherium
Pleuroceras
* Menoceras
Floridaceras
* Aphelops
new genus
* Peraceras
* Aceratherium
Chilotherium
Brachypotherium
* Teleoceras
Lartetotherium
* Dicerorhinus
Elasmotherium
Coelodonta
Stephanorhinus
Gaindotherium
Punjabitherium
* Rhinoceros
* Diceros
* Ceratotherium
RHINOCEROTIDAE
Aceratheriinae
Rhinocerotinae
FOUR LIVING GENERA
* Genera in this study.

FIGURE 2. Historical distributions of living and fossil rhinocerotoid genera. Arrows indicate potential migration routes (land bridges) during periods of lowered sea level.

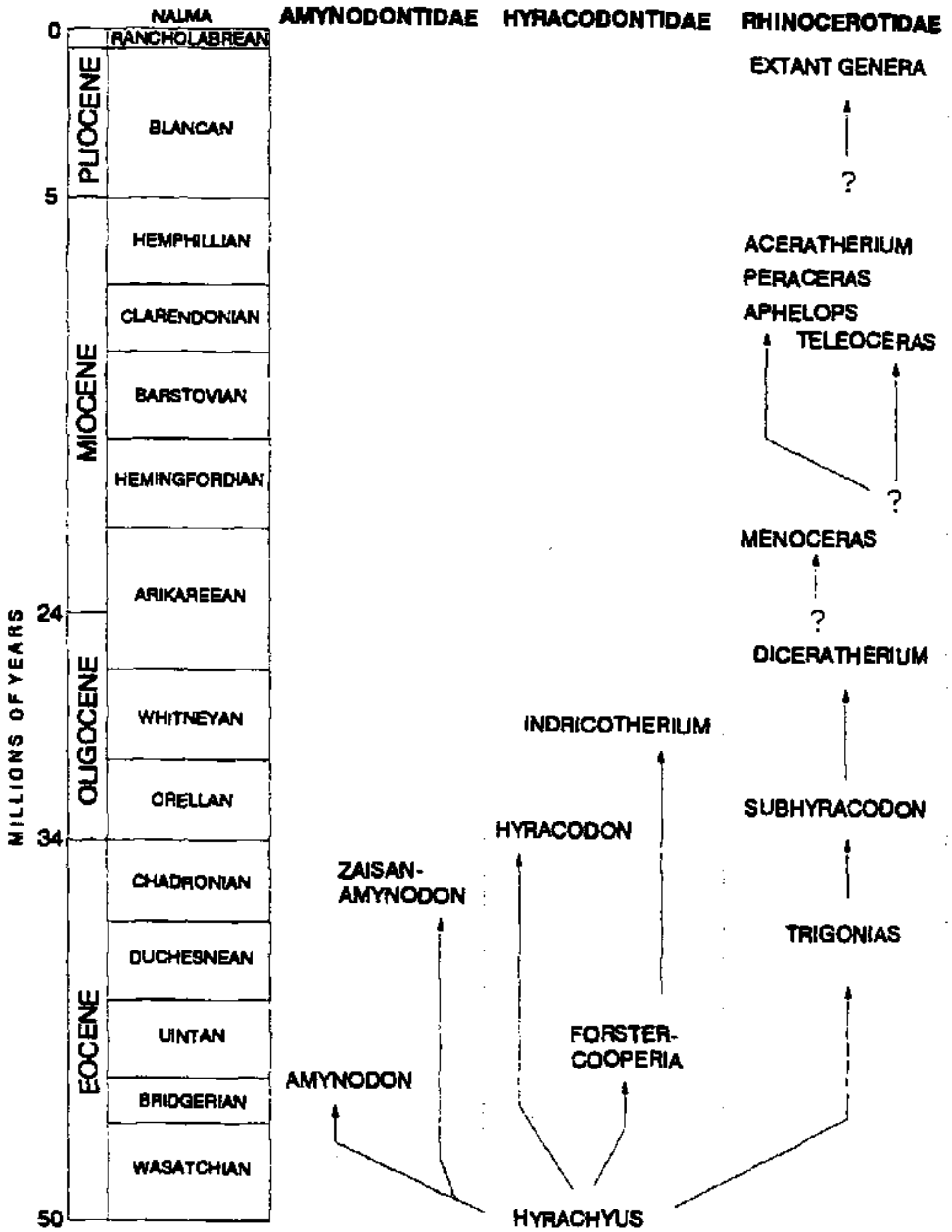

FOSSIL GENERA
RECENT GENERA
MIGRATION ROUTES

Previous studies of rhinocerotoid systematics and phylogeny include those of Osborn (1903, 1904), Matthew (1931, 1932), Wood (1941), Radinsky (1967a), Hooijer (1976, 1978), and Groves (1983), and Groves and Chakraborty (1983). Descriptive studies of specific genera including living forms include Cooper (1911, 1924, 1934), Matthew, (1924), Osborn (1923, 1924), Wood (1931), Granger and Gregory (1936), Tanner (1969), Groves (1972), Groves and Chakraborty (1983), Groves and Kurt (1972), Yatkola and Tanner (1979), Lucas et al. (1981), Russell (1982), Laurie et al. (1983), and Hanson (1989).

Recent reviews of the Rhinocertoidea and its families include, Prothero (in press, a and b), Prothero and Manning (1987), Prothero et al., (1986, 1989), Wall (1989), and Lucas and Sobus (1989). This study relies primarily on these most current views about rhinocerotoid systematics (Figure 1) and phylogeny (Figure 3).

Hyrachyus -- The most primitive rhinocerotoid genus is *Hyrachyus*, comprised of small animals (Great Dane-sized) resembling *Hyracotherium*, the most primitive equid. The status of *Hyrachyus* as the primitive sister-taxon to the three rhinocerotoid families is based primarily on dental characters (Prothero et al., 1986). Radinsky (1967b) considered this genus to be a helaletid tapiroid, but acknowledged its ancestry to the rhinocerotoids. In this study, *Hyrachyus* is used as the basal group ("primitive

FIGURE 3. Phylogeny and geochronology of the rhinocerotoid genera in this study (after Prothero, in press a). North American Land Mammal Age (NALMA) boundaries are approximate (after Tattersall et al., 1988).


NALMA
AMYNODONTIDAE
HYRACODONTIDAE
RHINOCEROTIDAE
MILLIONS OF YEARS
0
5
24
34
50
PLIOCENE
MIOCENE
OLIGOCENE
EOCENE
RANCHOLABREAN
BLANCAN
HEMPHILLIAN
CLARENDONIAN
BARSTOVIAN
HEMINGFORDIAN
ARIKAREEAN
WHITNEYAN
ORELLAN
CHADRONIAN
DUCHESNEAN
UINTAN
BRIDGERIAN
WASATCHIAN
EXTANT GENERA
?
ACERATHERIUM
PERACERAS
APHELOPS
TELEOCERAS
?
MENOCERAS
?
DICERATHERIUM
INDRICOTHERIUM
SUBHYRACODON
HYRACODON
ZAISAN-
AMYNODON
TRIGONIAS
FORSTER-
COOPERIA
AMYNODON
HYRACHYUS

morphotype") for comparisons of ancestor-descendent size-shape changes in each of the families. Although believed to be an emigrant from Asia, *Hyrachyus* is known predominantly from middle Eocene beds in the Bridger Formation of Wyoming where it is one of the most common genera of fossil mammals of this period.

Amynodontidae -- Amynodontids appeared in the middle Eocene where some had already achieved the size of cattle (*Amynodon*). Subsequent evolutionary size increases - to the size of modern rhinoceroses - made them among the largest land mammals of the late Eocene holarctic region (Wall, 1989). Family characters of amynodontids include conical incisors, enlarged male canines, reduced premolars, and preorbital fossae (Prothero et al., 1986). Other specializations within the family included high-crowned cheek teeth, convergence to hippopotamus-like proportions in the semi-aquatic riverine genus *Metamynodon*, and (possibly) a tapir-like proboscis in the terrestrial genus *Cadurcodon* (Wall, 1980).

Hyracodontidae -- The hyracodontids evolved in the late Eocene and Oligocene from *Hyrachyus* or a *Hyrachyus*-like form. Primitively sheep-sized and adapted for running (cursorial), this family evolved larger body sizes (cow-sized in North America). In Asia, *Paraceratherium* achieved a size greater than that of elephants but paradoxically retained limb proportions indicative of cursoriality. Members of this family have equal-sized incisors and small canines (i.e., tuskless) among other features upon which their classification is based (Radinsky, 1966). More recently, Prothero et al. (1986) considered limb characters to be more important taxonomically.

Rhinocerotidae -- Primitive rhinocerotids were sheep-sized animals which probably immigrated from Asia. Beginning in the early Oligocene, rhinocerotids became larger, culminating in *Diceratherium* which reached the size of modern rhinoceroses. *Diceratherium* was the only known genus of rhinocerotid in North America for approximately 14 million years. During this period (mid-Oligocene to mid-Miocene), they were the largest mammals found in terrestrial communities (with regard to large size, they were preceded by the titanotheres and paraceratheres, and followed by the mastodons). In the mid-Miocene, sheep-sized representatives of the divergent aceratherine (*Aphelops*) and teleoceratine (*Teleoceras*) lineages immigrated to North America from Europe or Eurasia. Species in both groups evolved to the size of modern rhinoceroses but dwarfing also occurred. Ecological diversity in later rhinocerotids is exemplified by a dichotomy between teleoceratine grazers and aceratherine browsers (Prothero, in press a). Characters which distinguish rhinocerotids from other families include facial bone arrangement and tooth size, shape and enamel patterns (Prothero et al., 1986). Horns are not a universal characteristic of the family, but occur in all extant genera.

Multivariate Morphometric Methods

This study relies primarily on the methods of principal components analysis (PC) and canonical variates analysis (CV) as ordination techniques where multivariate relationships of specimens or centroids (means) are observed in two or three variance-maximizing dimensions. These two methods are among the diversity of methods that have been developed for the analysis of multivariate morphometric data. Applications of these methods to diverse problems and organisms are discussed in several reviews and general references (Blackith, 1965; Sneath and Sokal, 1973; Reyment et al., 1984; Bookstein et al., 1985; Foote, 1991; Reyment, 1991). Mathematical background and discussions of multivariate methodology with examples can be found in many sources (Anderson, 1958; Bartlett, 1965; Marcus, 1990, Morrison, 1967; Cooley and Lohnes, 1971; Davis, 1973; Harris, 1975; Timm, 1975; Green, 1976, 1978; Pimentel, 1979; Neff and Marcus, 1980; Campbell and Atchley, 1981; Johnson and Wichern, 1982; Rohlf, 1990). Important early papers on both method and application have been collected into several volumes (Atchley and Bryant, 1975; Bryant and Atchley, 1975). The field of morphometrics currently is dynamic and growing as evidenced by a number of recent symposia and publications (Rohlf and Bookstein, 1990; Bookstein, 1991; Marcus et al., 1993; Rohlf and Marcus, 1993).

Among living vertebrates, PC has been applied to fish (Bookstein et al, 1985), painted turtles (Jolicoeur and Mosimann, 1960), birds (Schnell, 1970; Blondel et al., Vuilleumier, Marcus, and Terouanne, 1984), bats (Freeman and Lemen, 1991), voles (Flury and Riedwyl, 1988), martens (Jolicoeur, 1963), and primates (Albrecht, 1978, 1980). Studies of fossils using PC include horses (Winans, 1989) and Dinosauria (Chapman et al., 1981; Weishampel and Chapman, 1981).

Canonical variates analysis of living vertebrates include shrews (Gower and Ross, 1969), primates (Ashton et al., 1965; Oxnard, 1967; Albrecht, 1978; reviewed by Albrecht and Miller, 1991), anteaters (Reeve, 1941), and canids (Wayne, 1986). Applications of CV to fossil vertebrate groups, or to groups with both fossil and living representatives, have been less numerous than PC studies. Such groups include primates (Oxnard, 1969; Bilsborough, 1984) and moas (Cracraft, 1976).

CHAPTER 2.

MATERIALS AND METHODS

MATERIALS

Four hundred ninety seven specimens of extant and fossil rhinocerotoid taxa were measured in mammalogy and paleontology departments of the following museums: American Museum of Natural History (New York), National Museum of Natural History (Washington, D.C.), Museum of Comparative Zoology at Harvard University (Boston) Field Museum of Natural History (Chicago), Denver Museum of Natural History. At each museum, all specimens except the most fragmentary were measured, including both juveniles and adults.

Data for a given specimen was recorded on a single data sheet (Appendix 2) whose page number is the specimen number. Each specimen consisted of either: (1) skull and associated mandible (matched elements of the same animal), (2) skull only, or (3) mandible only. Most of the specimens of extant rhinoceroses were complete, with all or most measurements present. Many of the fossil specimens were partial (fragmentary) and had some regional plaster reconstruction. Most of the fossil mandible specimens were hemimandibles (partial or complete), representing one side of the mandible. When both sides of the mandible were present, one side was chosen for measurement based on completeness and other factors.

Sample sizes of measured living and fossil skulls and mandibles are given in Table 1. Because skulls and mandibles were treated separately and independently, total numbers of skull and mandible elements exceed the total number of specimens (data sheets). Aging of specimens was based on: (1) absence of deciduous teeth, (2) at least 3/4 eruption of the third molar (relative to a fully erupted second molar), and (3) presence of some first molar wear. The subsample of adults used in this study was derived by reduction of the sample of measured adults. Captive specimens of extant taxa were excluded. Incomplete fossil adult specimens were excluded because of the statistical need for complete data sets (discussed below under methods). The data reductions resulted in the following samples for analysis: skulls - 83 extant, 101 fossil; mandibles - 80 extant, 117 fossil. Identification of these specimens by museum number is given in Appendix 1. Individual specimen numbers arranged by genus are listed in Table 2 (skull) and Table 3 (mandible), with associated taxonomic, geographic, temporal, and sample size information.

TABLE 1. Comparison of sample sizes for numbers of specimens measured versus number of specimens used in analyses.

	SKULL		MANDIBLE	
	EXTANT	FOSSIL	EXTANT	FOSSIL
JUVENILES MEASURED	90	26	74	29
ADULTS MEASURED	117	131	119	133
ADULTS ANALYZED	83	101	80	117

TABLE 2. Generic and subgeneric group information for skull specimens used in the analysis. The four living genera are listed first alphabetically and are followed by 13 fossil genera, listed alphabetically.

Genus	Code[1]	N[2]	Species[3]	Locality[4]	Age[5]	Specimen #'s[6]
Ceratotherium	CERAS	19	"simum"	East Africa	Recent	22, 59, 99,101, 102,103,104,141, 142,298,360,366, 367,368,369,370, 371,372,431
Dicerorhinus	SUMAS	2	"sumatrensis"	Southeast Asia	Recent	21, 46
Diceros	BICOS	48	"bicornis"	East Africa	Recent	147,149,150,151, 152,155,157,161, 166,167,168,169, 170,174,176,177, 178,181,295,305, 379,382,384,386, 387,388,389,390, 393,394,395,396, 397,398,402,404, 405,407,408,409, 410,411,412,414, 418,436,437,441
Rhinoceras	UNICS	8	"unicornis"	India/Nepal	Recent	48, 53, 55,303, 348,426,427,430,
	JAVAS	4	"sondaicus"	Java	Recent	17, 18,299,351

Genus	Code	N	Species	Locality	Age	Specimens
Aceratherium	ACER1S	1	"depereti"	Mongolia	Hemphillian	245
	ACER2S	1	"incisivium"	Europe	Blancan	124
Amynodon	AMYNS	2	"advenus"	Washakie Basin, Wyoming Uinta Co., Utah	Uintan Uintan	111 461
Aphelops	APHE1S	1	megalodus	Box Butte Co., Nebraska	Hemingfordian	205
	APHE2S	8	megalodus	Cherry Co., Nebraska	Clarendonian	268,269,270,271, 272,330,334,335
Diceratherium	DICE1S	3	annectens "nanum"	Oregon	Oligocene	239
				Wyoming	Arikareean	203,204
	DICE2S	1	niobrarense	Nebraska	Arikareean	266
	DICE3S	2	"armatum"	Niobrara Co, Wyoming	Arikareean	240,267
Forstercooperia	FORSS	2	"sharamuranensis"	Inner Mongolia	Uintan-Duchesnean	127,130
Hyrachyus	HYRA1S	2	"modestus"	Wyoming	Bridgerian (B2)	4, 5
	HYRA2S	3	"princeps"	?	Bridgerian (C4)	10
			"eximius"	Wyoming	Bridgerian (D5)	6, 12
Hyracodon	HYCOS	4	"nebraskensis"	South Dakota & Nebraska	Orellan	116,117,120,460

Genus	Code	N	Species	Locality	Age	Specimens
Indricotherium	INDRS	1	transouralicum	?	?	258
Menoceras	MENOS	18	"arikarense"	Sioux Co., Nebraska	Arikareean	171,195,196,197, 198,200,201,453, 454,456,457
			?			452
			?	Platte Co., Wyoming	Arikareean	143,158,172,186, 187,188,
Peraceras	PERA1S	2	"hessei"	New Mexico	Barstovian	324
			"profectum"	New Mexico	"	276
	PERA2S	3	"superciliosum"	Nebraska	Clarendonian	326,327,329
Subhyracodon	SUBH1S	5	mitis	South Dakota	Chadronian	28, 29, 31
			"trigonodum"			
			"copei"	South Dakota	Orellan	27
			"mitis"	Wyoming	?	32
	SUBH2S	4	occidentalis	South Dakota	Orellan	38, 64
			"occidentalis"		"	35, 63
	SUBH3S	7	"tridactylum"	South Dakota	Whitneyan	228,229,231,233, 236,278,458

Genus	Code	N	Species	Locality	Age	Specimens
Teleoceras	TELE1S	2	americanum	Nebraska	Hemingfordian	341,342
	TELE2S	4	medicarnutum	Nebraske	Barstovian	317,318,344
			medicornutum "thomsoni"		"	255
	TELE3S	6	major	Nebraska	Clarendonian	311,312,313,314, 315,316
	TELE4S	3	"hicksi"	Calarado	Late Hemphillian	281,496,497
	TELE5S	4	fossiger	Nebraska	Early Hemphillian	284
			fosoiger	Kansas	"	287
			fassiger	Texas	"	291
			"fassiger"	Calorado	"	424
Trigonias	TRIGS	13	osborni	Washington Co., Colorado	Chadronian	462
			osborni	Weld Co., Calarado	"	422,443,468,469,
					"	470,471,472,476
			osborni "cooki"		"	475
			asborni "preoccidentalis"		"	492
			osborni "hypostylus"		"	490
			"osborni"	Shannon Co., South Dakota	"	23

1. Codes refer to the subgeneric groups determined in Chapter 3.
2. Sample sizes of the groups indicated under the Code column.
3. Species names in quotes are those associated with museum tags.
4. Localities are derived from information associated with museum specimens.
5. Age is given as North American Land Mammal Age where possible (see Figure 3).
6. Specimen numbers were assigned sequentially as specimens were measured and correspond to page numbers in the original data book.

TABLE 3. Generic and subgeneric group information for mandible specimens used in the analyses. The four living genera are listed first alphabetically and are followed by 13 fossil genera, listed alphabetically.

Genus	Code[1]	N[2]	Species[3]	Locality[4]	Age[5]	Specimens #,s[6]
Ceratotherium	CERAM	19	"simum"	East Africa	Recent	22, 59, 99, 101, 102, 103, 104, 141, 142, 297, 298, 360, 366, 367, 368, 369, 370, 371, 431
Dicerorhinus	SUMAM	2	"sumatrensis"	Sumatra	Recent	21, 46
Diceros	BICOM	47	"bicornis"	East Africa	Recent	147, 149, 150, 151, 155, 157, 161, 166, 167, 168, 169, 170, 174, 176, 177, 178, 181, 294, 295, 305, 379, 382, 384, 386, 387, 388, 389, 390, 392, 393, 394, 396, 397, 398, 402, 405, 407, 408, 410, 411, 412, 414, 418, 436, 437, 441, 443
Rhinoceros	UNICM	9	"unicornis"	India/Nepal	Recent	48, 53, 55, 303, 348, 349, 426, 427, 429
	JAVAM	3	"sondaicus"	Java	Recent	17, 18, 299

Genus	Code	N	Species	Locality	Age	Specimens
Aceratherium	ACER1M	2	"depereti"	Mongolia	Hemphillian	206,245
	ACER2M	2	"incisivium"	Europe	Blancan	124,212
Aphelops	APHE1M	4	megalodus "megalodus"	Nebraska	Barstovian "	209,211 207,208
	APHE2M	6	megalodus	Nebraska	Clarendonian	213,273,274 330,331,333
	APHE3M	4	malcorhinus " malacarhinus "longipes"	Oklahoma Texas Florida	Early Hemiphillian " "	214 215 216,275
	APHE4M	4	"mutilis" mutilis "P. ponderis"	Texas Colorado	Late Hemiphillian	322,338 339,494
Diceratherium	DICE1M	1	"armatum"	Niobrara Co., Wyoming	Arikareean	241
	DICE2M	1	"niobrarense"	Niobrara Co., Wyoming	Arikareean	451

Genus	Code	N	Species	Locality	Age	Specimens
Forstercooperia	FORS1M	1	"sharamurunensis"	Inner Mongolia, China	Uintan-Duchesnian	126
	FORS2M	2	"confluens"	Mongolia	?	128,129
Hyrachyus	HYRA1M	2	"modestus"	Wyoming	Bridger (B)	4,323
	HYRA2M	2	"eximius"	?	Bridger (D)	6, 8
Hyracodon	HYCOM	4	nebraskensis	South Dakota, Nebraska	Orellan	117,120,280,460
Indricotherium	INDRM	1	transuralicum	?	?	258
Menoceras	MENO1M	10	arikarense	Nebraska	Arikareean	189,190,191,192 194,454,457
			?	Wyoming	"	158,172,186
	MENO2M	1	barbouri "marslandiensis"	New Mexico	Hemingfordian	132

Genus	Code	N	Species	Locality	Age	Specimens
Penetrigonias	PENE1M	1	"dakotense"	South Dakota	Oligocene	15
Peracerss	PERA1M	3	"profectum" "hessei"	New Mexico	Barstovian "	276,340 324
	PERA2M	2	"superciliosum"	New Mexico	Barstovian	319,325
Subhyracodon	SUBH1M	8	"occidentalis"	South Dakota	Orellon	35, 43, 44 28, 29, 38 48, 65
	SUBH2M	2	"mitis"	Wyoming	?	32, 33
	SUBH3M	6	"tridactylum"	South Dakota	Whitneyan	231,232,234,279
			"	"	Whitneyon	458
			"	"	?	425
Teleoceras	TELE1M	3	americanum	Nebraska	Hemingfordion	249,250,253
	TELE2M	6	medicornutum	New Mexico	Barstovian	346,347
			"	"	"	259,260
			medicornutum "thomsoni"	Nebraska	"	254,255

Genus	Code	N	Species	Locality	Age	Specimens
Teleoceras (ctd)	TELE3M	12	major	Nebraska	Clarendonian	217,218,219, 221A,221B,262, 263,264,312, 313,314
				South Dakota	"	261
	TELE4M	4	hicksi	Colorado	Late Hemphillian	226,281,282,283
	TELE5M	2	"fossiger"	Kansas	Early Hemphillian	286,424
		6	fossiger	Oklahoma, Texas		223,224,225 227,290,292
Trigonias	TRIGM	13	osborni	South Dakota	Chadronian	421
			osborni "taylori"	Colorado	"	491
			osborni	Colorado	" "	423,470,474, 477,479,480, 481,483,484, 485,486
Zaisanamynodon	ZAIS1M	1	?	Inner Mongolia	Chadronian	107
	ZAIS2M	1	?	Oregon	Chadronian	114

1. Codes refer to the subgeneric groups determined in Chapter 3.
2. Sample sizes of subgeneric groups.
3. Species names in quotes are those associated with museum tags.
4. Localities are derived from information associated with muse4um specimens.
5. Age is given as American Land Mammal Age where possible (see Figure 3.)
6. Specimen numbers were assigned sequentially as specimens were measured and correspond to page numbers in the original data book.

METHODS

Measurements

A morphometric suite of 83 linear measurements (57 skull; 26 mandible) was designed to include both global and local information about size and shape, and to include information from sagittal, coronal, and horizontal planes. A major constraint on measurement design was the ease and probability of finding landmarks on fossil specimens. Measurement of horns was not considered because many fossil taxa are hornless, horns are not preserved in fossil taxa with horns, and rhinoceros horns are epidermal (keratinous), not osteological features. To maximize data retrieved from fragmentary and reconstructed specimens, measurements were estimated when: (1) bilateral symmetry allowed doubling of a measurement made to the median plane, (2) caliper placement could be done by eye, or (3) when a feature (landmark) could be reconstructed using clay. Further, measurements were noted as estimates when: (1) a landmark was part of a questionable reconstruction, (2) a landmark was good but distortion evident, or (3) a landmark was poorly defined on a good specimen. All measurements were taken to the nearest millimeter using a standardized sequence. Complete descriptions of instruments, landmarks, and all original measurements are given in Appendix 3. Of the original measurement suite, a subset (19 skull; 11 mandible) was used for analysis. Many original measurements were excluded to reduce the number of missing values in the data set (discussed below). Brief definitions and abbreviations of the measurements used are listed in Table 4 and are illustrated in Figure 4 (skull) and Figure 5 (mandible).

Data and Statistics

Initial screening of the data included inspection of means, standard deviations, skewness, kurtosis, histograms, bivariate plots, and preliminary principal components results. Identification of transcription and gross measurement errors resulted in some data corrections. In cases where simple mistakes were not obvious, modifications or exclusions of suspect data were based on all available biological, statistical, and procedural information available. When possible, measurements were checked against specimen photographs of known scale.

The incompleteness of fossil specimens resulted in many missing values in the data set. Because of the requirement for complete data by multivariate methods, the number of missing values was reduced by excluding: (1) specimens with many missing values across measurements, and (2) measurements with many missing values across specimens. Exclusions were done until no more than five percent of values were missing for any given specimen or measurement. The remaining 19 skull and 11 mandible measurements (Table 4) indicate which structures and landmarks have most often

TABLE 4. Short definitions of linear measurements used for analysis. Measurements are illustrated in Figures 4 (skull) and 5 (mandible). A complete list of all 83 original measurements with full definitions is given in Appendix 3.

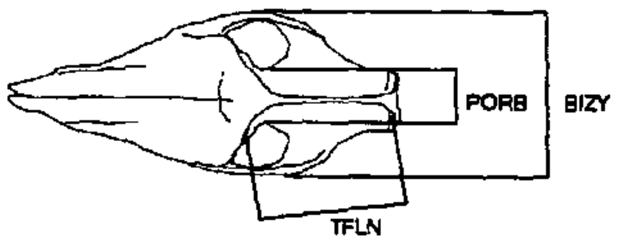
SKULL (19 measurements)

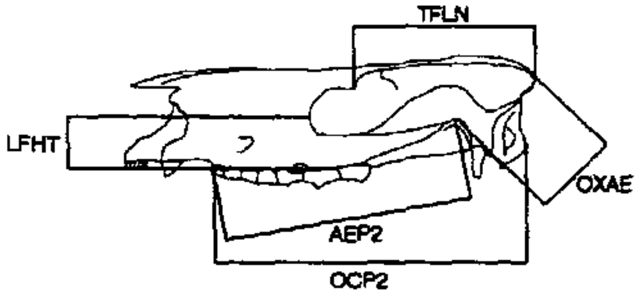
AEAE - Articular eminence to articular eminence
AEOR - Articular eminence to orbit
AEP2 - Articular eminence to second upper premolar
BICN - Bicondylar breadth
BIZY - Outer bizygomatic breadth
LFHT - Lower face height
LOXB - Lower occipital breadth
M1M1 - Breadth across upper first molars
M3M3 - Breadth across upper third molars
MGAE - Foramen magnum to articular eminence
MXGT - Maxillary grinding tooth row length
MXMO - Maxillary molar tooth row length
OCP2 - Occipital condyle to upper second premolar
OXAE - Occiput to articular eminence
OXOR - Occiput to anterior orbital margin
PORB - Postorbital constriction width
TFLN - Temporal fossa length
ZYHT - Zygomatic process height
ZYLN - Zygomatic process length

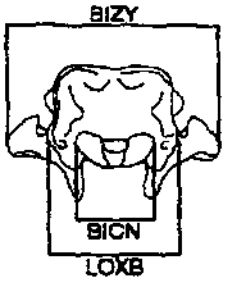
MANDIBLE (11 measurements)

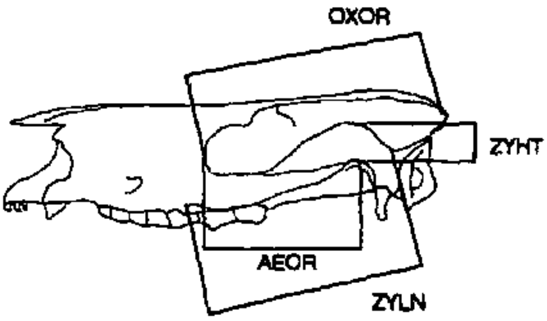
ANGD - Mandibular angle depth
ANGW - Mandibular angle width
BDBR - Mandibular body breadth
BDM1 - Mandibular body plus M1 height
BDHT - Mandibular body height
CNM3 - Mandibular condyle to third lower molar
LM1L - Lower first molar length
LM1W - Lower first molar width
MNMO - Mandibular molar tooth row length
RAMD - Mandibular ramus depth
RAMH - Mandibular ramus height

FIGURE 4. Illustration of the linear measurements taken on skulls. Endpoints of open rectangles indicate the landmarks for caliper placement. Measurement codes and short definitions are given in Table 4.


PORB
BIZY
TFLN


TFLN
LFHT
OXAE
AEP2
OCP2


BIZY
BICN
LOXB


OXOR
ZYHT
AEOR
ZYLN

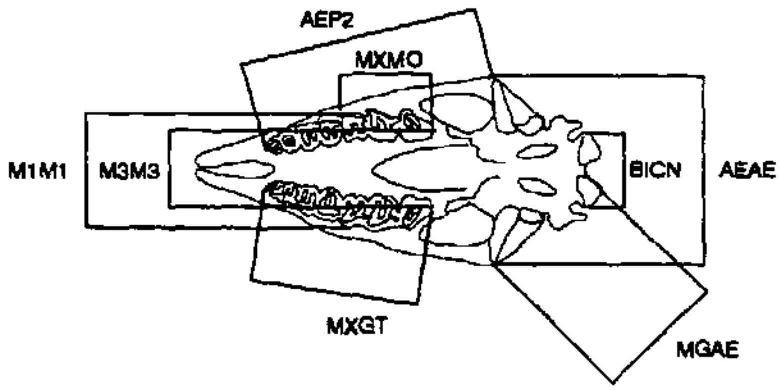
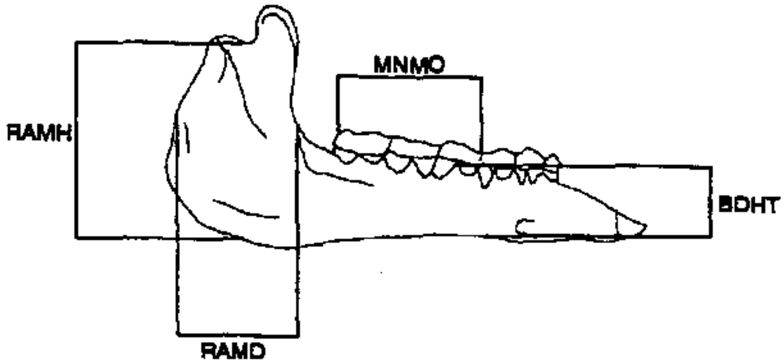
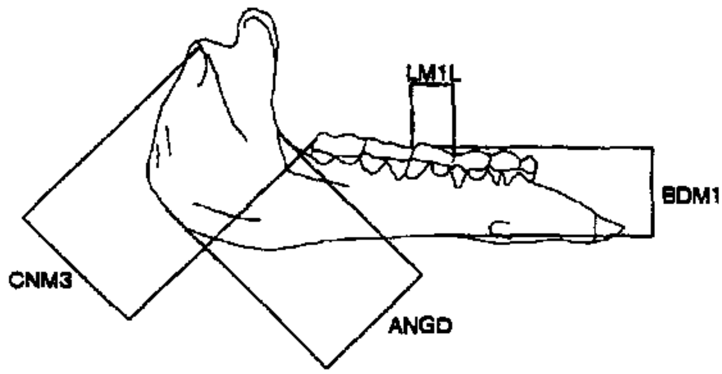
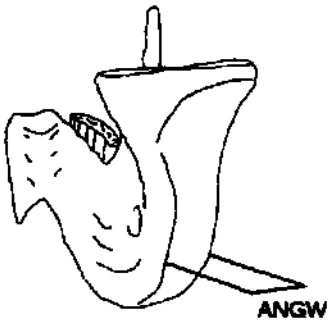
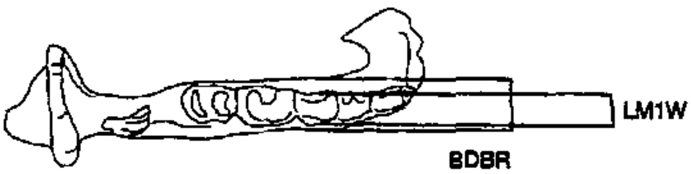

AEP2
MXMO
M1M1
M3M3
BICN
AEAE
MXGT
MGAE

FIGURE 5. Illustration of the linear measurements taken on mandibles. Endpoints of open rectangles indicate the landmarks for caliper placement. Measurement codes and short definitions are given in Table 4.


MNMO
RAMH
BDHT
RAMD


LM1L
BDM1
CNM3
ANGD


ANGW

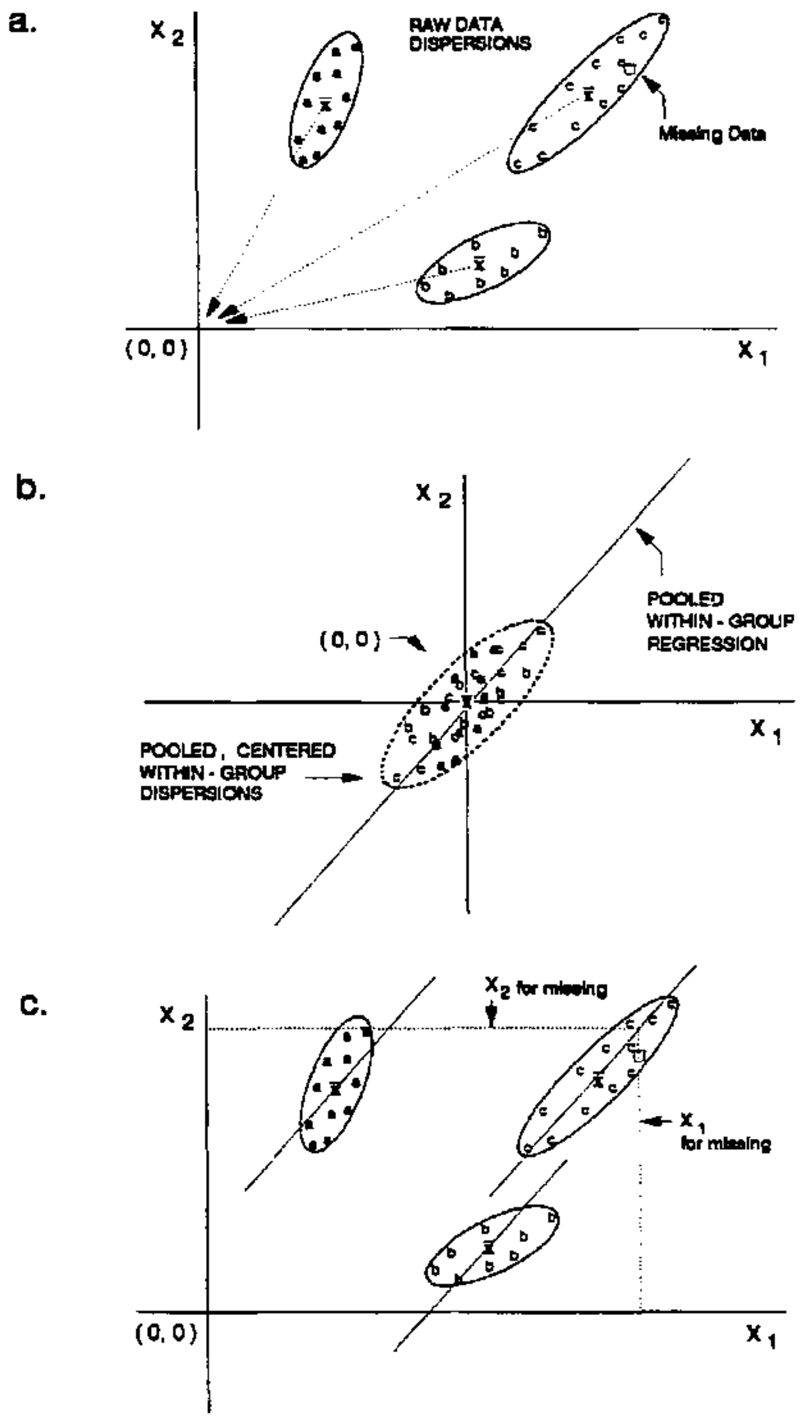

LM1W
BDBR

survived the geological burial-exposure cycle in fossil rhinoceroses.

The small number of remaining missing values were estimated by a multiple stepwise regression technique illustrated in Figure 6. Skull and mandible data sets were treated separately and independently. For each data set, all living and fossil genera were simultaneously mean-centered about the origin, producing a pooled within-group dispersion. For each measurement with missing values, a multiple regression equation was fit to the pooled data, where the measurement being estimated was the dependent variable and the remaining measurements were the independent variables. This resulted in a number of equations equal to the number of measurements with missing data. Missing values within each genus were estimated using the mean of that genus and the parameters of the appropriate multiple regression equation. A total of 39 values (27 skull; 12 mandible) were estimated and are indicated in the complete data sets for skulls and mandibles (Appendix 4).

Subsequent principal components analysis of the complete data sets (Chapter 3) resulted in the identification of subgeneric groups more closely representing species-level variation. Missing value estimation was repeated using a pooled within-group dispersion based on these new subgeneric groups. Estimates from the second iteration were used for all subsequent multivariate analyses, including reanalysis of the principal components results.

FIGURE 6. Bivariate example of the regression technique for estimating missing values. X_1 is the independent variable, X_2 is the dependent variable. (a) The raw data dispersions of all groups (generic or subgeneric) are mean-centered at the origin, producing a pooled within-group dispersion. (b) The least-squares regression line is determined for the pooled dispersion. (c) The pooled regression line is forced through the mean of each group and used to obtain estimates of missing values (X_2 predicted from X_1).


a.
RAW DATA DISPERSIONS
Missing Data
(0, 0)
X_1
X_2
b.
POOLED WITHIN - GROUP REGRESSION
(0, 0)
POOLED, CENTERED WITHIN - GROUP DISPERSIONS
X_1
X_2
c.
X_2 for missing
X_1 for missing
(0, 0)
X_1
X_2

A series of tests was run on the skull and mandible data to determine whether logarithmic transformation was required or advantageous. Means versus standard deviations for both raw and base-ten log-transformed data were plotted across all groups for each measurement. No consistent patterns of high correlation were observed between means and standard deviations for raw data. Additionally, no systematic reductions of correlation were observed as a result of logarithmic transformation. The assumption that larger animals exhibit greater relative variation was not supported by the rhinoceros data sets. Therefore, all analyses were performed on the raw, untransformed data.

CHAPTER 3.

WITHIN-GROUP RELATIONSHIPS
- PRINCIPAL COMPONENTS ANALYSIS

MULTIVARIATE VARIATION AND PRINCIPAL COMPONENTS ANALYSIS

Multivariate cranial and mandibular variation of living and fossil genera were analysed using principal components analysis (PC). This method allows the multivariate data to be "observed" from the perspective of orthonormal (mutually perpendicular), variance maximizing axes, derived as linear combinations of the original variables. The PC axes are ordered such that variation explained is greatest along the first axis, next greatest along the second axis, and so on until all of the variation of the original variables is accounted for by the new axes. Principal components is a dimension reduction technique because much of the original sample variation (and variation of interest) is usually included in the first two or three PC axes. Size differences among specimens often contribute much to the total variation and are usually maximized along the first PC axis. Specimens with large size differences but subtle shape differences will be separated more along the first axis, less on higher axes. Specimens of similar size but with greater shape differences may be separated in different ways across a number of PC axes. Because the PC axes define a unique morphological space, the closer specimens or group means plot together, the more similar they are in overall morphology as defined by the particular measurement suite used.

STRATEGY AND SIGNIFICANCE OF PRINCIPAL COMPONENTS RESULTS

The variation of skulls and mandibles for each genus of living and fossil rhinoceros was observed in the plane defined by the first (PC1) and second (PC2) principal component axes (first principal component plane, PCP1). For most genera, these two axes account for 60% or more of the variation originally dispersed among the 19 skull variables or 11 mandible variables. The generic dispersions of individuals were subdivided where possible into biologically significant subgroups based on geographic, chronologic, taxonomic, and variational information. These subgeneric groups represent estimates of biological populations separated by time and/or space, and in most cases approximate the species-level variation shown by the living analogues. A secondary purpose for dissection of the generic variation was to obtain a pooled within-group dispersion whose variation is an estimate for an "average" rhinoceros population (species?). This pooled dispersion is used by canonical variates analysis to maximize among group variation (Chapter 4). To summarize, the analyses of generic and subgeneric variation, described in detail below, provide: 1) insight about the nature and extent of variation within and among the genera of a large, diverse, and evolutionarily significant vertebrate taxon, and 2) provide a standard (pooled within-group variation) by which the morphological relationships among groups can be assessed.

SEX DIMORPHISM

Systematic differences in size and/or shape of males and females may contribute to intraspecific osteometric variation. It may, thus, be important in comparisons of interspecific and intergeneric differences both within and between living and fossil groups. Taxonomic errors can occur (especially in fossils) when males and females are so dissimilar as to be interpreted as two taxa (Kurten, 1969). Among the living rhinos, Nowak and Paradiso (1983) state bluntly that females are smaller than males. Because many of the living rhino specimens were sexed at the time they were shot, it was possible to investigate multivariate sex dimorphism in two of the living genera (*Diceros* and *Ceratotherium*). Among the fossil taxa, evidence for multivariate morphometric sex dimorphism can be assessed by correlation of morphological clustering of specimens with qualitative characters believed to represent dimorphism *a priori*. In this study it was possible to investigate sex dimorphism of skull morphology in the fossil genus *Menoceras*.

PRINCIPAL COMPONENTS ANALYSES OF INDIVIDUAL GENERA

Total PC variation (sum of all eigenvalues) and the first three eigenvalues for each genus are summarized in Table 5. Among the living genera, *Diceros* and *Ceratotherium* have similar amounts of total variation for both skull and mandible data sets. Since these two taxa represent good single species and the sample sizes are reasonably large (n=48 and n=19, respectively), their total variation is the best estimate by which the fossil samples may be compared. Also significant is the higher total variation in *Rhinoceros*, representing two species. Least significant for comparison with fossils is the total variation for *Dicerorhinus* skulls and mandibles. The large total variation is probably an artifact of inadequate sample size (n=2). Thus, when comparing total variation between living and fossil genera, sample sizes must be considered. For smaller sample sizes, it is the relative dispersion of the points rather than the numeric value of the total variation which is important.

Scatter plots of PC1 versus PC2 for each genus are summarized in Figure 7 and Figure 8. Axes were set to include the extremes of the most variable genera and are the same across all of the generic PC plots. They thus allow direct comparisons of multivariate

TABLE 5. Eigenvalues, percent of total, and total variation for the first three axes of each generic principal components analysis. Total variation is for all axes (19 skull; 11 mandible).

SKULL

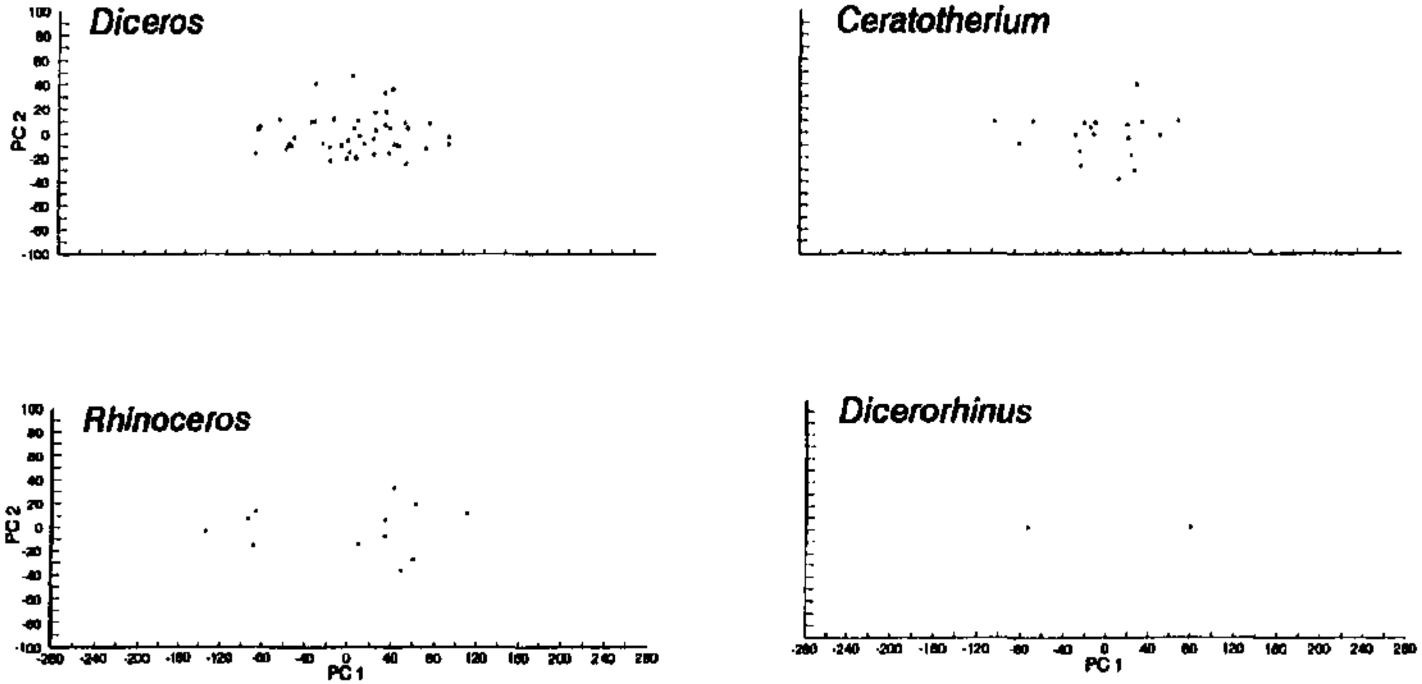
GENUS	PC1	%	PC2	%	PC3	%	Total
Dicerorhinus	11445.0	100.0	0.0	0.0	0.0	0.0	11445.0
Diceros	1996.1	60.2	263.9	7.9	218.1	6.5	3314.4
Ceratotherium	1978.6	59.9	335.5	10.1	214.5	6.5	3298.8
Rhinoceros	6176.8	82.2	416.7	5.5	378.9	5.0	7512.3
Aceratherium	12120.0	100.0	0.0	0.0	0.0	0.0	12120.0
Amynodon	3570.0	100.0	0.0	0.0	0.0	0.0	3570.0
Aphelops	6178.2	73.9	1017.8	12.1	472.3	5.6	8353.2
Diceratherium	10276.6	88.8	809.1	6.9	351.3	3.0	11669.0
Forstercooperia	3731.5	100.0	0.0	0.0	0.0	0.0	3731.5
Hyracodon	718.8	65.9	313.3	28.7	57.4	0.1	1089.7
Hyrachyus	7896.3	88.3	839.7	9.3	128.3	1.4	8939.4
Menoceras	1316.3	53.9	353.3	14.4	186.9	7.6	2437.9
Peraceras	43566.0	96.8	555.9	1.2	481.7	1.0	44969.1
Subhyracodon	5529.3	79.2	439.7	6.3	346.2	4.9	6980.5
Teleoceras	5988.3	61.2	1273.1	13.0	1068.1	10.9	9775.2
Trigonias	2106.2	43.2	1309.1	26.8	515.8	0.1	4869.6

MANDIBLE

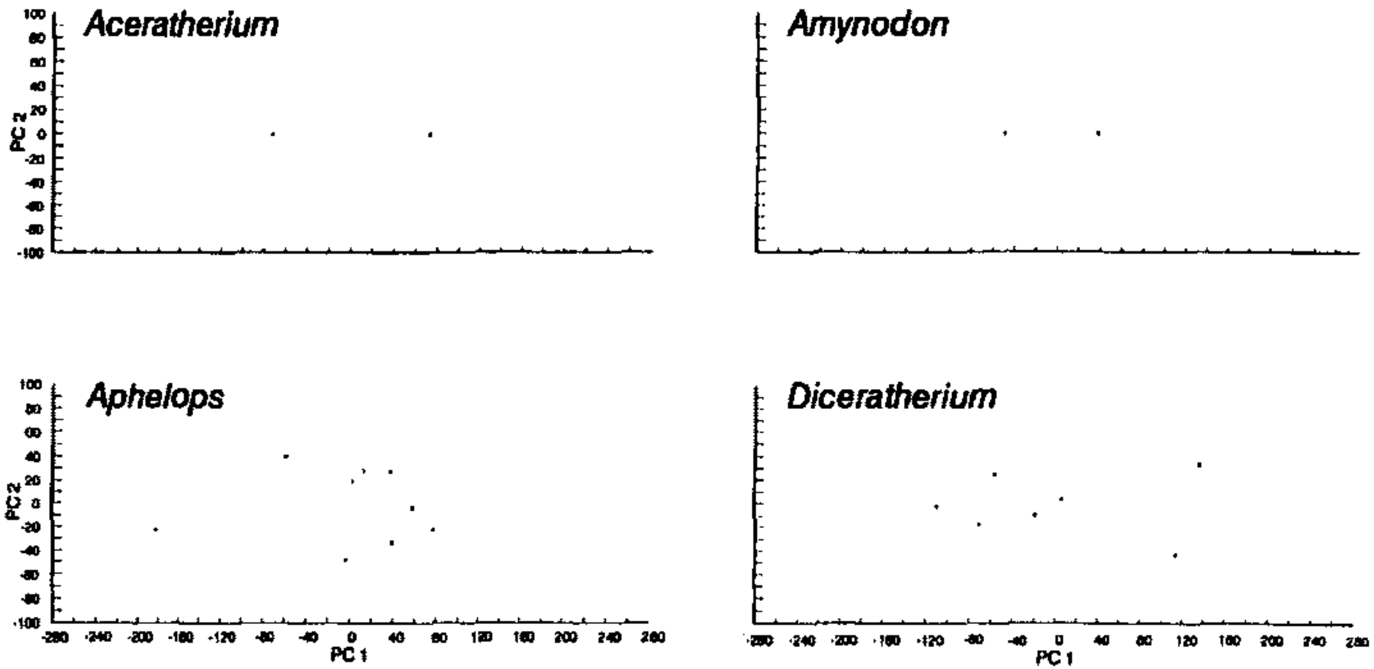
GENUS	PC1	%	PC2	%	PC3	%	Total
Dicerorhinus	3958.5	100.0	0.0	0.0	0.0	0.0	3958.5
Diceros	373.7	50.7	152.0	20.6	72.2	9.8	735.8
Ceratotherium	342.2	44.1	155.1	19.9	123.7	15.9	775.7
Rhinoceros	2069.1	87.8	130.2	5.5	68.7	2.9	2354.3
Aceratherium	294.5	59.3	135.6	27.3	65.6	13.2	495.9
Aphelops	3204.8	86.1	206.6	5.5	160.7	4.3	3720.0
Diceratherium	1204.7	85.9	121.0	8.6	33.6	2.3	1401.0
Forstercooperia	1769.9	93.2	127.0	6.6	0.0	0.0	1897.0
Hyracodon	140.0	66.6	41.5	19.7	28.6	13.6	210.1
Hyrachyus	1461.3	96.5	33.3	2.1	19.1	1.2	1513.9
Menoceras	308.4	69.7	86.5	17.0	49.9	9.8	507.9
Peraceras	2512.4	92.8	151.0	5.5	36.4	1.3	2722.4
Subhyracodon	696.9	71.3	112.7	11.5	79.5	8.1	977.4
Teleoceras	1120.7	61.6	301.9	16.5	136.2	7.4	1819.3
Trigonias	212.9	47.1	85.3	18.9	84.0	18.6	451.2
Zaisanamynodon	1008.0	100.0	0.0	0.0	0.0	0.0	0.0

FIGURE 7. Summary of principal components plots of skulls for living and fossil genera. Living genera are shown first followed by fossil genera in alphabetical order. All plots are to the same scale.

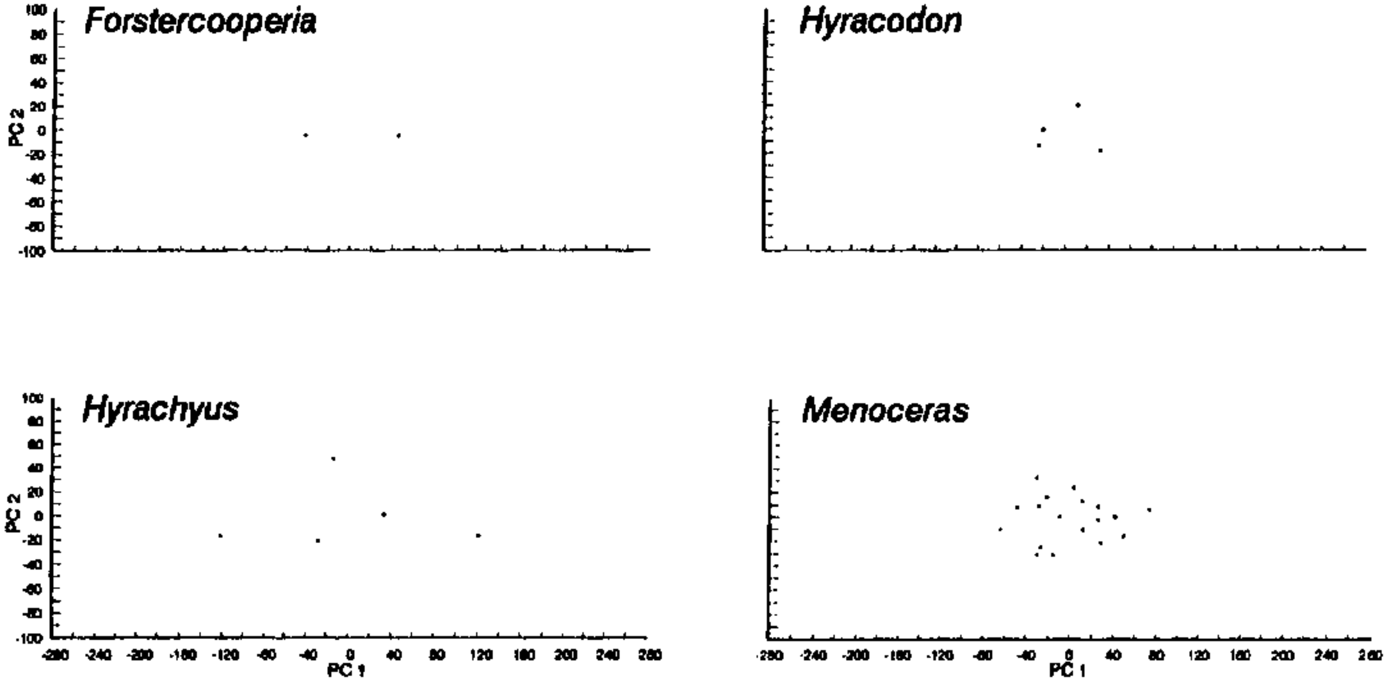
SUMMARY OF PRINCIPAL COMPONENTS ANALYSES - SKULLS



SUMMARY OF PRINCIPAL COMPONENTS ANALYSES - SKULLS



SUMMARY OF PRINCIPAL COMPONENTS ANALYSES - SKULLS



SUMMARY OF PRINCIPAL COMPONENTS ANALYSES - SKULLS

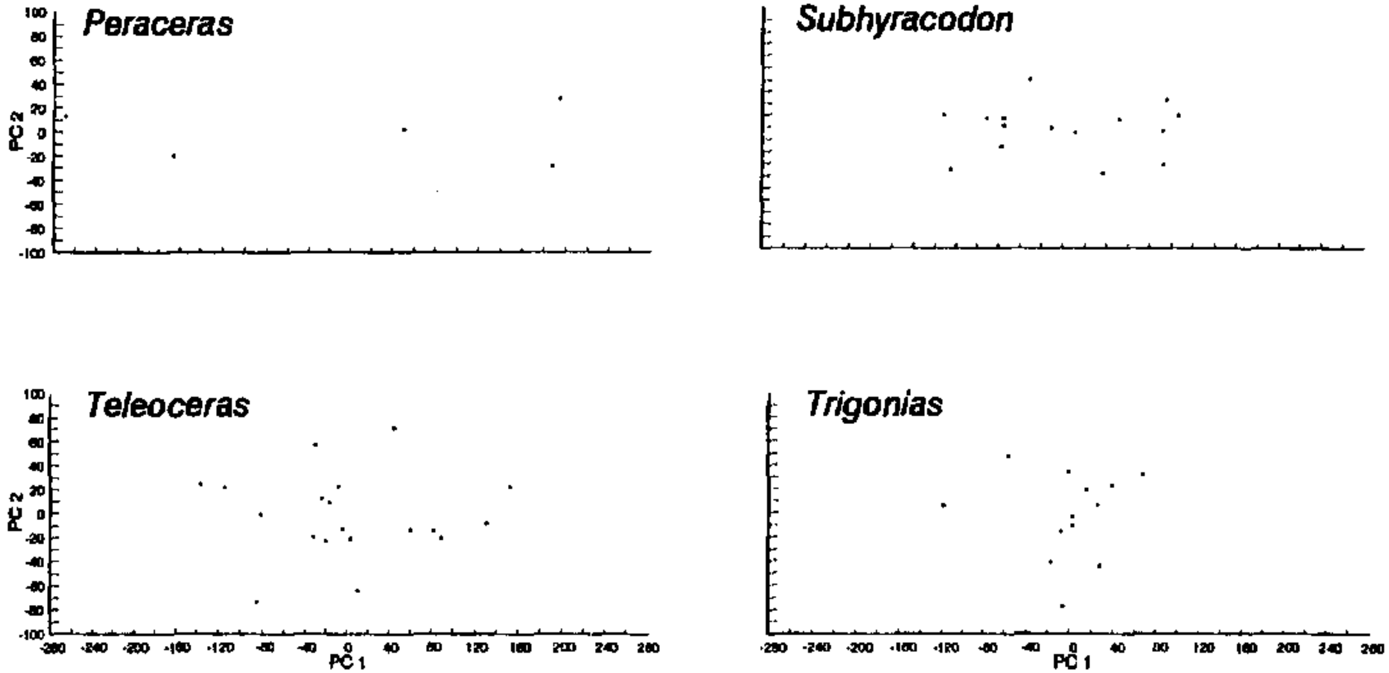
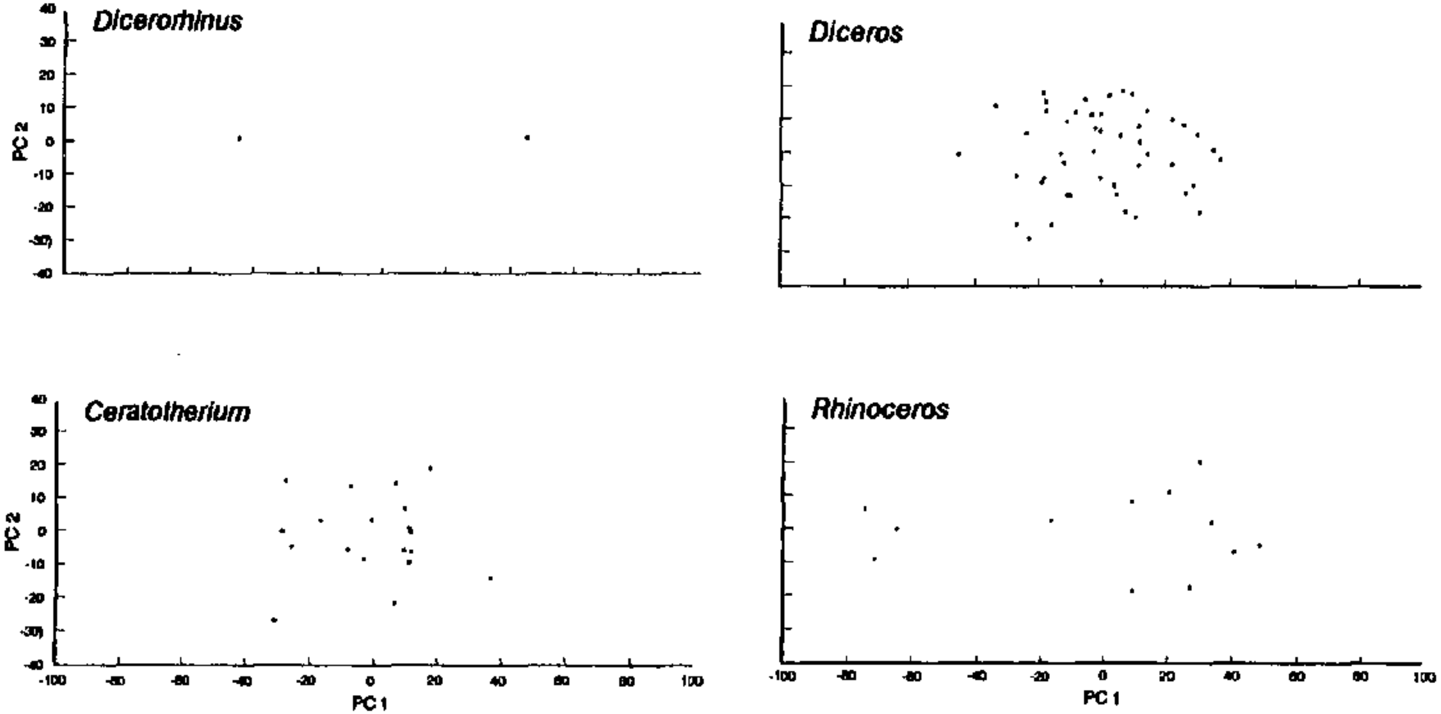
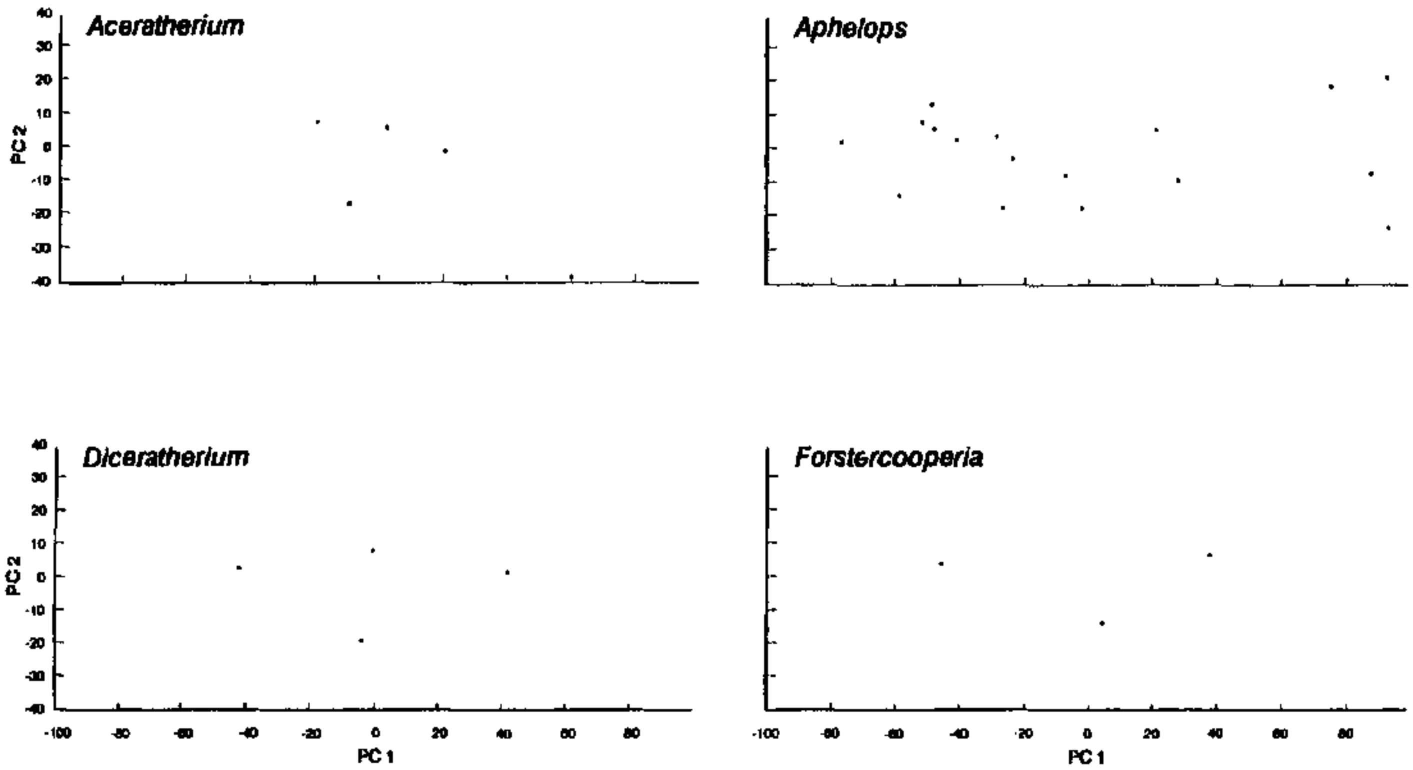


FIGURE 8. Summary of principal components plots of mandibles for living and fossil genera. Living genera are shown first followed by fossil genera in alphabetical order. All plots are to the same scale.

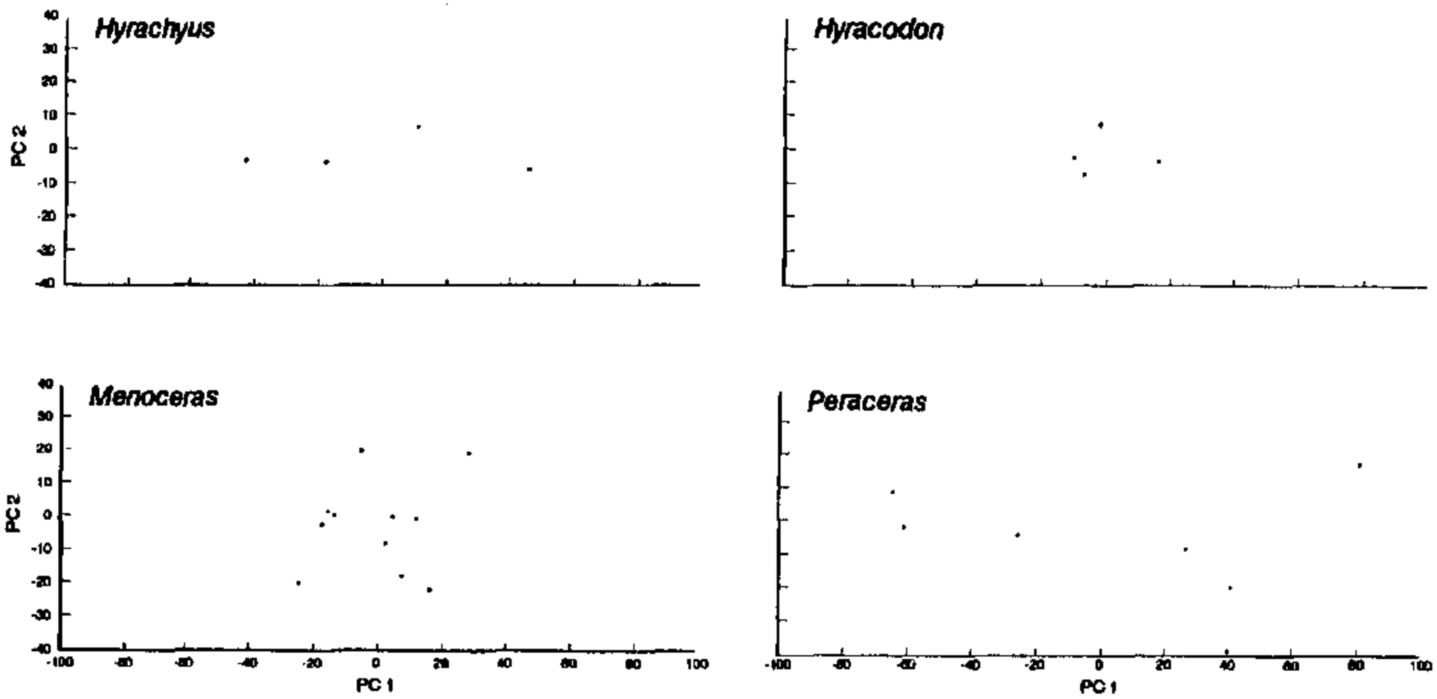
SUMMARY OF PRINCIPAL COMPONENTS ANALYSES - MANDIBLES



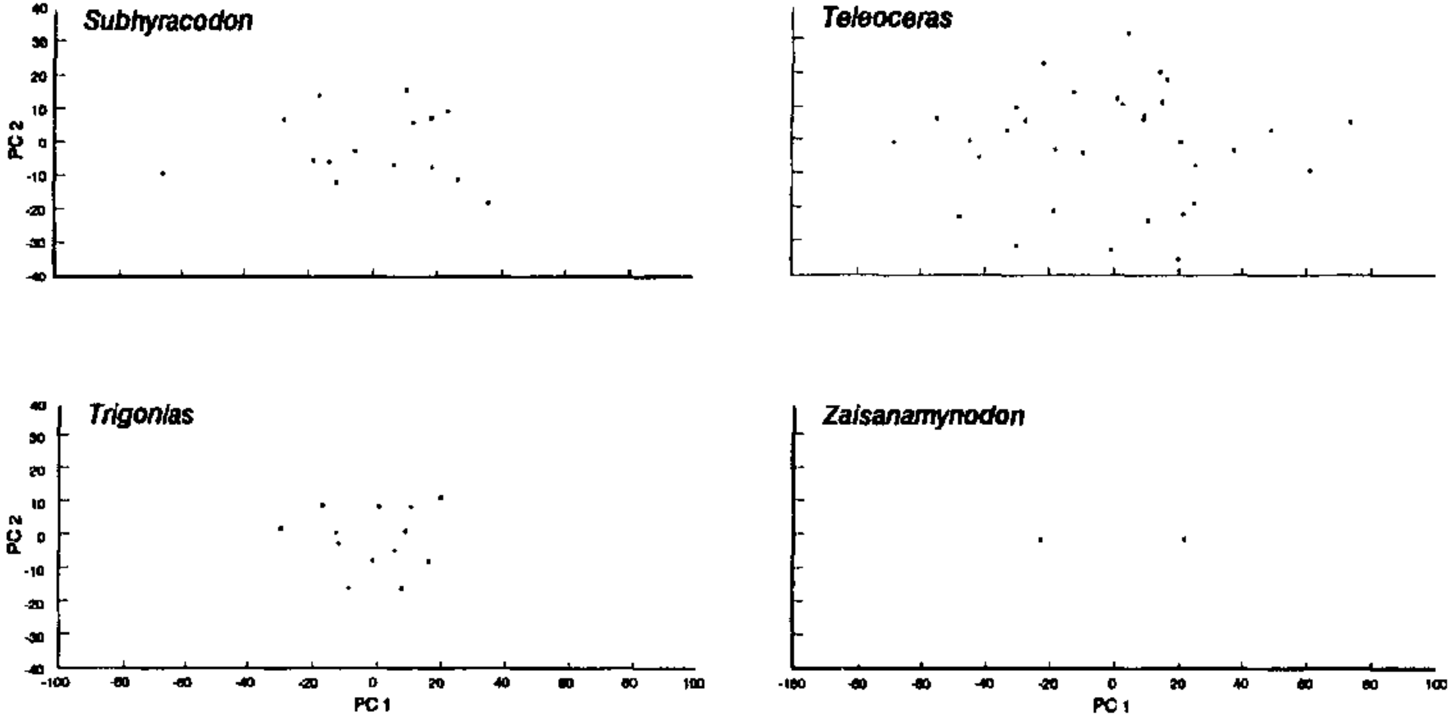
SUMMARY OF PRINCIPAL COMPONENTS ANALYSES - MANDIBLES



SUMMARY OF PRINCIPAL COMPONENTS ANALYSES - MANDIBLES



SUMMARY OF PRINCIPAL COMPONENTS ANALYSES - MANDIBLES



variation for skull and mandible characters. For example, among the skull samples, patterns range from *Diceros*, with the most homogeneous clustering of points, to *Peraceras* with a few widely scatterd points. Significantly, among all genera, *Rhinoceros* with its two component species shows the clearest bimodal clustering of specimens.

The PC analyses of each genus are discussed in detail below. Living rhinos are discussed first followed by the fossil genera. Each genus discussion begins with a brief introduction to the taxon followed by separate discussions of skull and mandible morphometric results.

Living Rhinoceroses

Locality data on the living rhinoceroses varies from relatively precise (e.g, the name of a town or river) to overly broad (e.g., "Africa"). Most often, the localities given indicate the political units in effect at the time the rhinos were collected (e.g., "British East Africa" or "Tanganyika"). Such regional geographic designations represent maxima since species inhabit patches within a given range at a given scale. For example, Goddard (1970) reported that the largest population of black rhinos existed within the 23,500 km^2 confines of Tsavo National Park (Kenya) and that within this range thirteen habitat types with local populations were recognized. In the Serengeti (Tanzania), "green regions", driven by rainfall, vary spatially and temporally (Sinclair, 1979), and this probably influences the ranges of local populations of rhinos. When the name of a town is given for the locality of several rhinos, it only indicates they are from the same region but not necessarily from the same local population. The locality data allow a limitied analysis of regional differentiation among the rhinoceros specimens.

Diceros

Diceros is comprised of a single species, *D. bicornis*, the black rhinoceros. It inhabits primarily brush and scrub transitional zones between grassland and forest where it browses on a variety of bushes and shrubs. Historically, the black rhino ranged over much of sub-Saharan Africa (Kingdon, 1979; Meester and Setzer, 1971, cited in Nowak and Paradiso, 1983). The specimens used were collected in "British East Africa" which was comprised mostly of the modern countries Kenya and Tanzania. Areas <u>not</u> sampled or included in this study include (1) South Africa and the Limpopo River drainage, (2) southwestern Angola, (3) the Zambesi River drainage, (4) Sudan (upper Nile), and (5) the Lake Chad region. Thus, the morphological variation represented by the specimens used may not represent the total range of variation for the species. As a standard of comparison for the fossils, therefore, the black rhino variation must be considered relative to the geographic range of sampled specimens as well as the amount of environmental heterogeneity within that range.

Two modern studies of black rhinoceros variation are those of Zukowsky (1964) and Groves (1967). Zukowsky proposed at least 16 "well differentiated" subspecies for *D. bicornis* based on observations of 95 skulls from European museums, zoo animals, photographs, and bibliographic sources. This amount of subspecific variation is questionable because of the small sample sizes (averaging six skulls per subspecies) and Zukowsky's own admission of great individual variation in the shape and structure of black rhino skulls. Groves criticized Zukowsky's work on the above grounds and noted that skull measurements do not often discriminate between the proposed subspecies. Using additional material, Groves studied East African populations in more detail and reported the existence of two size clines within the region formed by several subspecies and "intergrades" (Groves, 1967). The locality information for the specimens used in this study was insufficient for a detailed analysis of geographic variation in the black rhino. However, this study shows evidence of some geographic differentiation, supporting two of Grove's subdivisions (see below).

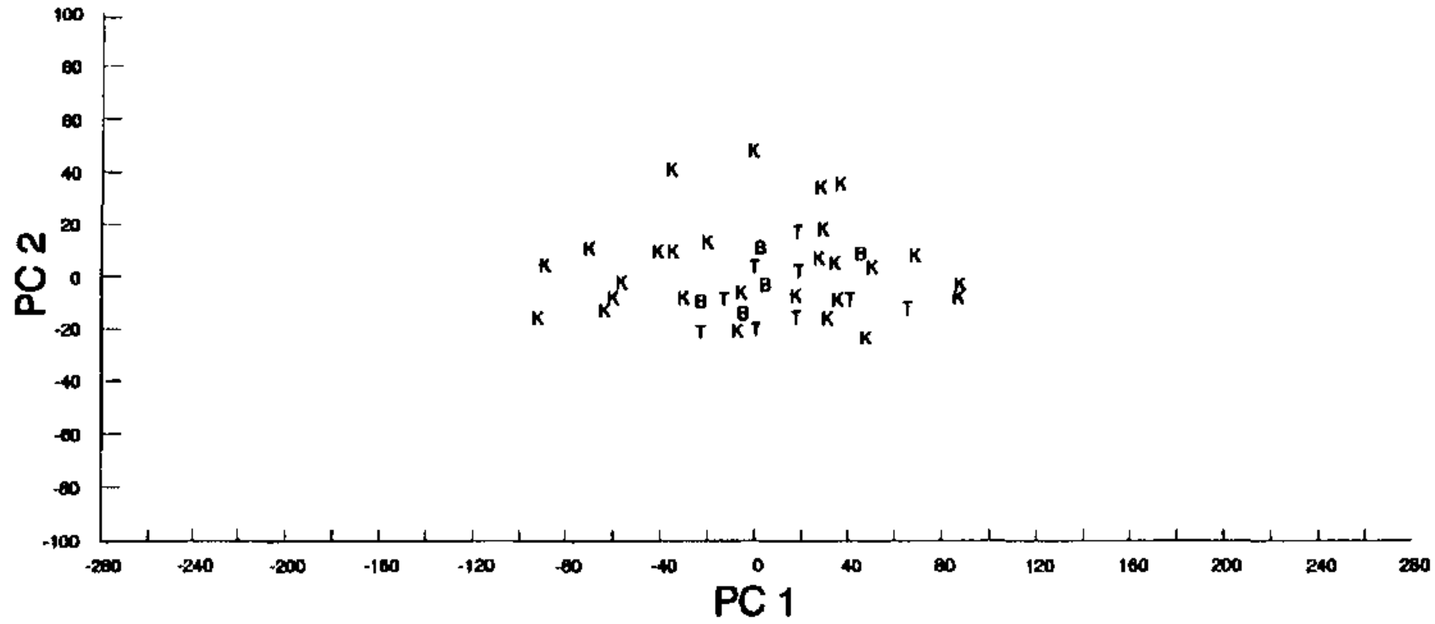
Neither Groves (1967) nor Zukowsky (1964, English summary) discussed sex dimorphism in the black rhino. Jarman (1983) suggested that male and female black rhinos reached similar weights and shapes. Ralls (1976), in a review of mammal species with larger females, did not include rhinoceroses. Evidence for sex dimorphism in the black rhino is presented below under separate discussions of skull and mandible.

Skull (Figures 9-13) -- Principal components ordination of the black rhino skulls with respect to PC1 and PC2 is shown in Figure 9 (same result as *Diceros* plot in Figure 7). This multivariate dispersion represents 68.1 percent of the total variation in the sample. Generally, in PC studies, specimens are ordinated by size along the first PC axis (size axis). This was confirmed here and is true for all subsequent plots. Higher axes (PC2, PC3, etc.) are related to aspects of specimen shape. This basic ordination plot (Figure 9) is used several times (Figures 10 - 13) where the only difference in is how the individual specimens are labelled.

Figure 9 also shows the provenience of the specimens with respect to the geographical units within which they were collected. The extremes of variation on both PC axes are represented by the Kenyan specimens. Both sets of specimens from British East Africa (BEA) and Tanzania (Tanganyika) are overlapping within the Kenyan cloud of variation. Whether or not BEA specimens are Kenyan or Tanzanian, these data suggest that there are no significant factors contributing to morphological differentiation between rhinos

FIGURE 9. Principal components plot of *Diceros* (black rhino) skulls with specimens identified to the largest geographic political unit based on museum tag information: B - British East Africa, K - Kenya, T - Tanzania. Scales are the same as all other skull plots in this chapter (see Figure 7). Corresponding plot of mandibles is shown in Figure 14.

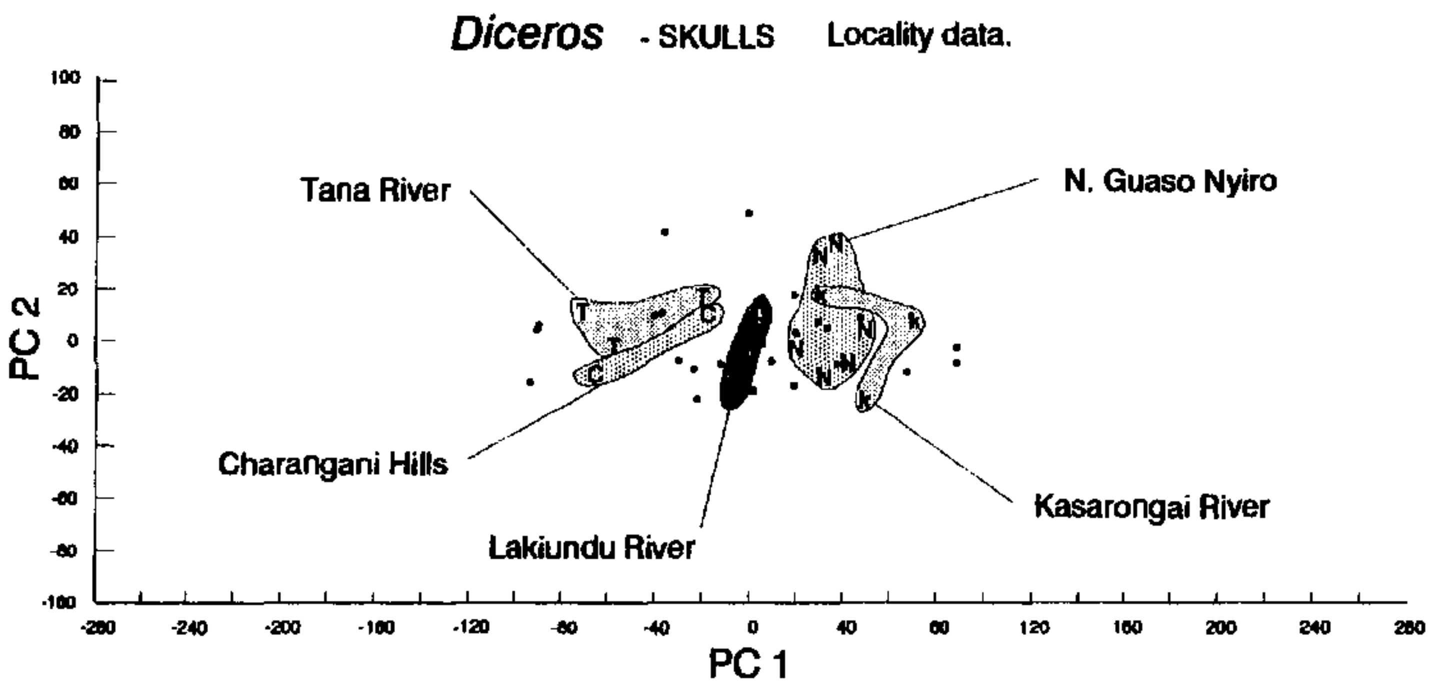
Diceros - SKULLS Geographic provenience by country.



collectively inhabiting Kenya versus those inhabiting Tanzania. A more detailed analysis of geographic variation is shown in Figure 10, based on limited locality data associated with the specimens. Although nothing can be concluded about differences between specimens from N. Guaso Nyiro and Kasarongai River, or between specimens from Tana River and Charangani Hills, N. Guaso Nyiro and Tana River specimens are distinct with respect to size. This supports Groves' (1967) observation of a west-to-east size cline among East African rhinos. The position of the Lakiundu River specimens confirms Grove's statement that Lakiundu populations are intermediate in the cline.

As mentioned previously, the nature and number of black rhino subspecies is not well established. Two relatively recent studies varied from 7 subspecies (Groves, 1967) to at least 16 subspecies (Zukowsky, 1964). The former study relied more on osteometric data, the later study on skull morphology and visual appearance. Many, if not most, of the original subspecific classifications of wild-caught specimens are probably meaningless in terms of biological information about real subspecies. More likely, in many cases, they represent local populations and were classified arbitrarily by non-experts. However, although the subspecific names may be wrong, there may be other important information confounded with them, such as geographic variation. Figure 11 shows specimens identified according to the subspecific

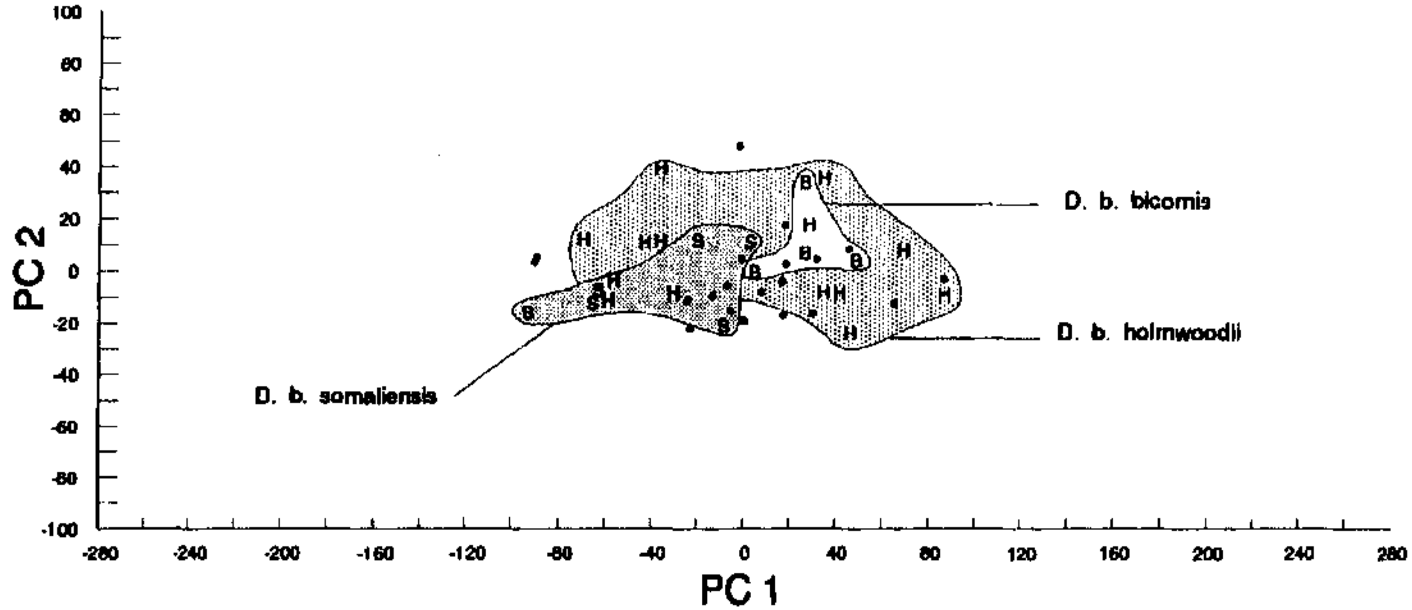
FIGURE 10. Principal components plot of *Diceros* (black rhino) skulls with specimens identified to regional locality based on museum tag information. Shaded areas include all specimens from the same locality. Dots represent specimens for which no locality data is known. Corresponding plot of mandibles is shown in Figure 15.



Diceros - SKULLS Locality data.
Tana River
N. Guaso Nyiro
Charangani Hills
Lakiundu River
Kasarongai River
PC 2
PC 1
100
80
60
40
20
0
-20
-40
-60
-80
-100
-280
-240
-200
-160
-120
-80
-40
0
40
80
120
160
200
240
280

FIGURE 11. Principal components plot of *Diceros* (black rhino) skulls with specimens identified by subspecies designations given on museum tags. Shaded areas include all members of the same subspecies. Dots represent specimens for which no subspecies designation was given: **H** - *D. b. holmwoodi*, **B** - *D. b. bicornis*, **S** - *D. b. somaliensis*. Corresponding plot of mandibles is shown in Figure 16.

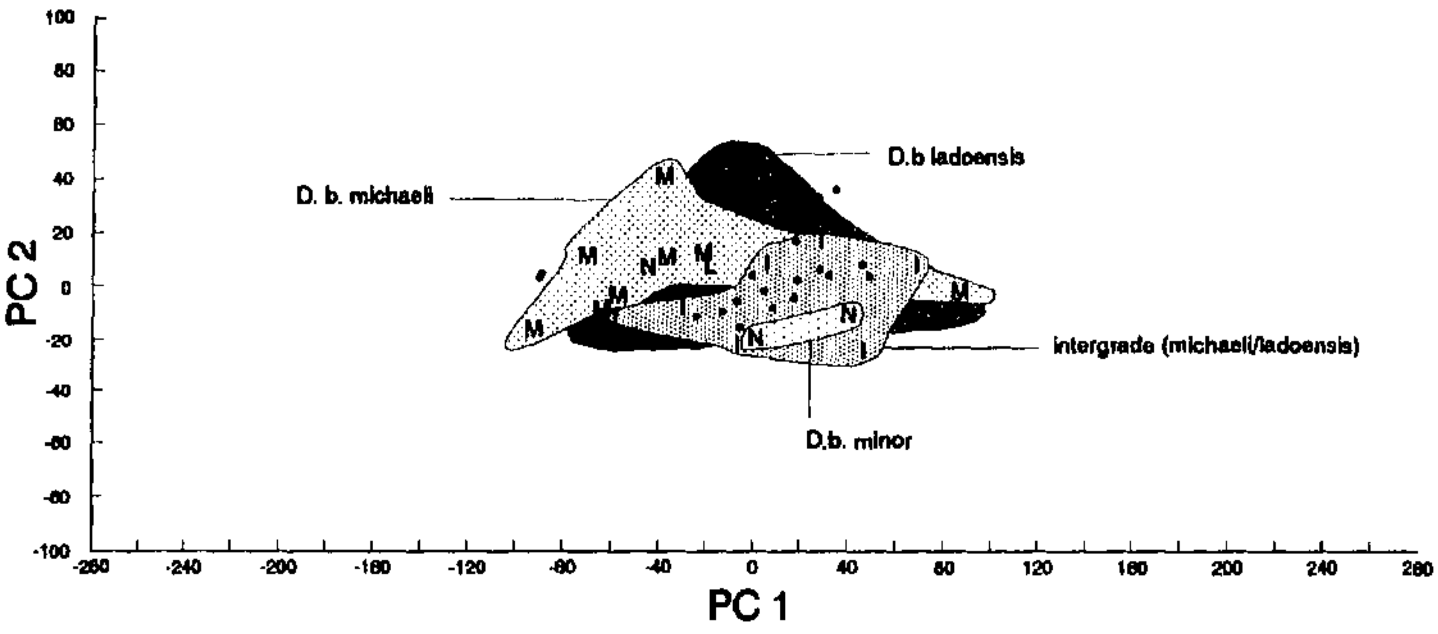
Diceros - SKULLS Subspecies by museum tags.



designations given on museum tags. Based on Groves' analysis, the subspecific epithets of Figure 11 would be mostly incorrect for the following reasons: (1) *D. b. holmwoodi*, now synonymous with *D. b. minor*, probably represented a wastebasket taxon since few of the orginal *holmwoodi* specimens are attributable to *D. b. minor*, (2) *D. b. somaliensis* is now a synonym of *D. b. brucii*, and found only in northern Somalia, and (3) *D. b. bicornis* is now restricted to animals from southern and southwestern Africa. Of interest morphometrically, however, is the separation of specimens labelled *D. b. bicornis* versus those labelled *D. b. somaliensis* which may indicate that the original subspecific classifications of those two groups were based on real biological differences. Further analysis of subspecific variation is shown in Figure 12 where locality data was used to matched specimens with Groves' (1967) subspecies and intergrades. The majority of identifiable specimens were assignable to *D. b. michaeli* or to a *D. b. michaeli - D. b. ladoensis* intergrade category. The morphometric separation of these two groups lies along an oblique axis (upper left to lower right) and suggests that the intergrade category is perhaps more of a real group than Groves gave it credit for. Conversely, the *D. b. ladoensis* specimens appear not to be distinguishable from either group.

FIGURE 12. Principal components plot of *Diceros* (black rhino) skulls with specimens identified to subspecies based on those of Groves (1967). Shaded areas include all specimens of the same subspecies. Dots indicate specimens for which no subspecific assignment was determinable: M - *D. b. michaeli*, N - *D. b. minor*, I - *D. b. michaeli|ladoensis intergrade*, L - *D. b. ladoensis*. Corresponding plot of mandibles is shown in Figure 17.

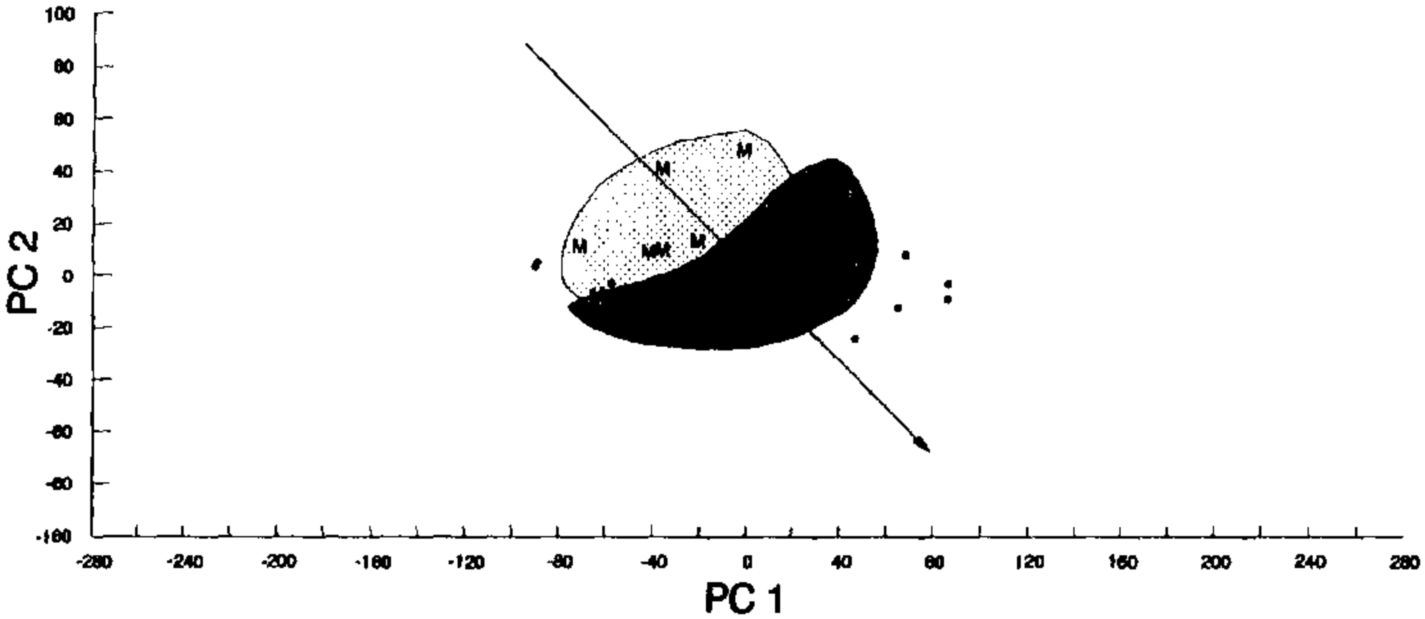
Diceros - SKULLS Subspecies after Groves, 1967.



An analysis of sex dimorphism of the black rhino skulls is shown in Figure 13 based on museum tag information. Sexing of the rhinos probably occurred at the time of collection but was not consistently recorded. The largest specimens in the analysis (right side of PC1) were not sexed. Most or all of these specimens could be males if males are actually larger than females on average and if there was a bias by the expeditions to take the larger (presumably bull) members during hunts. The following discussion of the pattern of the sexed specimens takes the data at face value. Inspection of the first axis indicates a tendency for females to be larger than males, contrary to Nowak and Paradiso (1983) who state that females are smaller than males (for all rhinos). The hypothesis that the female sample represents generally larger animals was tested using a Wilcoxan Rank Sum Test which gave a marginally insignificant result ($SUM_{male} = 67$; $SUM_{female} = 104$; $T_L = 66$; $T_R = 105$). The suggestion that females are larger than males in black rhinos would place this species among the minority of mammals exhibiting this phenomenon (Ralls, 1976). Although there is no significant size dimorphism, there is evidence for sex dimorphism in terms of shape or of size and shape combined. The principal component separation of males and female skulls shown in Figure 13 lies along an oblique axis (upper left to the lower right) which would be a linear composite of PC1 and PC2. The

FIGURE 13. Principal components plot of *Diceros* (black rhino) skulls with specimens identified by sex based on museum tag information. Shaded areas include specimens of the same sex. Dots represent specimens for which sex was not determined: M - male, F - female. Arrow represents an approximate axis (vector) of skull sex dimorphism in the PC morphospace. Corresponding plot of mandibles is shown in Figure 18.

Diceros - SKULLS Sex dimorphism.



details of these shape differences and their possible explanations have not been determined.

In summary, species level variation in *Diceros* skulls includes variation associated with geographic factors (interlocality and subspecific level variation) and with sex differences in skull shape. Demonstration of these factors of variation in this living analog is important and useful because fossil species can be expected to have exhibited these same kinds of variation.

Mandible (Figures 14-18) -- Principal components ordinations for black rhinoceros mandibles are given in Figures 14-18, which are different versions of the same PC plot. These plots parallel those of the skull studies in terms of the way specimens are labelled. Similarly, PC1 appears to be largely a size axis with smaller specimens on the left.

The results of geographic analyses are generally similar to those of the skull. At the lowest geographic resolution (country, Figure 14), Kenyan specimens determine the ranges of PC1-PC2 variation, while Tanzanian and BEA specimens lie within that dispersion. The Tanzanian mandibles, however, are more dispersed relative to the Kenyan mandible variation than are the Tanzanian skulls relative to Kenyan skull variation. Locality data for the black rhino mandibles (Figure 15) supports the skull data with respect to: existence and extent of local geographic variation,

FIGURE 14. Principal components plot of *Diceros* (black rhino) mandibles with specimens identified to the largest geographic political unit based on museum tag infromation.B - British East Africa, K - Kenya, T - Tanzanian. Scales are the same as all other mandible plots in this chapter (see Figure 8). Corresponding plot of skulls is shown in Figure 9.

Diceros - MANDIBLES Geographic provenience by country.

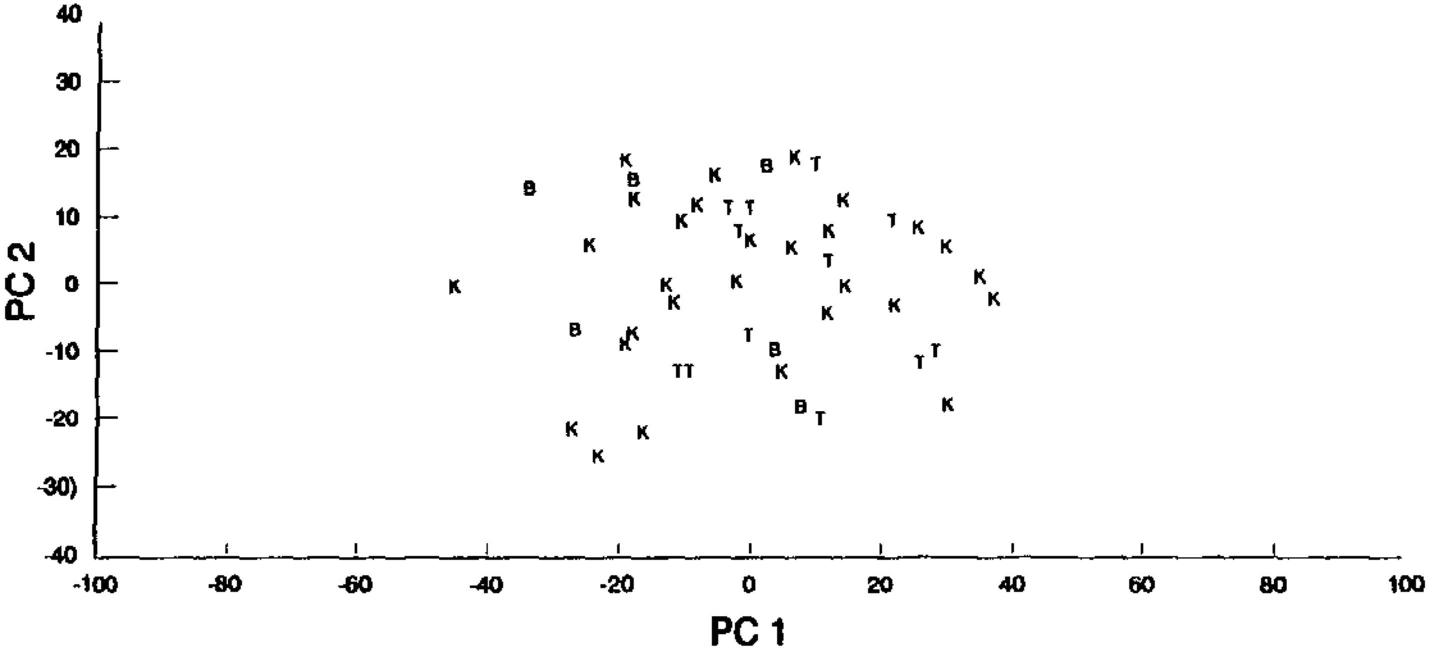
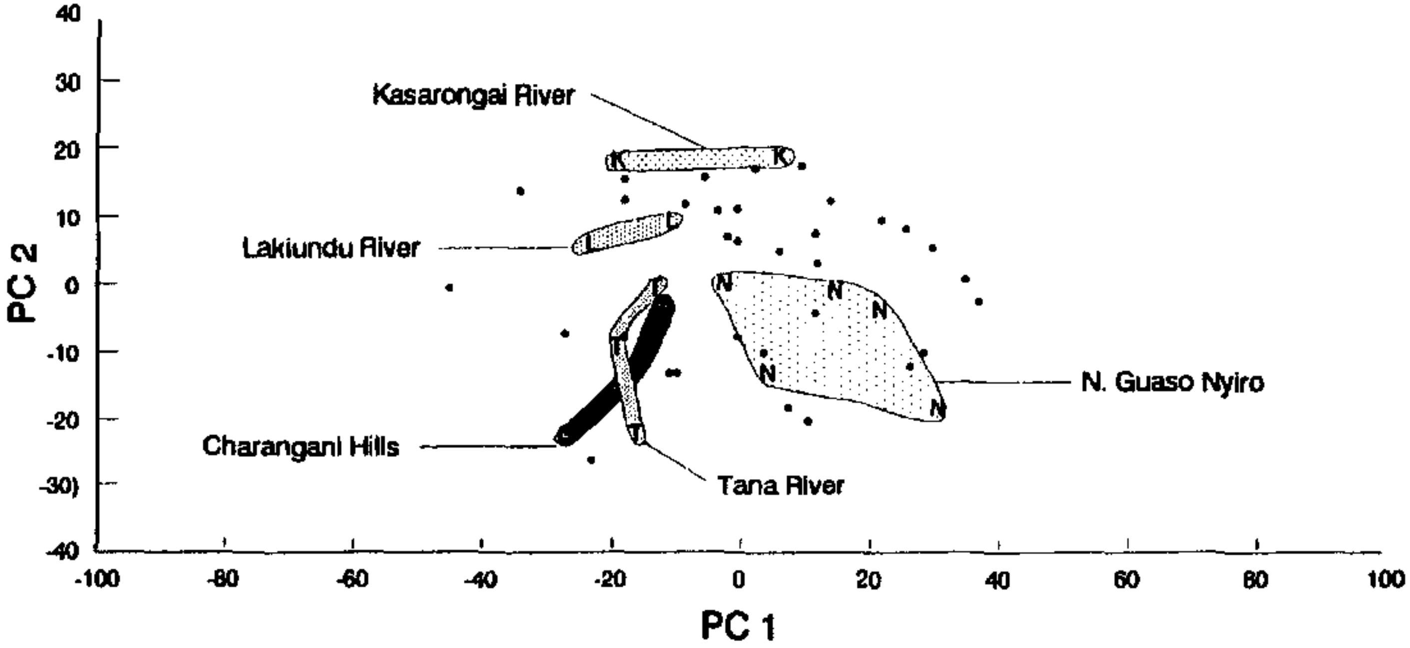


FIGURE 15. Principal components plot of *Diceros* (black rhino) mandibles with specimens identified to regional locality based on museum tag information. Shaded areas include all specimens from the same locality. Dots represent specimens for which locality was not determined. Corresponding plot of skulls is shown in Figure 10.

Diceros - MANDIBLES Locality data.



similarity of Charangani Hills and Tana River specimens, and an east-west size cline (N. Guaso Nyiro - Tana River). The pattern of morphological variation of the mandibles differs from that of the skulls in the following ways: Lakiundu River specimens are not intermediate in the size cline, Kasarongai River specimens are not similar to N. Guaso Nyiro specimens, and there is relatively more PC2 variation with respect to localities.

Results of subspecies analyses on the mandibles are also similar to the skull results. Figure 16 supports the morphological difference between those specimens originally assigned to *D. b. bicornis* and those assigned to *D. b. somaliensis*. Figure 17 supports the skull result that the *D. b. michaeli\ladoensis* intergrades form a group distinct from *D. b. michaeli* while *D. b. ladoensis* is not distinct. This result is less convincing because of the greater overlap in the mandible plot. It is interesting, however, that the separation of the intergrades and *D. b. michaeli*, to the extent that it is real, lies predominantly along the second axis. Thus, as in the locality analysis, mandibles appear to differ more by shape while skulls differ more by size.

Sex dimorphism was not observed in the black rhino mandibles (Figure 18). Both the largest and smallest sexed specimens were females, and the results of a Wilcoxan Rank Sum Test relative to PC1 were not significant ($SUM_{male} = 77$; $SUM_{female} = 76$; $T_L = 54$; $T_R = 90$). Thus, the sex dimorphism in black rhinos observed in

FIGURE 16. Principal components plot of *Diceros* (black rhino) mandibles with specimens identified by subspecies designations from museum tags. Shaded areas include all members of the same subspecies. Dots represent specimens for which no subspecies designation was given: H - *D. b. holmwoodi*, B - *D. b. bicornis*, S - *D. b. somaliensis*. Corresponding plot of skulls is shown in Figure 11.

Diceros - MANDIBLES Subspecies by museum tags.

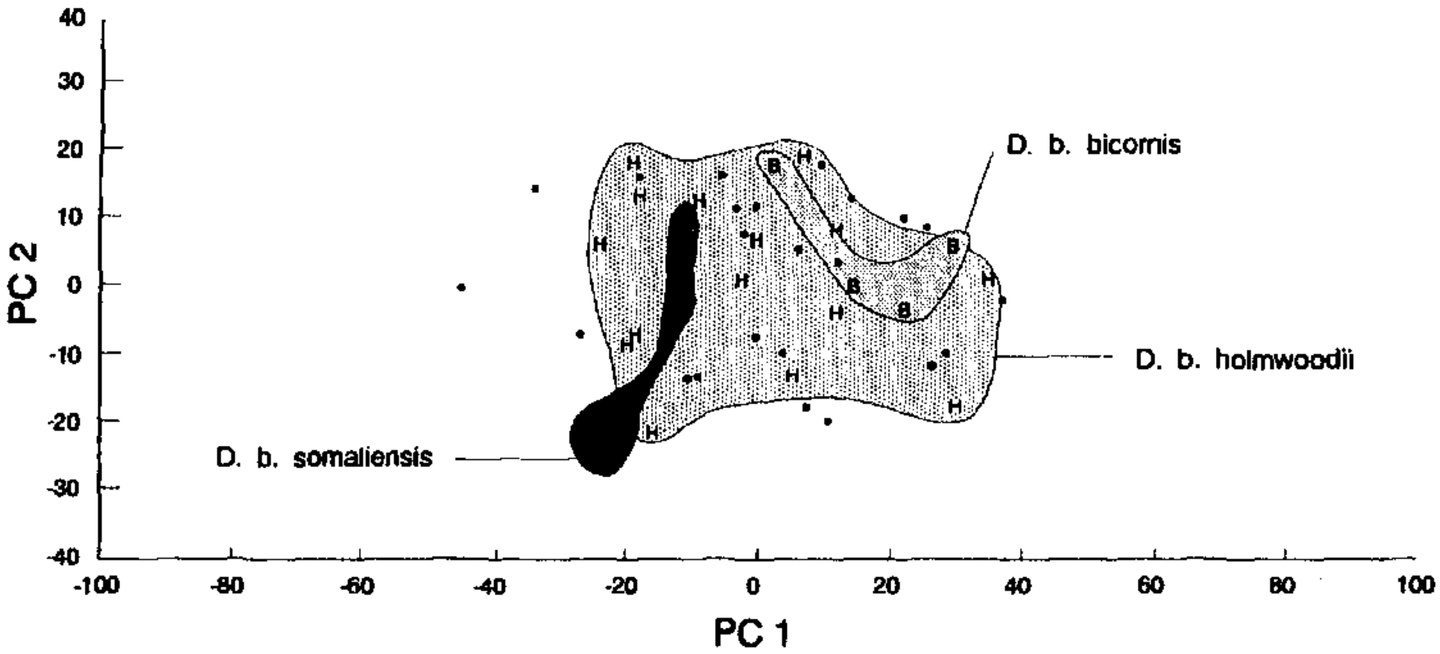


FIGURE 17. Principal components plots of *Diceros* (black rhino) mandibles with specimens identified to subspecies based on those of Groves (1967). Shaded areas include all specimens of the same subspecies. Dots indicate specimens which were not assignable to one of Grove's subspecies: M - *D. b. michaeli*, N - *D. b. minor*, I - *D. b. michaeli/ladoensis* intergrade, L - *D. b. ladoensis*. Corresponding plot of skulls is shown in Figure 12.

Diceros - MANDIBLES Subspecies after Groves, 1967.

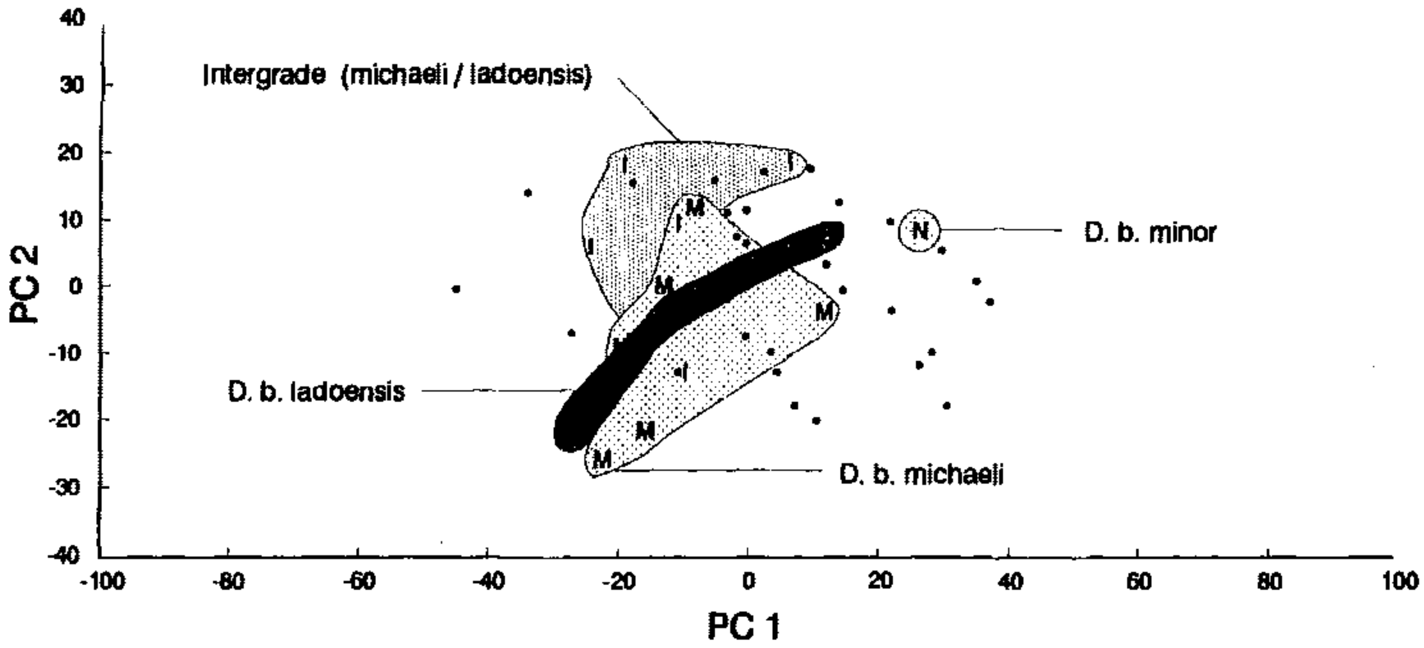
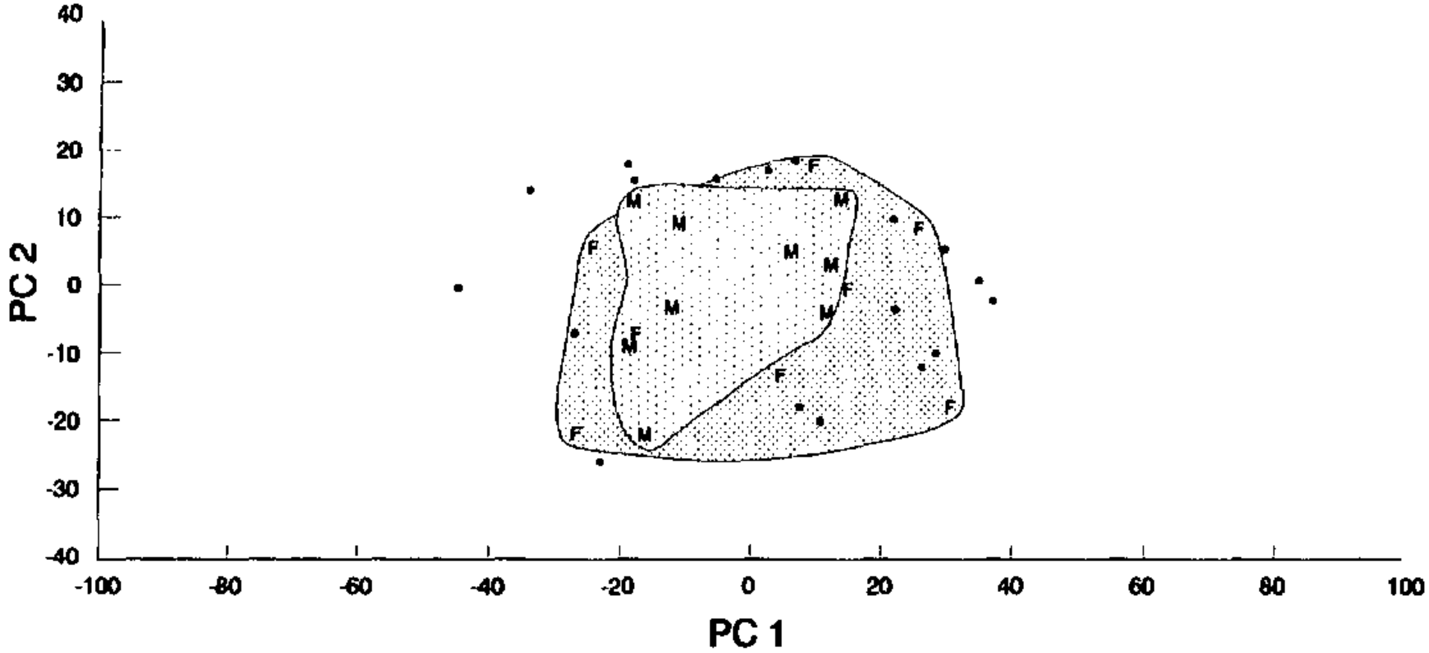


FIGURE 18. Principal components plot of *Diceros* (black rhino) mandibles with specimens identified by sex based on museum tag information. Shaded areas include all specimens of the same sex. Dots represent specimens for which sex was not determined. Corresponding plot of skulls is shown in Figure 13.

Diceros - MANDIBLES Sex dimorphism.



this study is regionalized to some features of the craniorostral skeleton (see discussion under *Ceratotherium*).

In summary, as compared to the skull sample, species level variation of the mandible sample appears to be less confounded by geographic and sex differences and is more often associated with PC2. It should be noted that, unlike the fossils, the living analog samples represent matched skull-mandible pairs. Mandibles might give systematically different results, perhaps due to regionalized differences in development and selection (mosaic evolution). This should be considered when interpreting the fossils.

Ceratotherium

Ceratotherium is represented by a single species, *C. simum*, the white rhinoceros. It primarily inhabits grassland and open forest (bushveldt in southern Africa) where it grazes unselectively on grasses. Historically, this species' geographic distribution consisted of two disjunct regions in Africa including a northern range (Chad, Central African Republic, S.W. Sudan, N.E. Zaire, and N. W. Uganda) and a southern range (S.E. Angola, S. W. Zambia, Mozambique, Rhodesia, Botswana, E. Namibia, and W. and E. South Africa) (Groves, 1975; Nowak and Paradiso, 1983). Each of the two geographic groups is considered a single subspecies with *C. s.*

cottoni in the north and *C. s. simum* in the south (Groves, 1972; 1975). Groves found differences between these subspecies to be very slight, but stressed the flatter skull and shorter maxillary tooth row in *C. s. cottoni*. All of the specimens in the sample studied here are *C. s. cottoni* from the region northwest of Lake Victoria including parts of Zaire, Uganda, and Sudan. The two most important collecting centers were Faradje (N.E. Zaire) and Lado Rhino Camp (Albert Nile, Uganda). This range is approximately similar in area to that for the black rhino sample, and similarly, may only represent a subsample of the total white rhino variation. Because no studies have suggested that *C. s. cottoni* represents more than one true subspecies, it was not possible to demonstrate variation due to subspecific variation in *Ceratotherium*. PC1 and total variation in the white rhino skull and mandible samples at the species level are approximately the same as that of the black rhino samples (Figure 7) despite differences in subspecific differentiation. This similarity of total variation between two distinct species lends support for the use of the living analogues as a gauge of specific level variation in fossil groups. Total variation for the white rhino skulls is second lowest among all the genera (only *Menoceras* is lower) and, among the mandible groups, only four fossil genera have lower total variation (Table 5).

<u>Skull</u> (Figures 19-20) -- The principal components results for *Ceratotherium* skulls were analyzed with respect to locality (Figure 19) and sex (Figure 20). These plots have the same scales (as for all skull plots), and PC1 is a size axis. The white rhino sample was collected, as noted above, from two relatively specific geographic foci: Faradje and Lado Rhino Camp. Although it is not known how far, nor in how many directions collectors may have forayed from these hubs, the PC results indicate that the regional populations being sampled were morphologically different. As shown in Figure 19, the Faradje and Lado specimens, which are separated along PC2 with little overlap, are distinguished by significant interlocality shape variation. Interlocality differences (in both black and white rhinos) suggest that rhino populations are sensitive to habitat heterogeneity and/or are partially isolated by barriers to gene flow. Fossil species are presumed to have the same potential for interlocality variability depending on the various biological and physical factors operating at the time.

Evidence for sex dimorphism in white rhino skulls is shown in Figure 20. Females are smaller than males (Wilcoxan Rank Sum Test: $SUM_{female} = 43$; $SUM_{male} = 77$; $T_L = 49$; $T_R = 79$) but appear to be similar in shape. This supports Jarmans (1983) conclusion that male rhinos are larger than females but similar in shape, but is

FIGURE 19. Principal components plot of *Ceratotherium* (white rhino) skulls with specimens identified to the most specific geographic locality known. Shaded areas include all specimens from the same locality: F - Faradje (Zaire), L - Lado Rhino Camp, (Upper Nile, Uganda), W - Wadelia Rhino Camp (?), S - Sudan, U - Uganda, V - Vanckerhovenville (Zaire).

Ceratotherium - SKULLS Locality data.

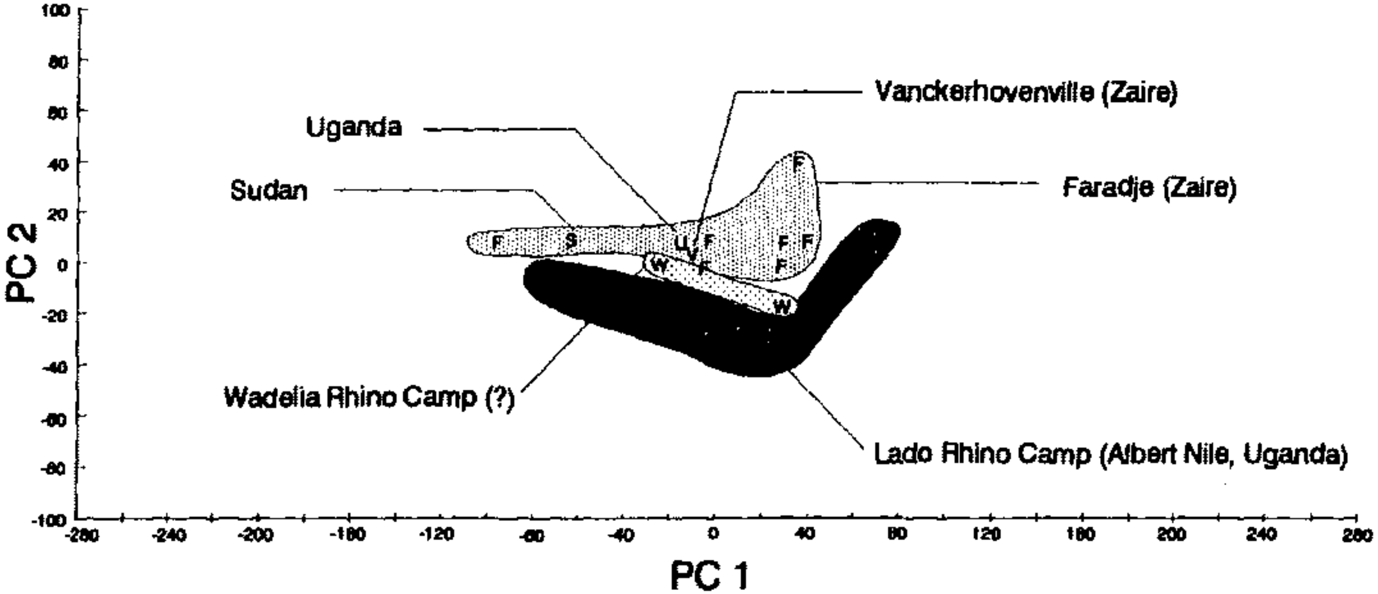
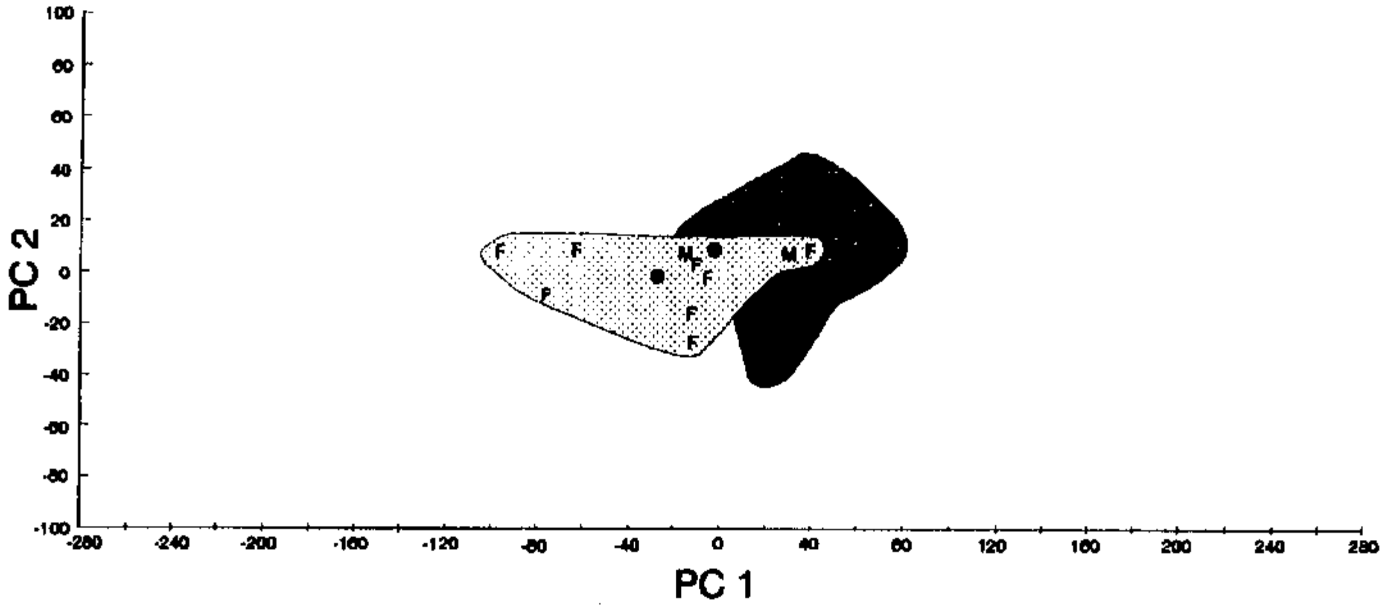


FIGURE 20. Principal components plot of *Ceratotherium* (white rhino) skulls with specimens identified by sex. Shaded areas include all specimens of the same sex. Dots indicate specimens for which sex information is unavailable: M - Male, F - Female.

Ceratotherium - SKULLS Sex dimorphism.



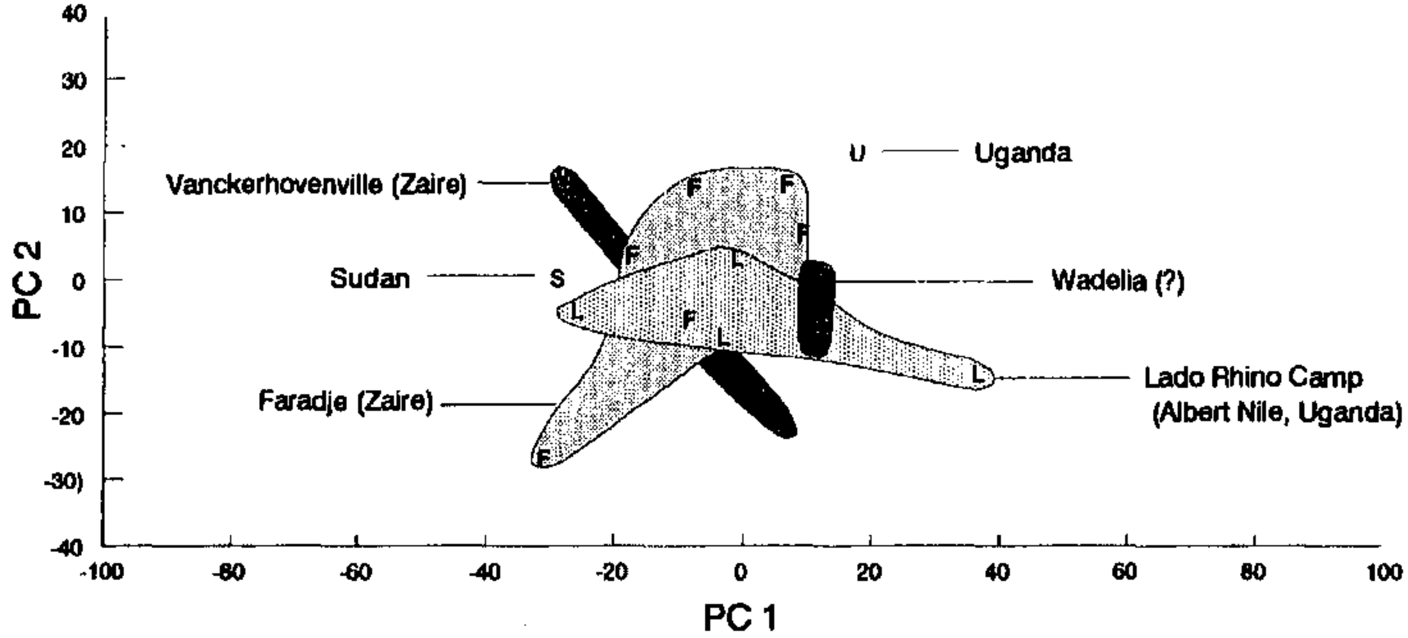
different than the dimorphism in the black rhino which includes a significant shape aspect.

In summary, the multivariate variation of white rhino skulls includes both interlocality and sex differences within a widely dispersed subspecies. In comparison with the black rhino, white rhino locality differences are similar in magnitude, sexes differ more in size than shape, and subspecific differentiation is less well-developed. Thus, although the black and white rhinos exhibit similar multivariate variation in the principal components space, the nature and causes underlying that variation are substantially different.

Mandible (Figures 21-22) -- Locality results for the mandible sample are shown in Figure 21. Overlap of Faradje and Lado specimens indicates that the mandibles are not as different in shape as are the skulls from these two localities. This discordant result between mandible and skull samples (consisting mostly of matched pairs) has important consequences for interpreting fossils. Since fossils are less often found as matched pairs, regional geographic differences in variation are less testable, but should be considered in interpretations based on only one element. Additionally, fossil mandibles and skulls might be susceptible to different kinds or amounts of distortion during burial.

FIGURE 21. Principal components plot of *Ceratotherium* (white rhino) mandibles with specimens identified to the most specific geographic locality known. Shaded areas include all specimens from the same locality: F - Faradje (Zaire), L - Lado Rhino Camp (upper Nile, Uganda), W - Wadelia Rhino Camp, S - Sudan, U - Uganda, V - Vanckerhovenville.

Ceratotherium - MANDIBLES Locality data.



Ceratotherium mandibles (Figure 22) show the same sex difference with respect to size as seen in the skulls (Figure 20). Males are larger than females (PC1) with little dimorphism in shape along PC2.

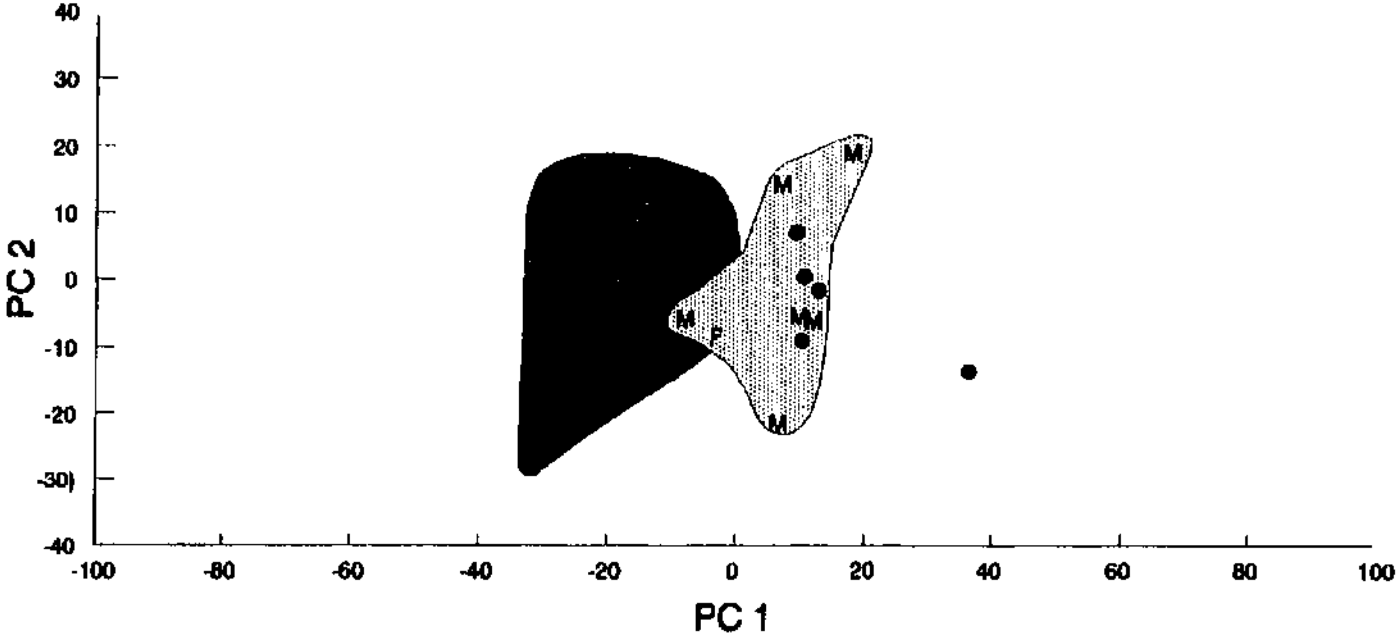
Rhinoceros

The genus *Rhinoceros* comprises two species of Asian one-horned rhinoceroses: *R. unicornis*, the greater Indian rhinoceros, and *R. sondaicus*, the Java rhino. Nowak and Paradiso (1983) state that both species live in the tall grass or reed beds of swampy jungles and eat grass, reeds, and twigs. Whitten et al. (1987) reported the diet of the Javan rhino as succulent secondary growth.

The historical range of the Indian rhino included northern Pakistan, northern India, Nepal, and Assam. Recorded localities for the specimens of this study are "India", "Nepal", and "Royal Chittawan National Park" (Nepal). The Indian specimens are most likely from the Ganges River Valley or from the Brahmaputra River Valley in the eastern province of Assam. The historical range of the Javan rhino included Sikkim, eastern India to Viet Nam and southern China, the Malay Peninsula, Sumatra, and Java. The specimens of this study were collected in western Java in the area of Bantam.

FIGURE 22. Principal components plot of *Ceratotherium* (white rhino) mandibles with specimens identified by sex. Shaded areas include all specimens of the sam sex. Dots indicate specimens for which sex data is unavailable. M - Male F - Female

Ceratotherium - MANDIBLES Sex dimorphism.



PC results for skulls and mandibles are similar and are discussed together. No analysis of sex dimorphism was possible for *Rhinoceros* because of the absence of sex data.

Skulls and Mandibles (Figures 23-24) -- Principal components results for *Rhinoceros* are shown in Figure 23 (skulls) and Figure 24 (mandibles). The two species are clearly distinct and, in the context of this study, are considered subgeneric groups based on taxonomy, locality, and morphology (size). Within species, little can be said about the nature of the variation because of the paucity of data. *R. unicornis* has a larger dispersion than *R. sondaicus*, at least partly due to a larger sample size, and among the specimens, those from Chittawan park are identified as the largest. The lesser variation among Javan specimens might be a sampling artifact, but several other factors may be involved, including the relict status and insular distribution of the species. Groves and Guerin (1980) state that the entire size range of the Javan rhino is represented on Java but it is not known whether the Bantam specimens represent that size range.

More important for this study is the larger generic variation associated with two well-defined species. The total variation among the *Rhinoceros* skulls is more than twice that of *Diceros* or *Ceratotherium* and total variation among the mandibles is more than three times that of the black or white rhinos (Figure 7, Table 5).

FIGURE 23. Principal components plot of *Rhinoceros* (Indian and Javan rhinos) skulls with specimens identified to locality. Shaded areas include all specimens from the same locality.

Rhinoceros - SKULLS Locality data.

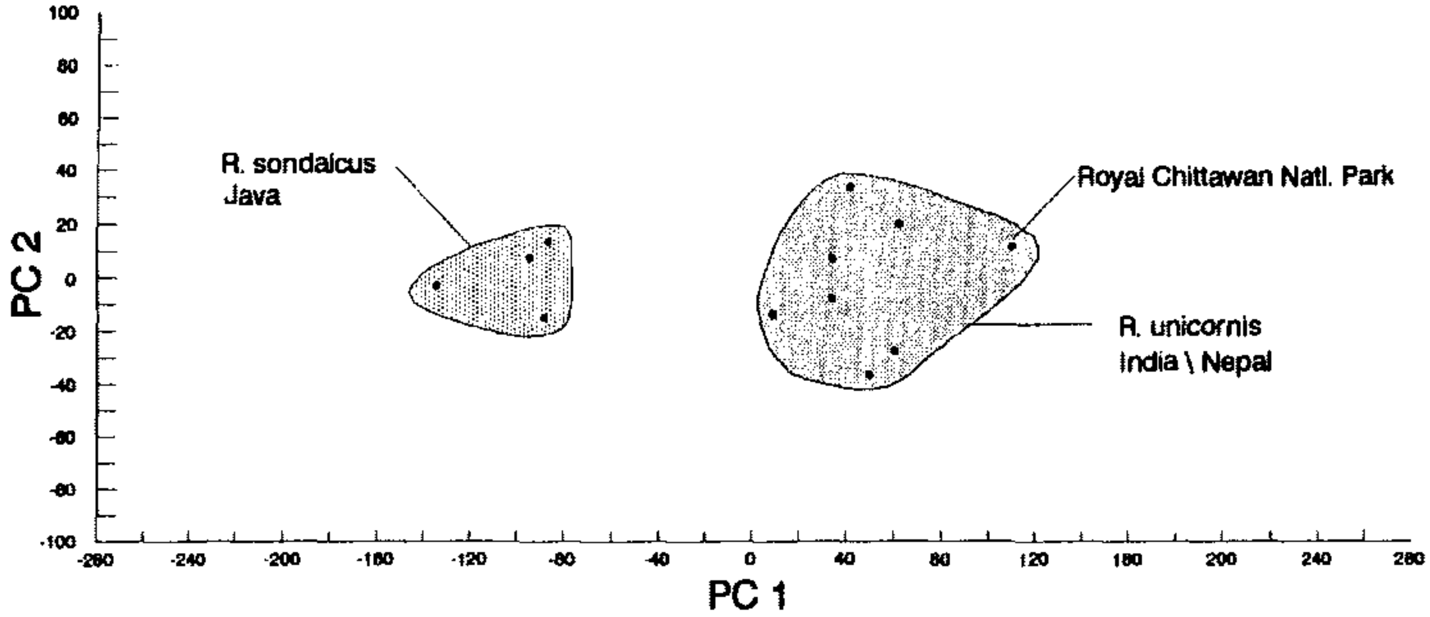
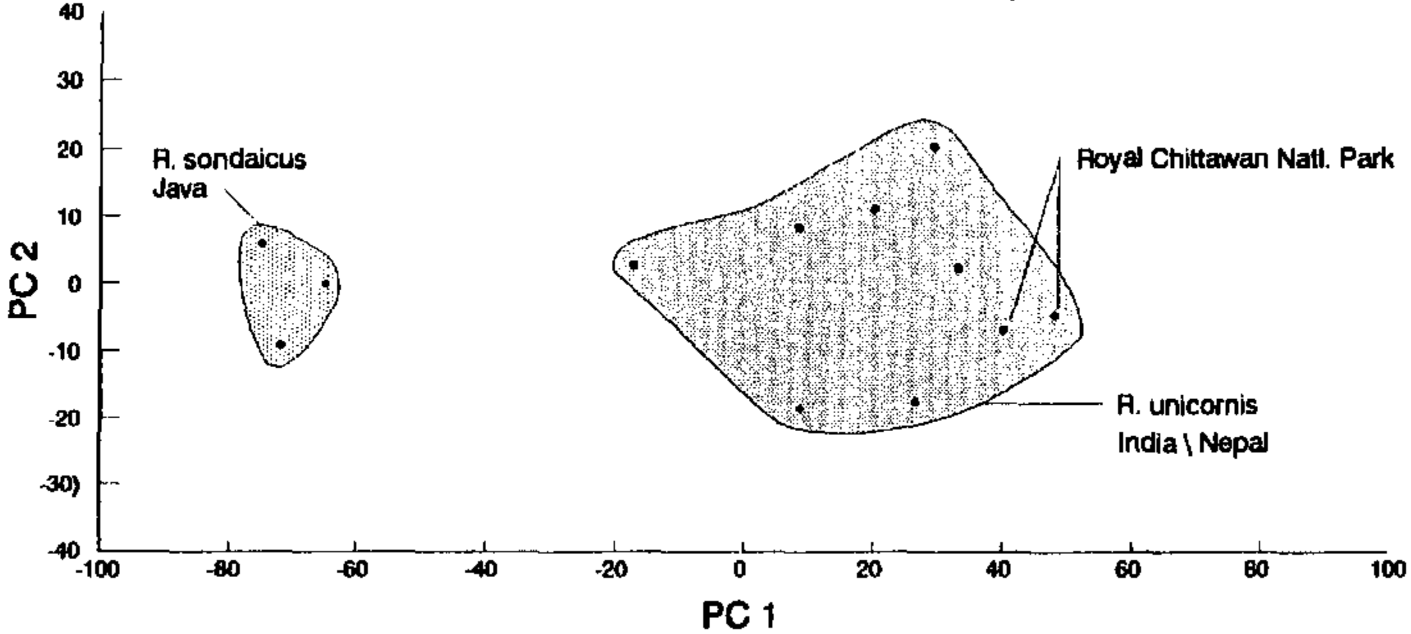


FIGURE 24. Principal components plot of *Rhinoceros* (Indian and Javan rhinos) mandibles with specimens identified to locality. Shaded areas include all specimens from the same locality.

Rhinoceros - MANDIBLES Locality data.



Because *Rhinoceros* is the only multispecies genus among the living analogues, it provides a valuable contribution as a clear example of interspecific level variation. Thus, the Asian one-horned rhinos together with the black and white rhinos, as living analogues, provide a gauge of subspecific, specific, and interspecific (intrageneric) variation to which the fossil genera may be compared.

Dicerorhinus

Dicerorhinus, like *Diceros* and *Ceratotherium*, is a single species genus comprised of *D. sumatrensis*, the Sumatran rhino. The generic name is derived from the two-horned condition which distinguishes it from the one-horned Asian rhino. Historically, this species was found in Assam, southeastern Bangladesh to the Malay Peninsula, and perhaps Vietnam, Sumatra, and Bornea. This rhino is found in areas of secondary growth in tropical forests across a range of elevations, but prefers more hilly habitats where it feeds on fruits, leaves, twigs, bark, and bamboos (Nowak and Paradiso, 1983). Only two adult specimens were available for this study, one collected from Burma (just north of Rangoon) and one from peninsular Malaysia (near Kuala Lumpur). Results for skulls and mandibles are similar and are discussed together.

Skull and Mandible (Figures 25-26) -- Principal components results for *Dicerorhinus* are shown in Figure 25 (skulls) and Figure 26 (mandibles). The small sample size and wide separation of the two specimens make *Dicerorhinus* one of the most problematic genera. The large total variation (Table 5) associated with this result is not useful as an indicator of either interspecific or large intraspecific levels of variation. If the specimens are normal individuals from a single species with variation similar to that of the black or white rhino, then they must be representative of the extremes of that variability. This is consistent with the geographic disjunction (approximately 1000 miles) between the specimens. Differences in habitat and limitations to gene flow could result in geographic/subspecific variants at these localities. A larger sample size in such a case might reveal the bulk of the variation in intermediate forms and intergrades as in the case of the black rhino. Alternatively, these two specimens might have been sampled from distinct groups representing incipient or unidentified species with a variational pattern similar to the Indian and Javan rhinos. A third possibility is that one or both of the specimens are abnormal outliers, falling outside the range of normal variability for that group. There is evidence that the Malay specimen is abnormal, and perhaps pathological. Notations taken during measurement indicate that this skull is highly rugose

FIGURE 25. Principal components plot of *Dicerorhinus* (Sumatran rhino) skulls with specimens identified to locality. Shaded area includes all specimens of the same spcies.

Dicerorhinus - SKULLS Locality data.

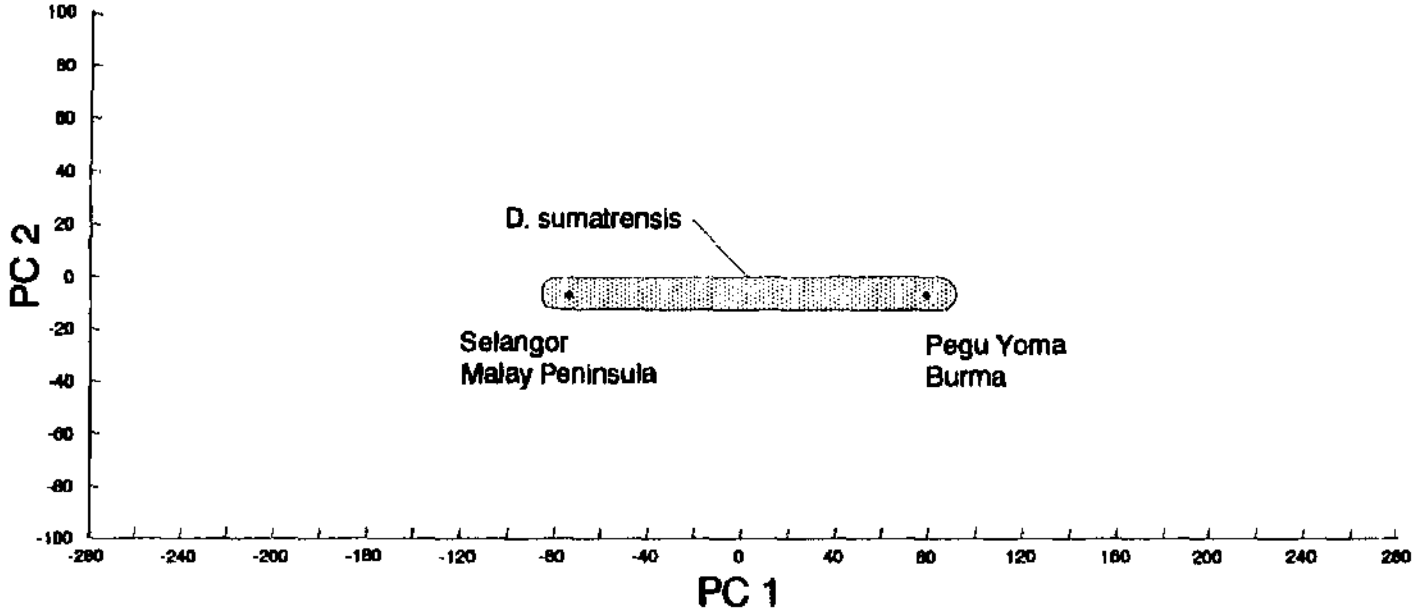
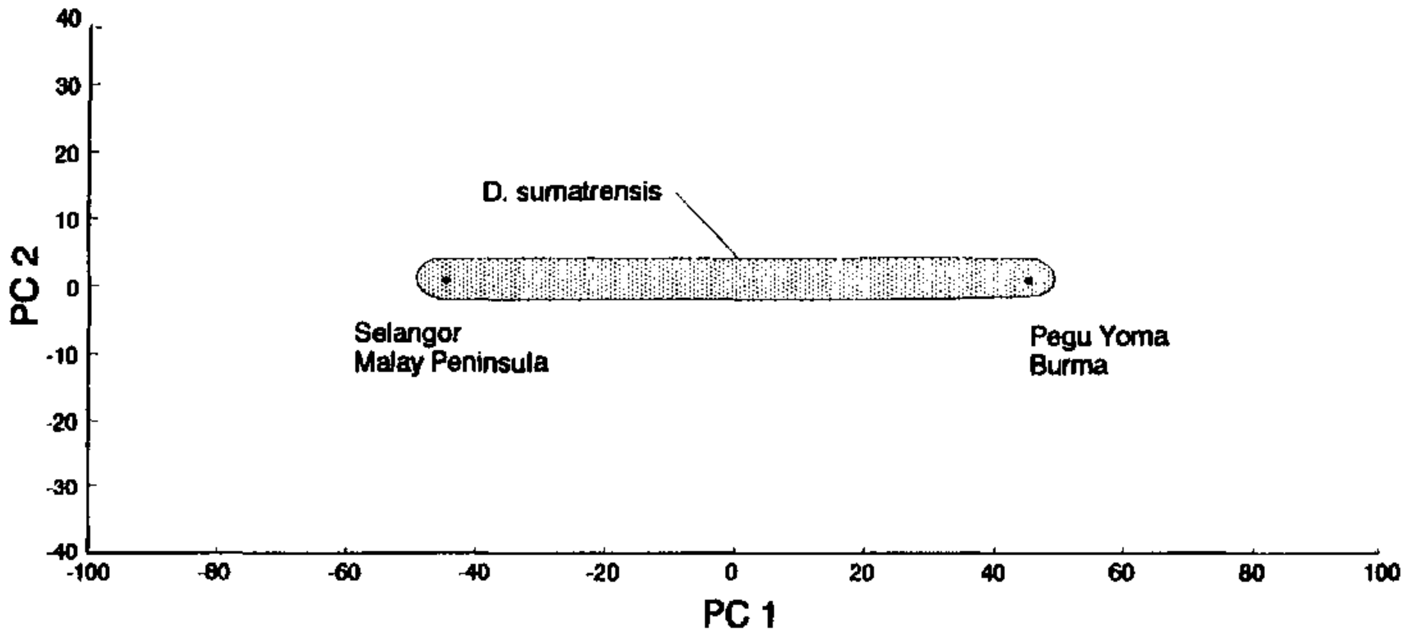


FIGURE 26. Principal components plot of *Dicerorhinus* (Sumatran rhino) mandibles with specimens identified to locality. Shaded area includes all specimens of the same species.

Dicerorhinus - MANDIBLES Locality data.



(almost ornately sculptured), is very light for its size, and has an abnormally curved tooth row. Justification for including it derives from the fact that it survived well into adulthood and was wild caught. Bizarre pathological or mutational variations occasionally occur in nature and are an aspect of variation to be considered when assessing fossil samples.

Fossil Rhinoceroses

Aceratherium

Aceratherium is a Miocene genus of the family Rhinocerotidae related to *Aphelops* and *Peraceras*. These genera are included in the Subfamily Aceratheriinae, which was contemporaneous, and often sympatric, with primitive members of the Subfamily Rhinocerotinae (especially *Teleoceras*). *Aceratherium* is a hornless rhino with reduced premaxillae, relatively low-crowned teeth, and a deeply incised nasal notch. The latter two features and other evidence suggest that members of this taxon were browsing feeders with prehensile upper lips or perhaps short probosci. Prothero et al. (1986) state that many of the specimens assigned to *Aceratherium* actually belong to other genera, and that this has been a "wastebasket" genus for primitive hornless fossil rhinoceroses.

Because taxonomic revision is not the purpose here, the two specimens used are considered to represent *Aceratherium*.

<u>Skull</u> (Figure 27) -- The small sample size precludes grouping of specimens based on subgeneric variational patterns. Separation of the two specimens is similar to that of the Sumatran rhino skulls and, in the absence of other information, the same arguments would apply. The two specimens might be extremes of a single species or they might represent distinct taxa. The geographic and temporal information associated with the specimens indicates that they are from distinct populations in time and space, and probably represent species level variation consistent with the species classifications of the specimens. Each specimen is retained as a subgeneric group (ACER1S; ACER2S).

<u>Mandible</u> (Figure 28) -- The total variation (Table 5) and PC1-PC2 dispersion for this sample are similar to those of *Menoceras* (discussed below) which is one of the least variable of the fossil genera and is mostly comprised of a single-species quarry sample. The similarity with *Menoceras* and the absence of obvious clustering of the specimens would not lead to subdivision of this generic sample. However, the two specimens on the left of Figure 27 are from the late Miocene of Inner Mongolia and classified as *A. depereti* (ACER1M), while the two specimens on the right are from the late Miocene of Europe and classified as *A. incisivum* (ACER2M). The separation of the two subgroups is similar

FIGURE 27. Principal components plot of *Aceratherium* skulls with specimens identified by species, locality, and age. Shaded areas include all specimens in the same subgeneric group.

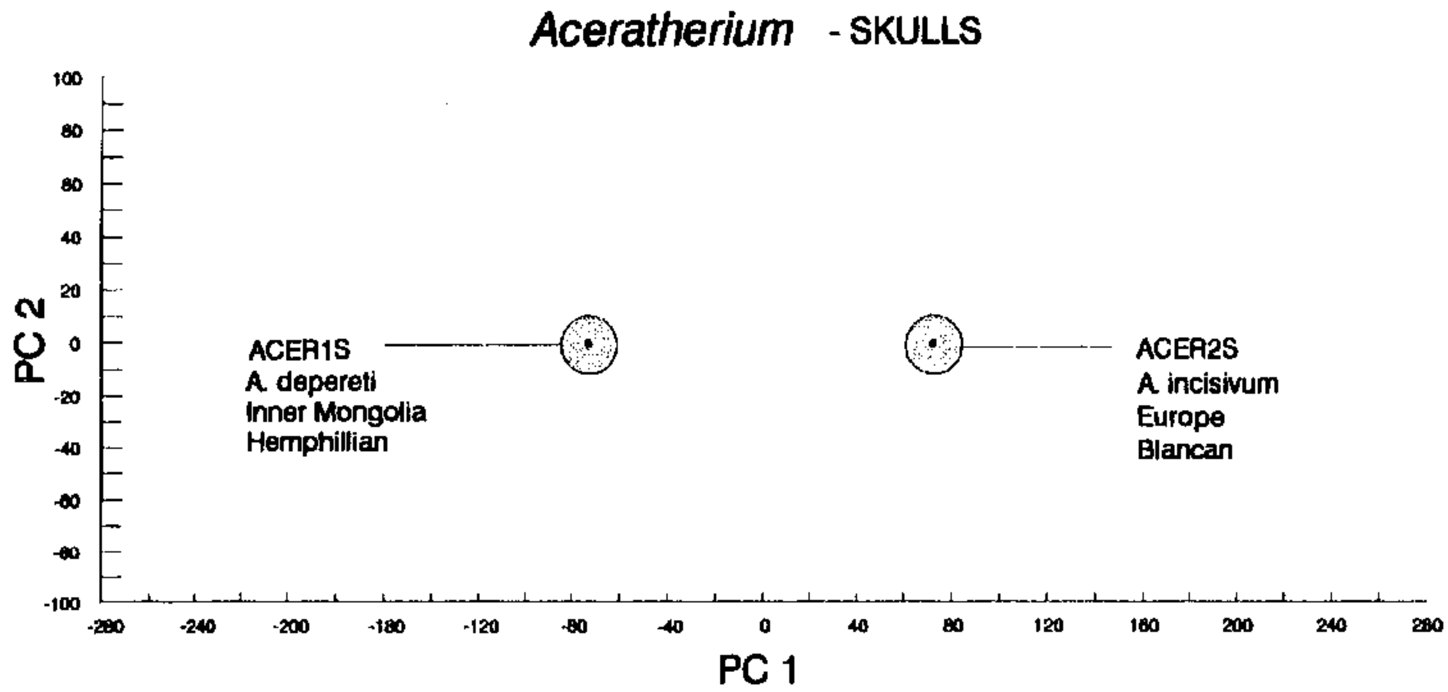
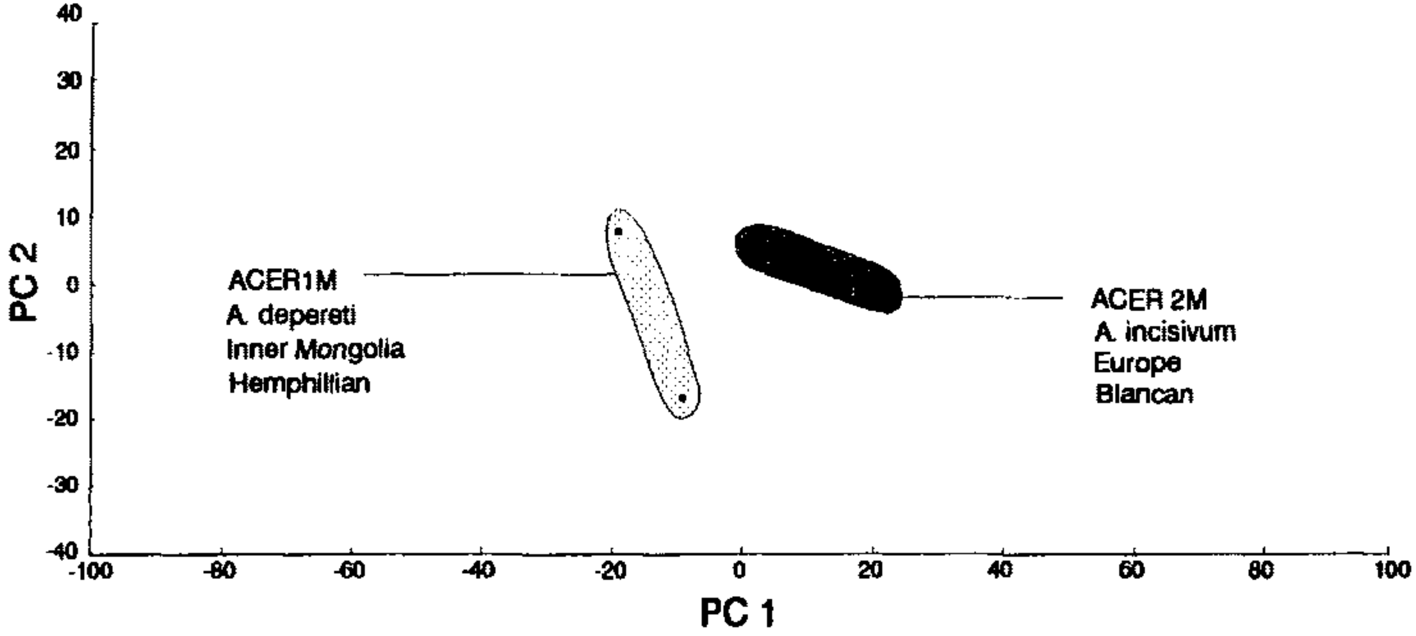

Aceratherium - SKULLS
PC 2
PC 1
ACER1S
A. depereti
Inner Mongolia
Hemphillian
ACER2S
A. incisivum
Europe
Blancan

FIGURE 28. Principal components plot of *Aceratherium* mandibles with specimens identified by species, locality, and age. Shaded areas include all specimens of the same subgeneric group.

Aceratherium - MANDIBLES



to that of some of the geographic subgroups in *Diceros*. Thus, *Aceratherium* mandibles exhibit some minor levels of morphological variation related to time and geography, which has been reflected in their taxonomic assignments.

Amynodon

Amynodon is an evolutionarily and morphologically intermediate genus in the family Amynodontidae, falling between basal forms (more like *Hyrachyus*) and more derived genera (cadurocodonts and metamynodonts). Amynodontids are characterized in part by relatively large sagittal crests, enlarged canines, shortened facial regions, and well-developed preorbital fossae. Members of *Amynodon* were hornless rhinocerotoids restricted to the North American Eocene (Uintan A - Uintan C) and divided into two species, *A. reedi* and *A. advenus*, of which the latter was significantly larger (Wall, 1982, 1989). The paleoecology of amynodons has been little studied; they probably browsed on soft vegetation with their relatively low-crowned cheek teeth (molars and reduced non-molariform premolars). Two skulls of *Amynodon* were measured; no mandibles are included in the analysis.

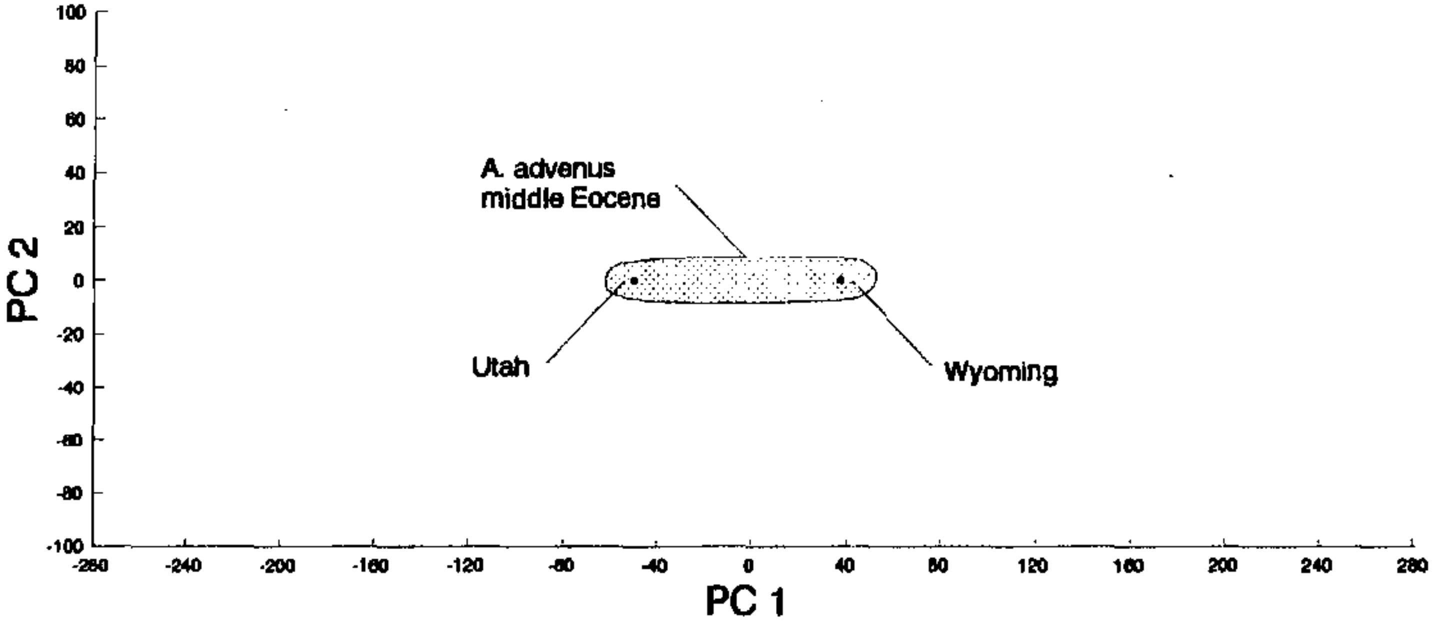
<u>Skulls</u> (Figure 29) -- Both specimens are from middle Eocene (Uintan) strata in adjacent western states and are classified as *A. advenus* (the larger specimen is tagged "*advenus*", the smaller unlabelled specimen was assigned to the species by Wall, 1982). The PC1 variation and dispersion of the *Amynodon* sample is consistent with that for single-species living analogs and supports Walls' conclusion. Based on the preceding evidence, *Amynodon* was not divided into subgeneric groups.

Aphelops

Aphelops is a common early Miocene to late Miocene rhinocerotid found from the Rocky Mountains to Florida, often dominating high plains quarries in association with abundant and probably sympatric *Teleoceras*. Generally, *Aphelops* is characterized by relative brachydonty, absence of incisors, molarized premolars, medium to long skull with a dorsally arched naso-frontal profile, deep narial notch with retracted nasals, modern rhino-like limb proportions, and absence of horns. From the late Hemingfordian to the late Hemphillian, a series of *Aphelops* species progressively increased in size accompanied by increases in relative tooth height and nasal retraction. Moderately low-crowned grinding (cheek) teeth and a deep nasal notch (and/or nasal bone

FIGURE 29. Principal components plot of *Amynodon* skulls with specimens identified by species, locality, and age. Shaded area includes all specimens in the same subgeneric group.

Amynodon - SKULLS

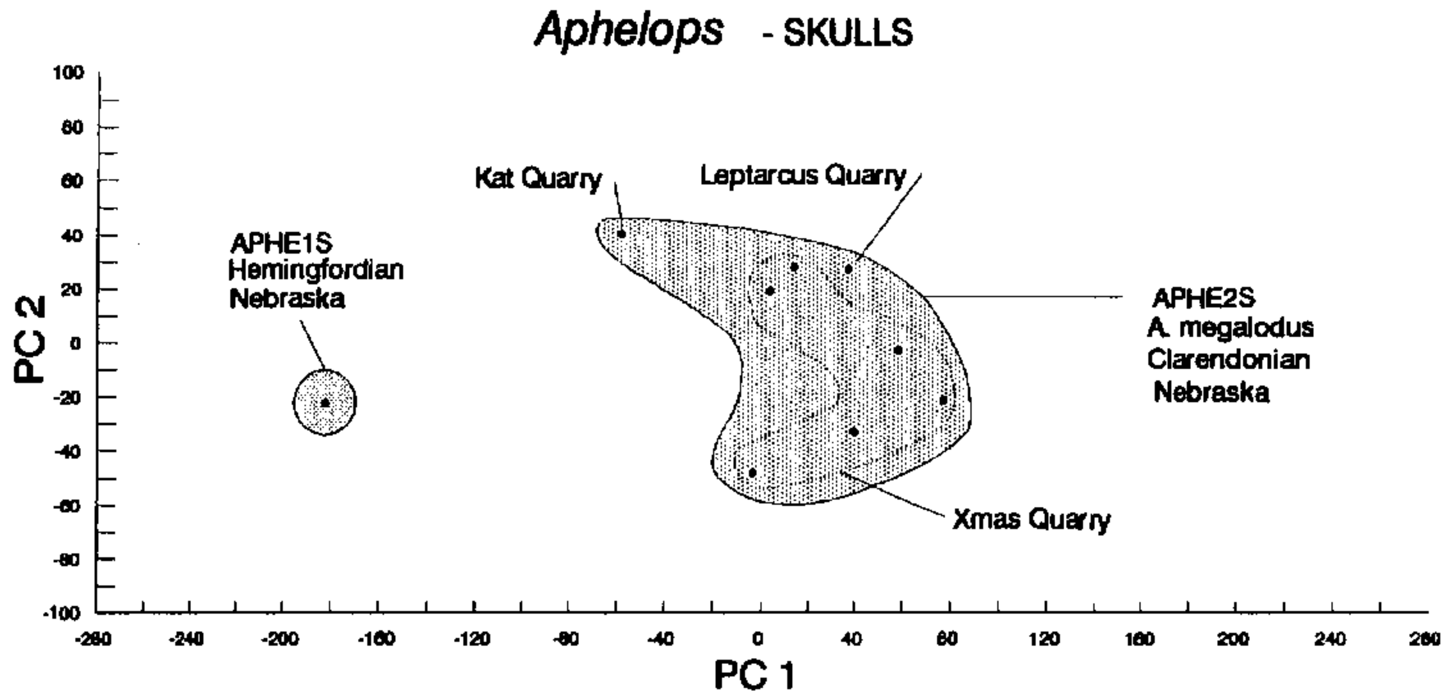


retraction) are characters associated by inference with a browsing lifestyle (Matthew, 1931; 1932; Prothero et al., 1989, in press a).

Among all the genera analysed, principal components results for *Aphelops* show the greatest difference between the skull and mandible samples in terms of locality-time diversity and subgeneric groupings (2 skull subgroups at 2 times, 4 mandible subgroups at 4 times). This is at least partly due to the larger numerical and broader geographic sampling represented by the mandible specimens.

Skull (Figure 30) -- The total variation is intermediate among the genera and is most similar to that of *Rhinoceros* which suggests that the fossil skulls may represent more than one species. The single Hemingfordian specimen (APHE1S), which is distinct temporally and morphologically, represents earlier, smaller forms within the *Aphelops* lineage. The other eight specimens are from Clarendonian localities (three quarries) in Nebraska (Harrison Formation, Cherry Co.). The majority (6 of 8) of the Clarendonian specimens are from the Xmas quarry. It is reasonable to assume that these skulls represent a single species given the temporal and geographic constraints of terrestrial sediments and the similarity in size of the morphometric dispersion compared to both the black and white rhinos. Quarry samples such as this one potentially provide the best overall estimate of within

FIGURE 30. Principal components plot of *Aphelops* skulls with specimens identified to locality and age. Shaded areas include all specimens in the same subgeneric group.

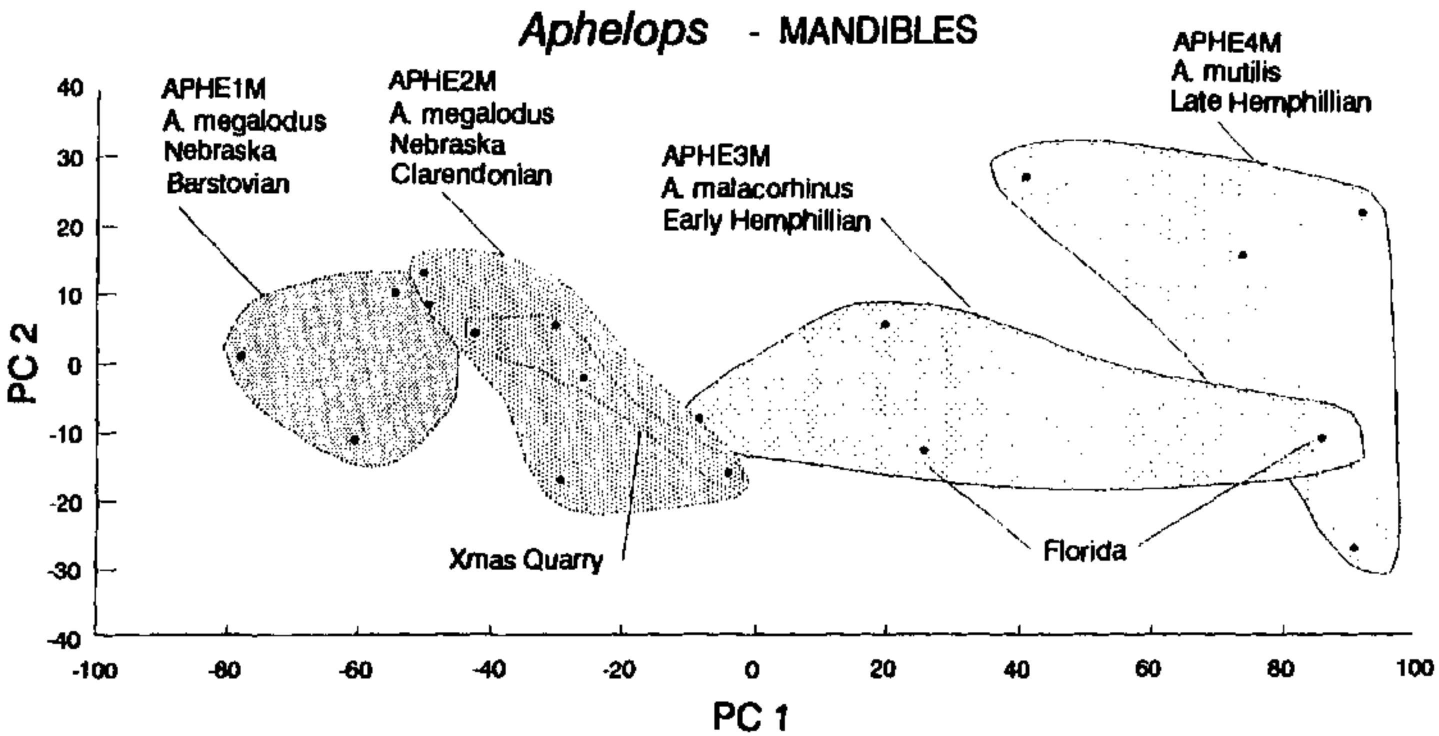


Aphelops - SKULLS
PC 2
PC 1
APHE1S
Hemingfordian
Nebraska
Kat Quarry
Leptarcus Quarry
APHE2S
A. megalodus
Clarendonian
Nebraska
Xmas Quarry

species variation (catastrophic burials such as volcanic ash falls only sample a single deme at one point in time). Intraquarry variation may include interdemic to subspecific or even chronospecific variation depending on the amount of time-averaging and size of the area sampled by the depositional system. The Kat and Leptarcus quarry specimens were grouped with the Xmas quarry skulls because of their temporal, geographic, and morphological similarity (APHE2S). Although the Kat specimen is an outlier, there is no other information to suggest that it represents a separate subgroup.

Mandible (Figure 31) -- Total and PC1 variation of the sample (Table 5), which is among the largest, is similar to that of *Peraceras*. Dissection of this large amount of variation into reasonable subgeneric groups consistent with living analog variation resulted in four groups showing minimal overlap. APHE1M unites four Barstovian specimens attributed to *A. megalodus*. APHE2M unites six Clarendonian specimens, including four from one quarry (Xmas), also attributed to *A. megalodus* (Prothero, personal communication). These two groups are straightforward and satisfactory based on their temporal, geographic, and morphological patterns. The fact that they are currently classified as one species may be interpreted in two ways: either significant, localized mandible size evolution occured within the species, or these two subgroups actually represent two species. Compared with

FIGURE 31. Principal components plot of *Aphelops* mandibles with specimens identified to locality and age. Shaded areas include all specimens in the same subgeneric group.



Aphelops - MANDIBLES
APHE1M
A. megalodus
Nebraska
Barstovian
APHE2M
A. megalodus
Nebraska
Clarendonian
APHE3M
A. malacorhinus
Early Hemphillian
APHE4M
A. mutilis
Late Hemphillian
Xmas Quarry
Florida
PC 2
PC 1
40
30
20
10
0
-10
-20
-30
-40
-100
-80
-60
-40
-20
0
20
40
60
80
100

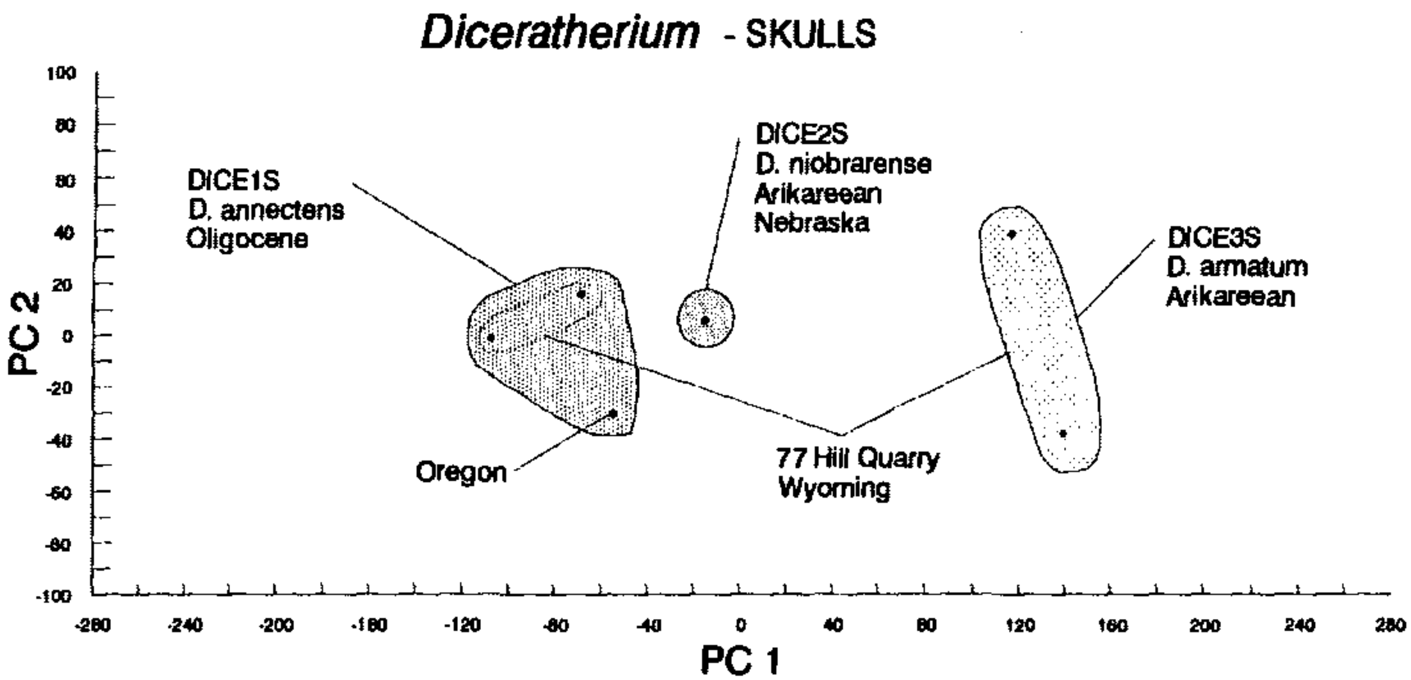
variation within and among other subgroups, the latter interpretation is not unreasonable. The remaining specimens are all Hemphillian and account for much of the *Aphelops* mandible variation. Subdivision of these specimens was based on time-taxonomic correlations such that some geographic confounding is present. APHE3M includes mandibles classified as *A. malacorhinus* from several early Hemphillian localities including Texas. The great size range of this subgroup might suggest two species by comparison with living forms, but much of this range is spanned by two specimens from the same locality (Florida). The wide separation of the Florida specimens is itself problematic but is accepted here, given the other problems. APHE4M comprises specimens attributable to an *A. mutilis* - late Hemphillian correlation and also includes specimens from Texas. The dispersions of APHE3M and APHE4M, as single species, are less satisfactory in comparison with other groups and probably represent compromises given limited data and sample sizes. Explanations for the large early Hemphillian diversity of *Aphelops* mandibles might include rapid size evolution within the species or, as indicated by the Florida specimens, greater than average variation.

Diceratherium

The genus *Diceratherium* is currently considered to include those fossil rhinoceroses exhibiting (probably in males only) paired (side-by-side), subterminal, antero-posteriorly elongated nasal flanges (ridges). These boney characters are believed to have underlain epidermal horns. Earlier definitions of the genus included all rhinoceroses with paired nasal protuberances (diceratheres *sensu obsoletum*). Those forms with terminal, spherical horn bosses are now classified as *Menoceras* (discussed below). *Diceratherium* is further separated from *Menoceras* by retaining simple, primitive cheek teeth lacking much development of crochets and cristae. *Diceratherium* species are found in upper Oligocene to lower Miocene localities (Whitneyan - Arikareean) from Oregon to the Great Plains. These species differ mostly in size, with later forms achieving relatively large size. For example, the holotype *D. armatum* from the John Day formation of eastern Oregon was approximately two-thirds the size of the Indian rhino. Rhinoceroses were not generically diverse during the time *Diceratherium* was extant. Rather, *Diceratherium* species were the predominant rhino members of faunas for approximately 10 million years spanning the Whitneyan and Arikareean ages. Prior to extinction, *Diceratherium* coexisted with *Menoceras* during the mid to late Miocene (Matthew, 1931; Peterson, 1920; Prothero, in press a; Prothero et al., 1986, 1989; Tanner, 1969; Troxell, 1921).

Skull (Figure 32) -- The total and PC1 variation, which is fourth highest among the skulls, is associated with a fairly wide scatter of a few data points. The small sample size results in relatively

FIGURE 32. Principal components plot of *Diceratherium* skulls with specimens identified by species, locality, and age. Shaded areas include all specimens in the same subgeneric group.

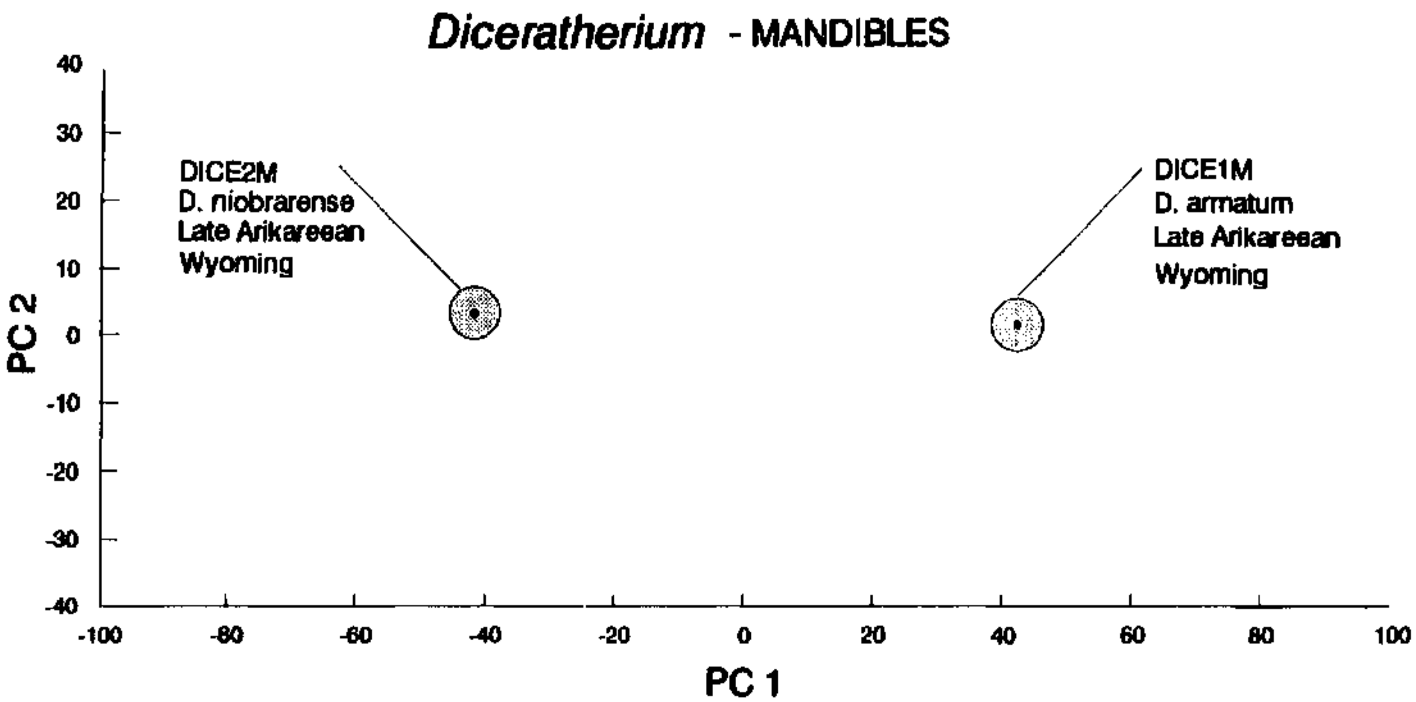


Diceratherium - SKULLS
DICE1S
D. annectens
Oligocene
DICE2S
D. niobrarense
Arikareean
Nebraska
DICE3S
D. armatum
Arikareean
Oregon
77 Hill Quarry
Wyoming
PC 2
PC 1

unsatisfactory subgroups in terms of dispersion. Two specimens are grouped as DICE3S representing Oligocene *D. armatum*. DICE1S and DICE3S are well separated and consistent with interspecies variation. However, DICE3S and two specimens of DICE1S are from the same quarry (77 Hill) in Wyoming. Thus, this interpretation accepts a polyphyletic sample from that locality. The single specimen of DICE2S is problematic. Although, consistent in time with DICE1S, it may be a distinct species (*D. niobrarense*). It's inclusion with DICE1S would also be consistent with variation in single species subgroups.

Mandible (Figure 33) -- The scatter of this small sample does not suggest any subgeneric morphometric grouping. Available data for three of the specimens suggests that they are taxonomically unique. Although similar in locality and age, the morphometric separation of *D. niobrarense* (DICE2M) and *D. armatum* (DICE1M) supports the notion of two species occurring at that time (also suggested by the skull analysis). In the absence of other data, locality alone was not considered sufficient to unite DICE3M and DICE4M. In summary, each of the specimens was retained as a single-specimen subgeneric group (DICE1M, DICE2M, DICE3M, DICE4M).

FIGURE 33. Principal components plot of *Diceratherium* mandibles with specimens identified by species, locality, and age. Shaded areas include all specimens in the same subgeneric group.



Diceratherium - MANDIBLES
DICE2M
D. niobrarense
Late Arikareean
Wyoming
DICE1M
D. armatum
Late Arikareean
Wyoming
PC 2
40
30
20
10
0
-10
-20
-30
-40
-100
-80
-60
-40
-20
0
20
40
60
80
100
PC 1

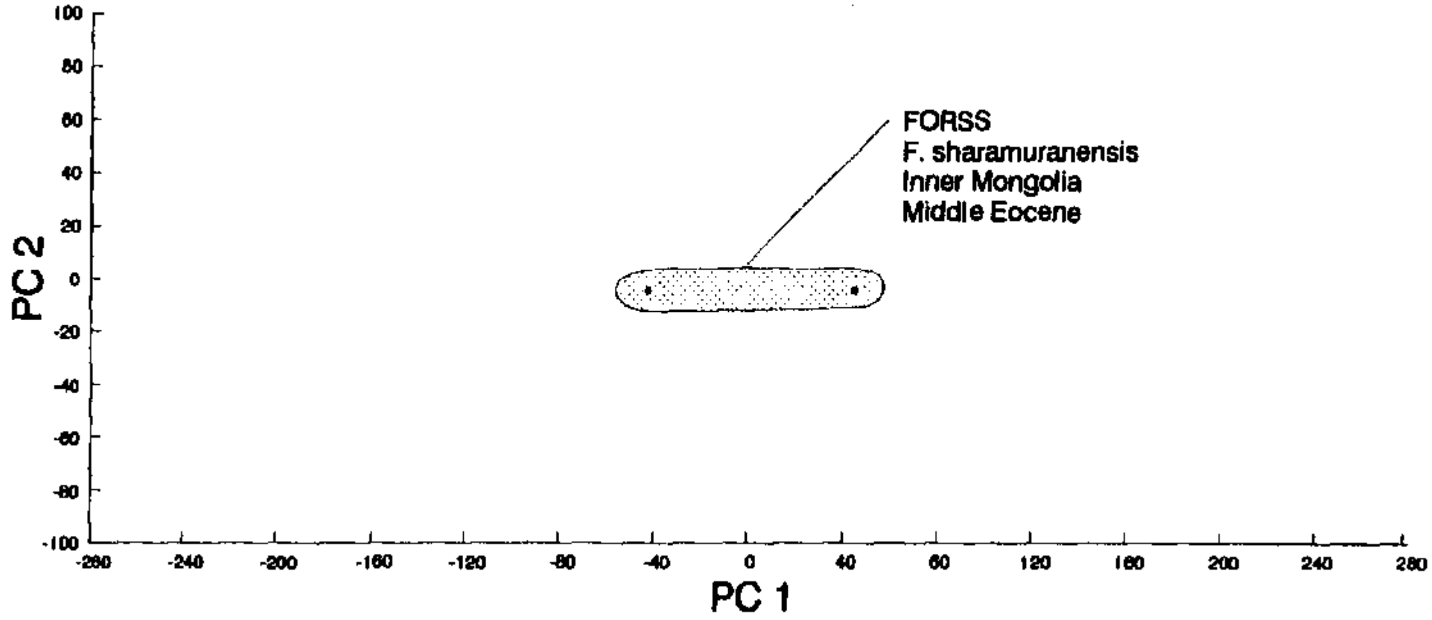
Forstercooperia

Forstercooperia is one of the three genera representing the family Hyracodontidae. It includes small, relatively primitive, hornless, cursorial rhinocerotoids from the middle Eocene of central Asia and North America. This lineage is believed to have later produced the largest known land mammals (see *Indricotherium* below). The primitiveness of *Forstercooperia* is illustrated by its inclusion of species once referred to the stem genus of rhinocerotoids (*Hyrachyus grandis*). Diagnostic features of the skull include nasal incision above the canine and an unreduced dentition with nonmolariform premolars. (Lucas et al., 1981; Prothero et al., 1986, 1989; Radinsky, 1967 b).

<u>Skull</u> (Figure 34) -- The two specimens are united by taxonomy, age, and locality (FORSS). The total skull variation, associated entirely with PC1, is similar to that of the black and white rhinos. It is not known whether the specimens are from the same quarry, from same level in the formation, or even from the same formation. The Shara Marun beds are tentatively assigned a mid to late Eocene (Lucas et al., 1981) which is consistent with the standard stage (Bartonian = upper Uintan-mid Eocene) age assigned to one of the specimens. Some authors have considered *F. sharmuranense* to represent a separate genus (*Juxia*).

FIGURE 34. Principal components plot of *Forstercooperia* skulls with specimens identified by species, locality, and/or geologic age. Shaded area includes all specimens in the same subgeneric group.

Forstercooperia - SKULLS



This taxonomic confusion is not important for this study since the two specimens represent smaller, more primitive hyracodontids regardless of their name.

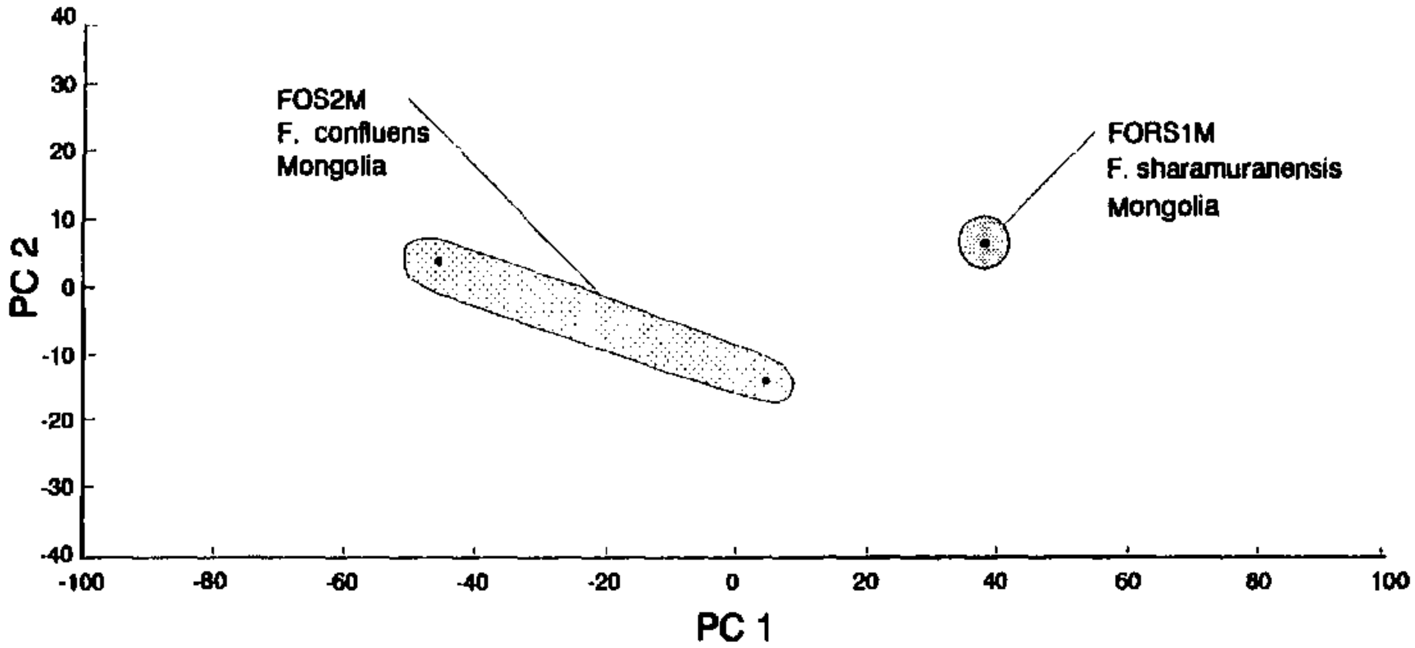
Mandible (Figure 35) -- Total variation, greater than in *Diceros* but less than in *Rhinoceros* (Table 5), is marginally consistent with a two-species hypothesis. The three specimens were divided into two subgeneric groups: FORS1M, a single specimen of *F. sharamuranense*, and FORS2M, two specimens classified as *F. confluens*. Variation within FORS2M is consistent with a single species when compared against the monotypic living taxa. In summary, total variation, taxonomic data, and morphological separation support the division of the mandibles into two subgeneric groups.

Hyrachyus

The Eocene genus *Hyrachyus* represents the most primitive rhinocerotoid condition. It is similar in size and shape to the most primitive members of other perissodactyl superfamilies, for example, *Hyracotherium*, a basal form of the Equoidea (horses), and *Heptodon*, a basal form of the Tapiroidea. Primitive features in *Hyrachyus* include small size, distinct sagittal crest, narrow posterior projecting occiput, convex dorsal skull profile, smooth

FIGURE 35. Principal components plot of *Forstercooperia* mandibles with specimens identified by species, locality, and/or geologic age. Shaded areas include all specimens in the same subgeneric group.

Forstercooperia - MANDIBLES.

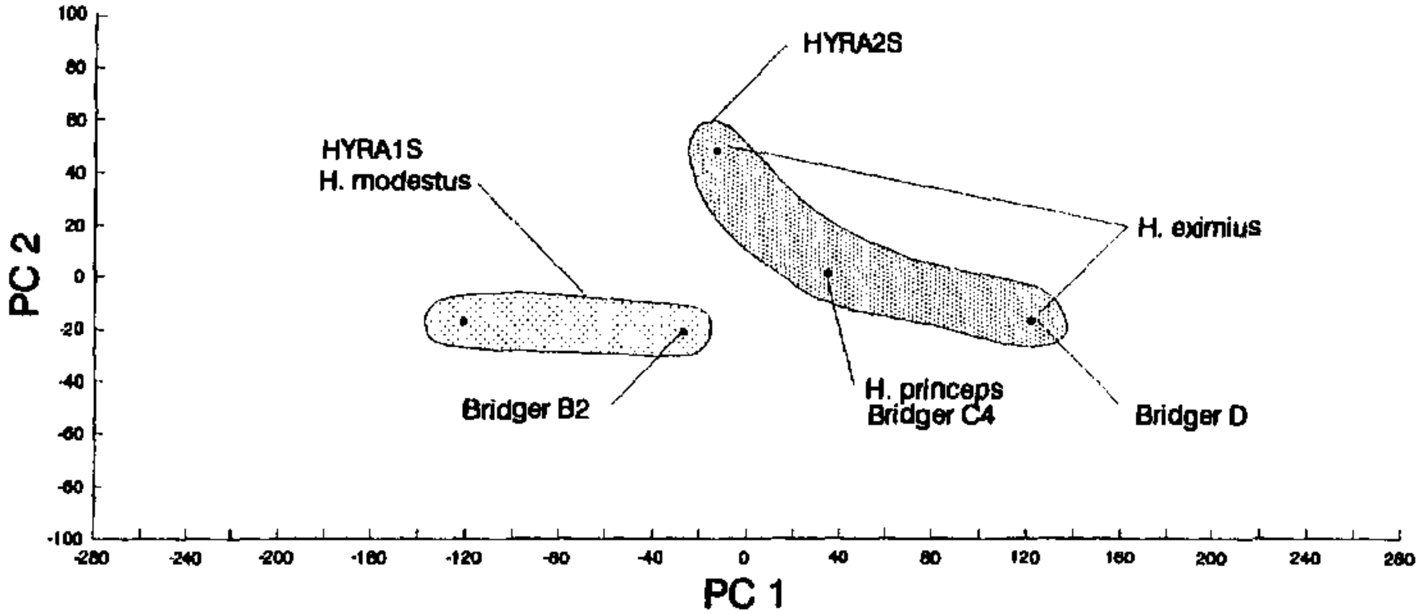


nasal bones (hornless), long basicranial region relative to the palate, unflared zygomatic arches, and an unspecialized anterior dentition. In the late Eocene, three families (Amynodontidae, Hyracodontidae, and Rhinocerotidae) evolved from this primitive condition. Species of *Hyrachyus*, differing mostly in size, were moderately cursorial browsers which achieved at least a holarctic distribution. It is among those taxa believed to have utilized the Euro-American land bridge (Wood, 1935; Radinsky, 1967b; Prothero et al., 1986, 1989).

Skull (Figure 36) -- The scatter of the small sample has an intermediate total variation, comparable to that of *Rhinoceros*. Because the data were not log-transformed, there remains the possibility that the variation of the very small *Hyrachyus* may not be comparable to the much larger living rhinos. Generally, larger species are expected to have larger variances. However, *Hyrachyus* skulls have a greater dispersion than *Diceros*, opposite of theoretical expectation, which adds weight to the conclusion that the *Hyrachyus* specimens comprise more than one species. This hypothesis is supported by the associated taxonomic and stratigraphic data. Two specimens labelled *H. modestus*, one of which is from the Bridger B2 stratum, were grouped as HYRA1S. The remaining specimens (HYRA2S) occur in higher beds (C and D) of the Bridger formation. Two of these are classified as *H. eximius*. The inclusion of the specimen labelled *H. princeps* (from Bridger C) in

FIGURE 36. Principal components plot of *Hyrachyus* skulls with specimens identified by species, locality, and/or geologic age. Shaded areas include all specimens in the same subgeneric group.

Hyrachyus - SKULLS



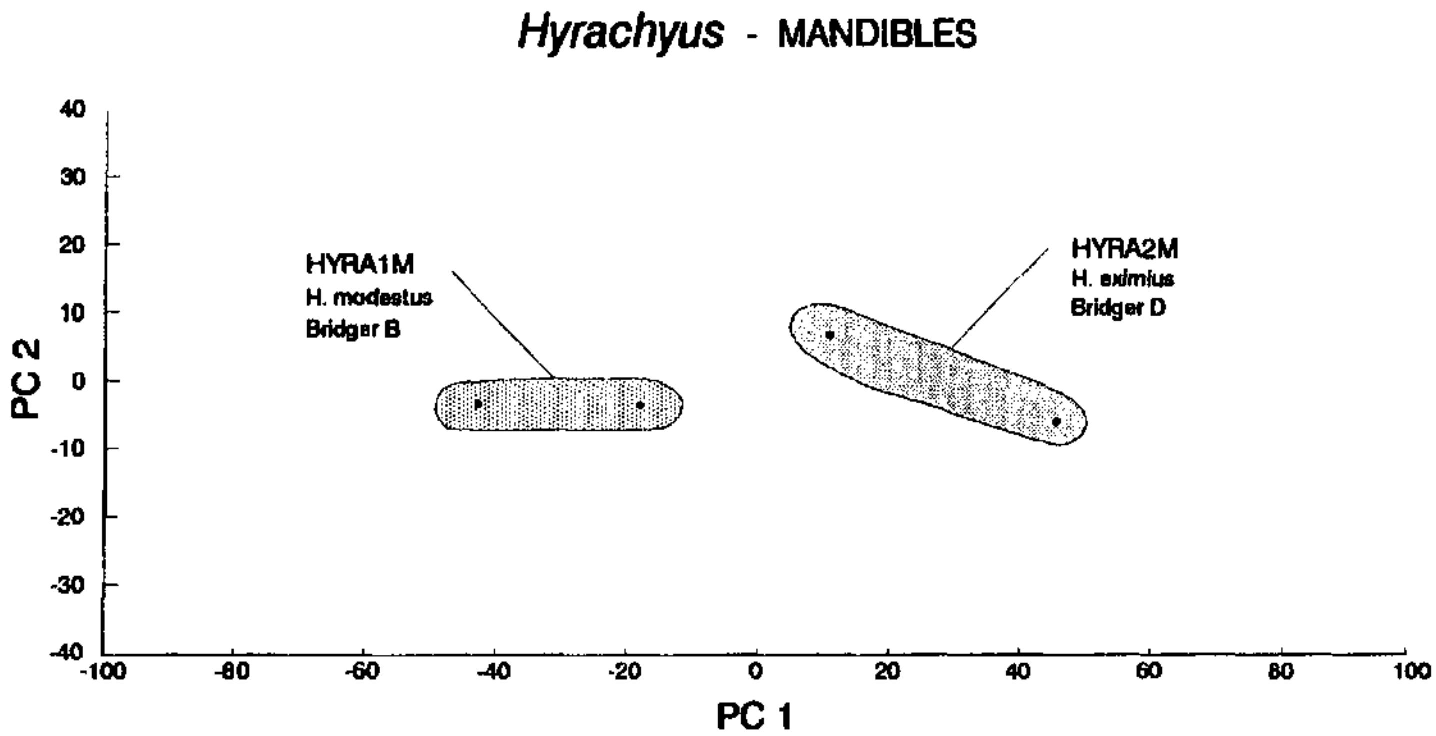
HYRA2S was based in part on the affinities of C and D faunas and on its morphological affinity with *H. eximius*. The *H. princeps* specimen is probably *H. eximius* (Prothero, personal communication). Several authors (Wortman, 1901, Wood, 1934, and Gazin, 1976) have considered the faunal differences between beds A-B and C-D sufficient to divide the Bridger Formation into two members (West, 1987). Their conclusions suppport the division of *Hyrachyus* skulls into two subgeneric groups.

Mandible (Figure 37) -- This analysis parallels that for the skulls. Two specimens of *H. modestus* from Bridger B form a group (HYRA1M) distinct from two specimens of *H. eximius* from Bridger D (HYRA2M). This pattern is consistent with the variation seen in the polytypic living analog *Rhinoceros*. Among the fossil genera, *Hyrachyus* shows the highest similarity between the skull and mandible principal components plots.

Hyracodon

Hyracodon is the most commonly found genus of hyracodontid. Skeletons and teeth are known from many localities spanning one of the longest time ranges of any mammalian genus (mid Eocene to late Oligocene). *Hyracodon* retained many of the primitive features of *Hyrachyus* including absence of horns and retention of a full complement of incisors and canines. Derived characters include: distinctive conical shape of incisors, flared

FIGURE 37. Principal components plot of *Hyrachyus* mandibles with specimens identified by species, locality, and/or geologic age. Shaded areas include all specimens in the same subgeneric group.

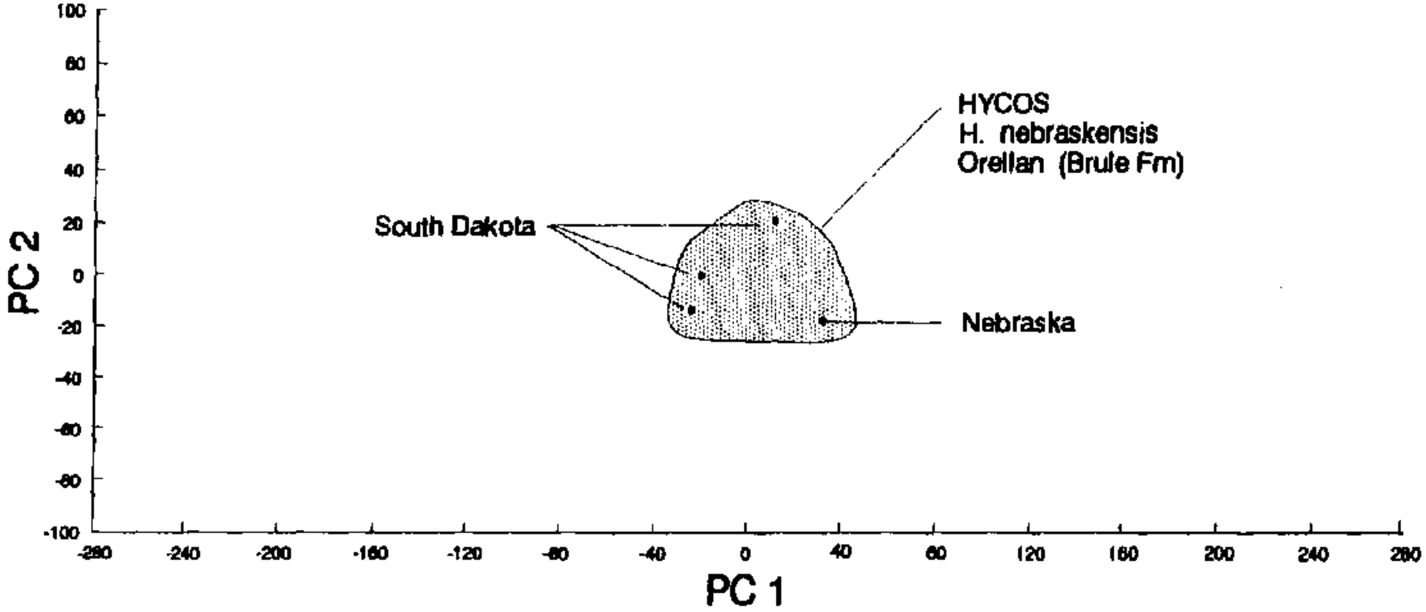

Hyrachyus - MANDIBLES
HYRA1M
H. modestus
Bridger B
HYRA2M
H. eximius
Bridger D
PC 2
PC 1
40
30
20
10
0
-10
-20
-30
-40
-100
-80
-60
-40
-20
0
20
40
60
80
100

zygomatic arches, and molarization of premolars. Though medium-sized in general, *Hyracodon* species differed mostly in size with the average or commonest forms usually described as sheep or great dane sized. Slender, elongated limbs and other postcranial features indicate that *Hyracodon* was very cursorial, a lifestyle usually associated with relatively open habitats such as savanna or grassland. The latter inference would suggest that *Hyracodon* was a grazer, which is supported by its relatively hypsodont cheek teeth. However, the teeth are otherwise simple and primitive which suggests a browsing habit. Further confusing this issue is the lack of any well-defined ecological facies associated with the fossils (Troxell, 1921; Sinclair, 1922; Wood, 1926; Radinsky, 1967b; Prothero, 1987, in press b; Prothero et al., 1986, 1989).

Skull (Figure 38) -- *Hyracodon* was the least variable of all genera with total variation considerably less than *Diceros*. This pattern is consistent with single-species variation in the context of this study and is consistent with the classification of all four specimens as *H. nebraskensis*. Relative to the living analogs, *H. nebraskensis* (as represented by these specimens) appears to be a well-defined morphologic species. The small separation between the South Dakota and Nebraska specimens may indicate some geographic differentiation within the species or temporal differentiation within the Orellan.

FIGURE 38. Principal components plot of *Hyracodon* skulls with specimens identified by species, locality, and/or geologic age. Shaded areas include all specimens in the same subgeneric group.

Hyracodon - SKULLS



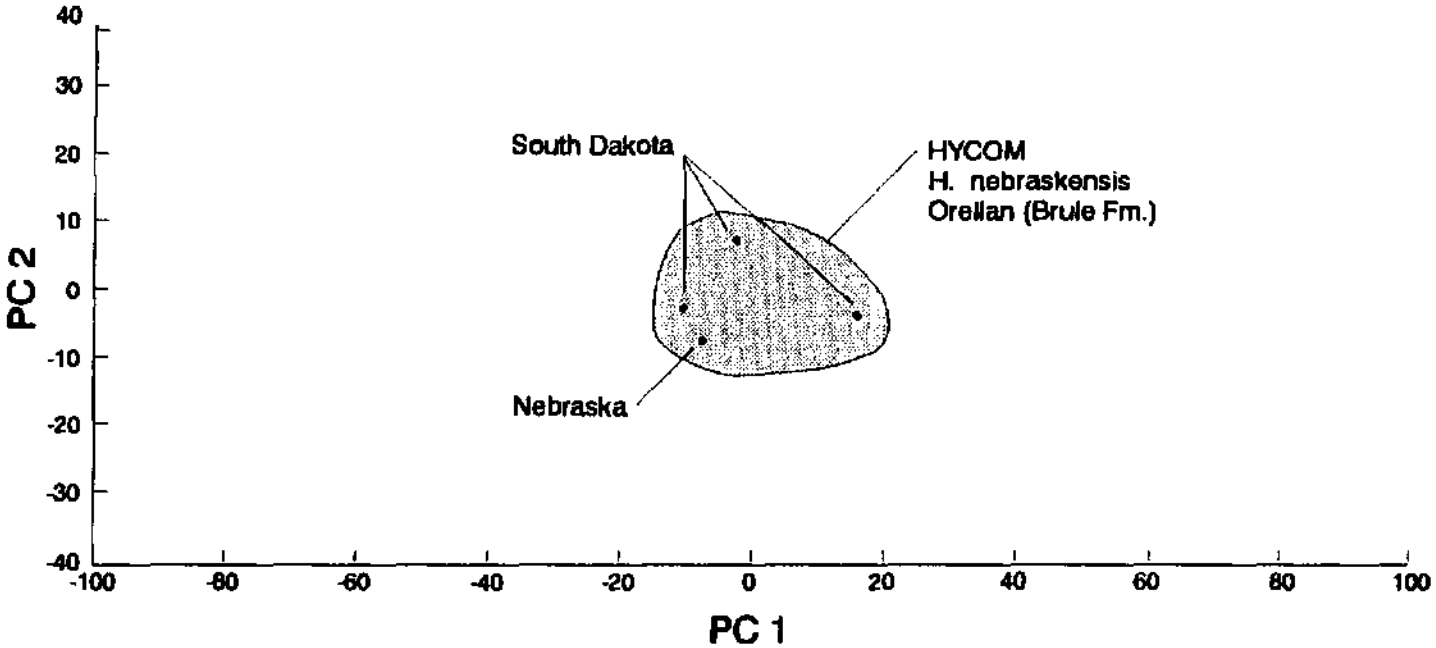
Mandible (Figure 39) -- The pattern of the mandible plot is very similar to that for the skulls and is based on the same four specimens (mandibles are matched with the skulls). They are therefore grouped similarly as HYCOS. However, in this case the "outlier" is a South Dakota specimen while the Nebraska mandible is more closely associated with other South Dakota specimens. The mandible results support the conclusions stated in the skull analysis.

Indricotherium

The *Indricotherium* specimen used in this study represents a lineage of Oligocene hyracodontids which became the largest land mammals yet discovered (approximately 15 to 18 feet at the shoulder). These rhinocerotoids retained many primitive characters including relatively long narrow skulls (dolichocephaly) without horns, long limbs with slender proportions, and retention of incisors. The incisors form a well-developed functional complex (vertical I^1 and procumbent I^2) considered to be an evolutionary novelty which unites the members as a monophyletic group. Slightly hypsodont, but otherwise primitive teeth, combined with large size suggest that indricotheres browsed on soft tree-top vegetation. Occipital and postcranial features indicate they fed in a head down position. Members of this group have historically been placed in

FIGURE 39. Principal components plot of *Hyracodon* mandibles with specimens identified by species, locality, and/or geologic age. Shaded area includes all specimens in the same subgeneric group.

Hyracodon - MANDIBLES



three genera: *Indricotherium*, *Baluchitherium*, and *Paraceratherium* all of which belong to the subfamily Indricotheriinae. The similarity of specimens in these genera has led to arguments for the synonymy of *Paraceratherium* and *Baluchitherium* (both are more similar in size and smaller than *Indricotherium*), or of all three genera. In either case *Paraceratherium* has priority (Forster-Cooper, 1911, 1924, 1934; Granger and Gregory, 1935, 1936; Lucas and Sobus, 1989; Osborn, 1923; Prothero et al., 1986, 1989, in press b).

Skull and Mandible (no figures) -- Single specimens cannot be analysed by PC since no axes can be found which maximize variance among specimens (a minimum of two specimens is required for PC). Hence, there are no principal components plots for the *Indricotherium* skull or mandible. However, the single specimen does represent a real population of indricotheres and is therefore an estimate of the mean of that population which will be used in later canonical variates analyses (Chapter 4). The amount and kind of variation represented in the indricotheres by this one specimen depends on systematic opinion: Lucas and Sobus (1989) considered the cranial differences between *Indricotherium* and *Paraceratherium* (= *Baluchitherium*) not to be of generic level importance and therefore the specimens constitute a single genus, *Paraceratherium*. Further, they argue that any differences which do exist between the forms can be interpreted as representing sex dimorphism.

Regardless of what taxonomic level is assigned to the differences between the originally defined genera, the specimen used here represents all of the indricotheres.

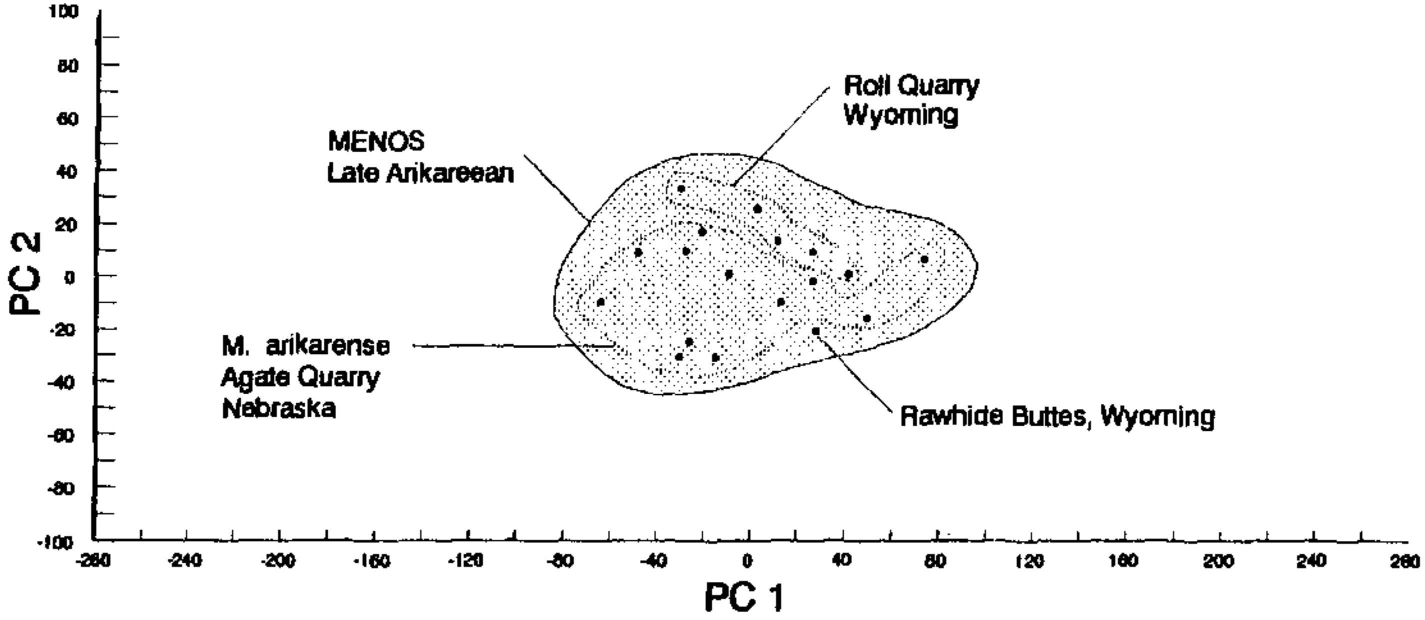
Menoceras

Menoceras comprises pig-sized, herding animals found in North America from New Mexico to Florida and in the Great Plains. This genus appeared suddenly in the latest Arikareean age and is believed to be an immigrant derived from unknown ancestors in Europe or Asia. This genus, and *Diceratherium*, which was already established in North America when *Menoceras* arrived, are often found at the same localities. This faunal association led to some taxonomic confusion because both have paired nasal swellings (presumably underlying horns). The two genera were subsequently shown to be only distantly if at all related, and the side-by-side nature of the horn bosses is considered to be an evolutionary parallelism at best, or an evolutionary convergence. The shape and position of the bosses are unique: in *Diceratherium* they are subterminal and ridge or flange-like, in *Menoceras* they are spherical (bulbous) and located at the tips of the nasal bones. Other features of the skull indicate that *Menoceras* is much more derived than *Diceratherium* and more closely related to the ancestors of modern rhinoceroses. These features include a shorter, broader skull, a broader non-overhanging occiput, reduced premaxillary bones, reduced sagittal crest, shortened basicranium, and heavy lower jaws with everted, rugose angles. Additionally, *Menoceras* and the higher rhinoceroses developed extensions of their molar cross-lophs resulting in crochets, antecrochets, and cristae, which fused to form fossettes and lakes in the dentine. The disappearance (extinction) of both *Diceratherium* and *Menoceras* in the Hemingfordian age is correlated with the appearance of aceratherine and teleoceratine rhinoceroses which were also probably immigrant taxa (Peterson, 1920; Prothero, in press a; Prothero and Manning, 1987; Prothero et al., 1986, 1989; Tanner, 1969; Troxell, 1921).

Skull (Figures 40-41) -- Principal components results for *Menoceras* skulls are shown in Figure 40. Among the fossil genera, *Menoceras* is one of the more homogeneous groups. Total variation among the skulls is below that of *Diceros* and therefore consistent with a hypothesis of a single species. This is further supported by the fact that the skull sample was not divisable into subgeneric groups by any criteria. The sample is primarily composed of specimens from two localities, the Agate Springs and Roll quarries. The Agate specimens are classified as *M. arikarense*. The unclassified specimens from Roll quarry form a nearly non-overlapping cluster separated from the *arikarense* group along the second PC axis. If the Roll specimens are *arikarense*, which is

FIGURE 40. Principal components plot of *Menoceras* skulls with specimens identified by species, locality, and/or geologic age. Shaded area includes all specimens in the same subgeneric group.

Menoceras - SKULLS



consistent with the single species hypothesis suggested by the variation pattern, then the small differences in shape between the quarries may be attributed to geographic and/or temporal factors. Confounding the total variation in *Menoceras* is variation due to sex dimorphism. Several specimens were labeled as to sex, which was probably determined by relative size differences of horn bosses. Mixed specimens from the same locality have either large horn bosses (presumably males) or little to no horn bosses (presumably females). Sexing of specimens was checked against photographs from which additional sexing was accomplished. An analysis of sex dimorphism in *Menoceras* is shown in Figure 41. The Roll quarry group is male except for one large female and does not provide evidence for sex dimorphism by itself. Dimorphism in the *M. arikarense* Agate quarry sample appears to be obvious when observed graphically (Figure 41b) and is marginally supported by a Wilcoxan Rank Sum Test (SUM_F=38; SUM_M=40; T_L=41; T_R=63). When sexes of the total sample are grouped (Figure 41c), the dimorphism is less obvious but the larger sample size results in a significant Wilcoxan test for differences between males and females (SUM_F=60; SUM_M=111; T_L=66; T_R=105).

<u>Mandibles</u> (Figure 42) -- Principal components results for *Menoceras* mandibles are shown in Figure 42. Except for a single specimen (MENO2M), the mandible results are similar to those for

FIGURE 41. Principal components plot of *Menoceras* skulls with specimens identified by sex. Shaded areas include all specimens of the same sex.

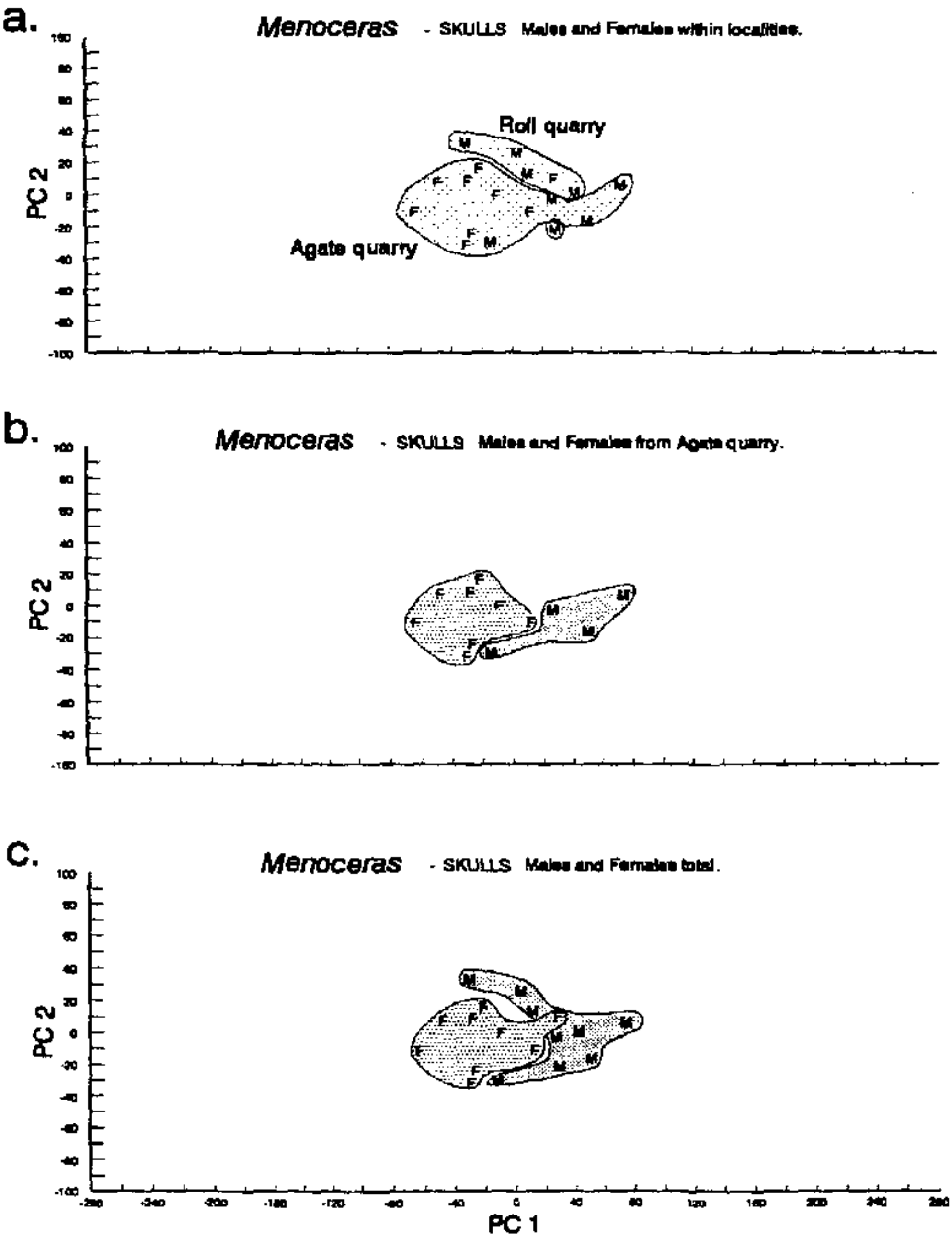
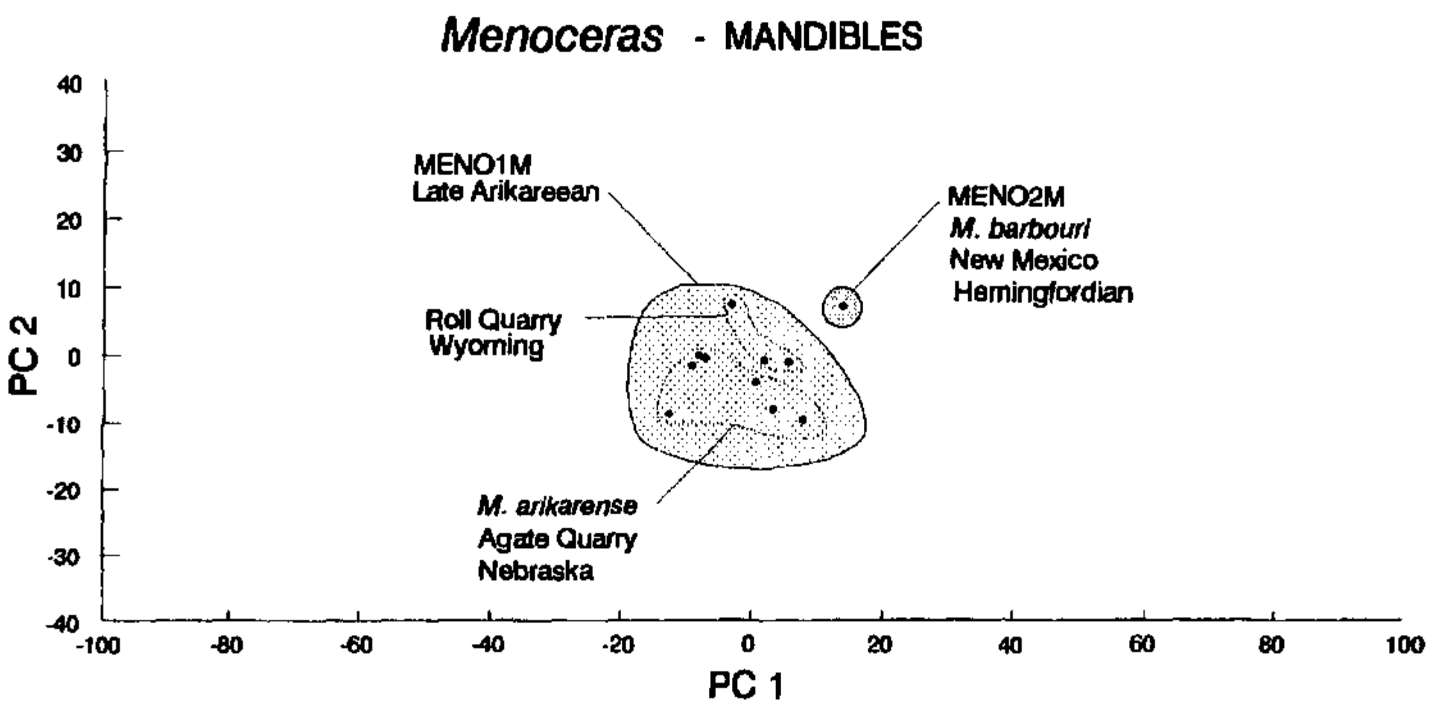

a.
Menoceras - SKULLS Males and Females within localities.
Roll quarry
Agate quarry
PC 2
b.
Menoceras - SKULLS Males and Females from Agate quarry.
PC 2
c.
Menoceras - SKULLS Males and Females total.
PC 2
PC 1

FIGURE 42. Principal components plot of *Menoceras* mandibles with specimens identified by taxonomy, locality, and/or geologic age. Shaded areas include all specimens in the same subgeneric group.



Menoceras - MANDIBLES
MENO1M
Late Arikareean
MENO2M
M. barbouri
New Mexico
Hemingfordian
Roll Quarry
Wyoming
M. arikarense
Agate Quarry
Nebraska
PC 2
PC 1
40
30
20
10
0
-10
-20
-30
-40
-100
-80
-60
-40
-20
0
20
40
60
80
100

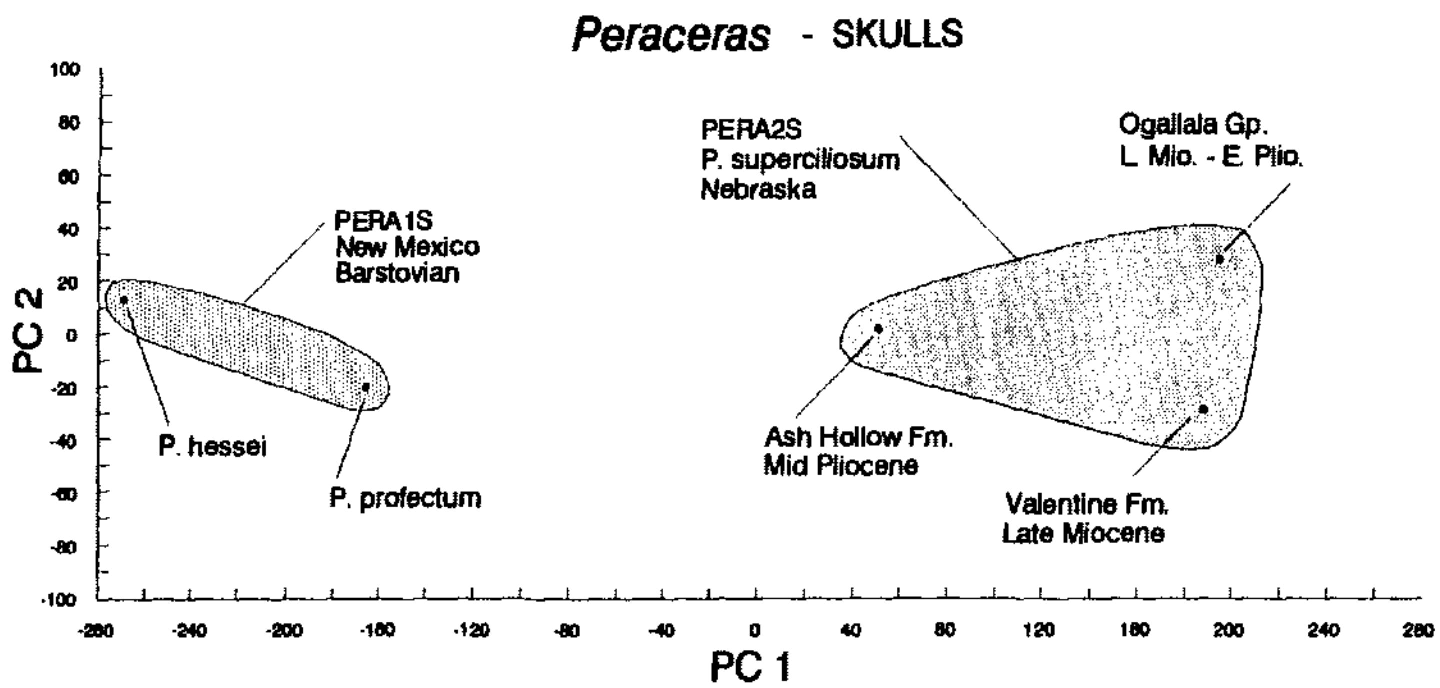
the skull. Within an Arikareean group of relatively low variation, the Agate (*M. arikarense*) and Roll specimens are distinct morphologically to a degree consistent with geographic and/or temporal variation within a species. Although the MEN02M specimen is not significantly outlying morphologically from MEN01M, it was retained as a subgeneric group based on information that suggests it represents a different biological population in time and space. Sex dimorphism was not analysed in the mandibles because of the lack of any characters comparable to the horn bosses for sexing specimens.

Peraceras

Peraceras probably migrated to North America from Eurasia in the early Miocene (late Hemingfordian), as did *Aphelops* and *Teleoceras*. These three genera displaced *Menoceras* and *Diceratherium* as the dominant rhinoceroses for most of the Miocene. For unknown reasons, *Peraceras* was the rarer of the three genera. It is found less often in local faunal association with the very common *Teleoceras* than is *Aphelops*. Characters which contribute to the uniqueness of *Peraceras* include brachycephaly, procumbent lambdoid crests and occiput, shortened and flattened nasal bones, retracted nasal incision, flat dorsal profile, reduced premaxillae with loss of the upper first incisor, brachydont teeth, and a short mandibular diastema. Significant size differences within the genus are associated with other characteristics. Smaller members (*P. profectum* and *P. hessei*) were primitive hornless browsers while larger members (*P. superciliosum*) had small terminal horns and may have been grazers (Osborn, 1904; Prothero in press a; Prothero et al., 1986, 1989; Prothero and Manning, 1987; Prothero and Sereno, 1982).

<u>Skull</u> (Figure 43) -- The total and PC1 variation for *Peraceras* skulls are the largest of all the genera. This suggests, by comparison with the living analogs and fossil genera analyzed thus far, that multiple species may be represented by the sample. Most of the variation is along the PC1 size axis. Indeed, the extremes of the PC1 scale were set for all of the skull PC plots by the *Peraceras* sample. It was possible to divide *Peraceras* into two subgeneric groups, but not without confounding information within each group. PERA1S consists of the two smallest specimens. Both are from the Barstovian of New Mexico but are classified as different species. This confounding of taxonomy (*P. hessei* and *P. profectum*) into a subgeneric group was based on geography, time, morphology, and variation. First, they are more morphologically similar to each other than either is to the three specimens of *P. superciliosum* (PERA2S). Second, the range of variation shown by the two specimens is consistent with that of a single species in

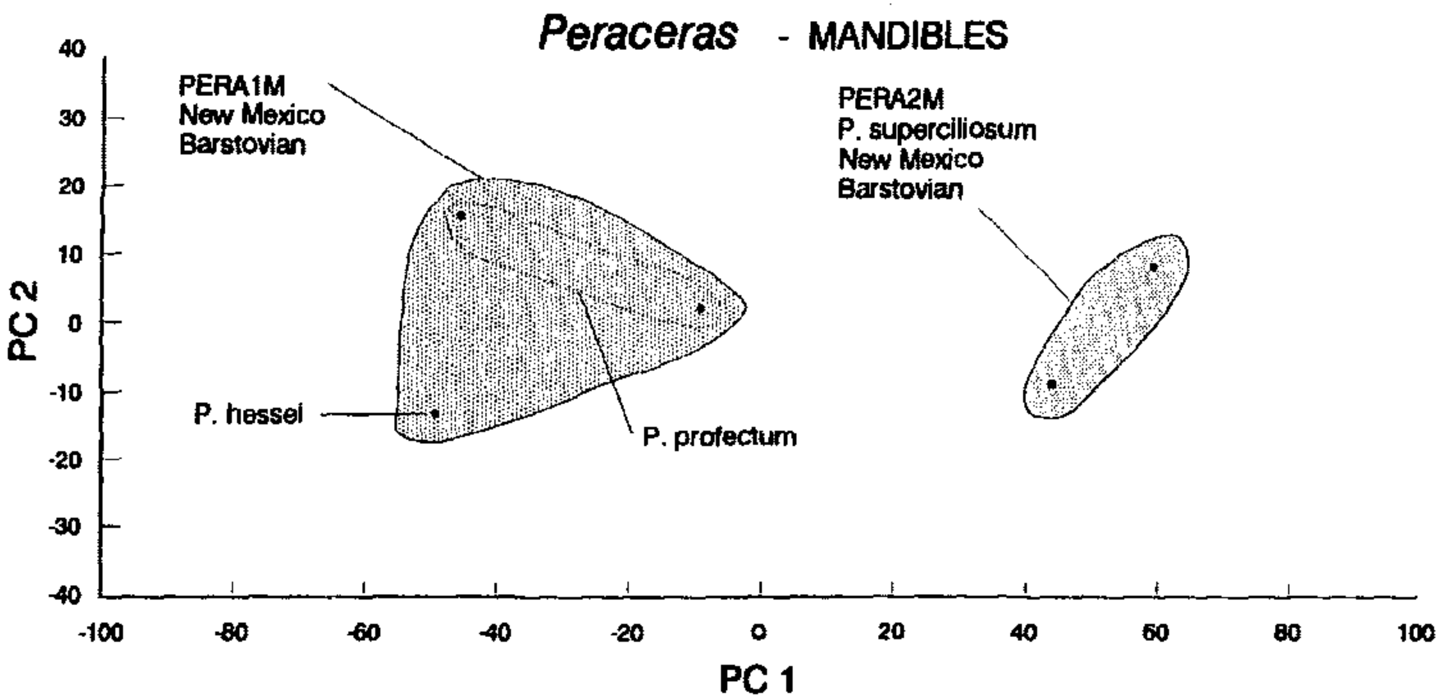
FIGURE 43. Principal components plot of *Peraceras* skulls with specimens identified by taxonomy, locality, and/or geologic age. Shaded areas include all specimens in the same subgeneric group.


Peraceras - SKULLS
PERA1S
New Mexico
Barstovian
P. hessei
P. profectum
PERA2S
P. superciliosum
Nebraska
Ogallala Gp.
L Mio. - E. Plio.
Ash Hollow Fm.
Mid Pliocene
Valentine Fm.
Late Miocene
PC 2
PC 1

the context of this study, and is no greater than that shown by the extreme specimens of *P. superciliosum*. *Peraceras hessei* was reported by Prothero and Manning (1987) as a new species of dwarf *Peraceras*; they described the specimen used in this study as "the best preserved of any skull referrable to this species". *Peraceras profectum* is described as a 20% larger, contemporary sister species. Species recognition by size difference alone is not compelling since two adult specimens of the black rhino may differ by this much. PERA1S may represent two species (given sample size and sampling error), but these specimens are sufficiently similar in time, space, and morphology in the context of this study to be considered as a single subgeneric group. PERA2S consists of three larger specimens whose dispersion is similar in size to the black rhino. All are classified as *P. superciliosum* and all are from Nebraska. Because two of the specimens are from different ages, time is confounded in this subgroup. The smallest specimen of PERA2S is from an older stratum than one of the larger specimens. This may be interpreted two ways: either *P. superciliosum* decreased in average size over time, or it maintained a wide range of adult size variation during the time represented by the sample. In summary, although each subgeneric group confounds some information, the two subgroups represent the most reasonable partitioning of the great variation exhibited by the *Peraceras* skulls.

Mandible (Figure 44) -- Total PC variation, which is among the highest of the genera (Table 5), suggests the presence of multiple subgeneric groups. Two subgeneric groups were identified based on taxonomy, geography, morphology, and relative amounts of variation. PERA1M (like PERA1S) includes specimens from the New Mexico Barstovian which are classified as either *P. profectum* or *P. hessei*. These specimens form a morphometric group, consistent with other fossil and living groups, which supports the grouping of *P. hessei* and *P. profectum*. Here, the two *profectum* specimens exhibit a range of size nearly inclusive of the *hessei* specimen, with one of the *P. profectum* more similar to *hessei* than to the other *P. profectum*. PERA1M is clearly distinct from PERA2M which represents *P. superciliosum* from the New Mexico Barstovian. The separation of PERA1M and PERA2M is similar to the separation of PERA1S and PERA2S but an important difference is that the *P. superciliosum* mandibles are from the same locality and time as the *hessei/profectum* subgroup. The relative contemporaneity and sympatry of PERA1M and PERA2M, combined with the size difference between the two groups, further emphasizes the morphometric similarity of *P. profectum* and *P. hessei*. Prothero (1989) recognized *hessei* as a valid species.

FIGURE 44. Principal components plot of *Peraceras* mandibles with specimens identified by taxonomy, locality, and/or geologic age. Shaded areas include all specimens in the same subgeneric group.



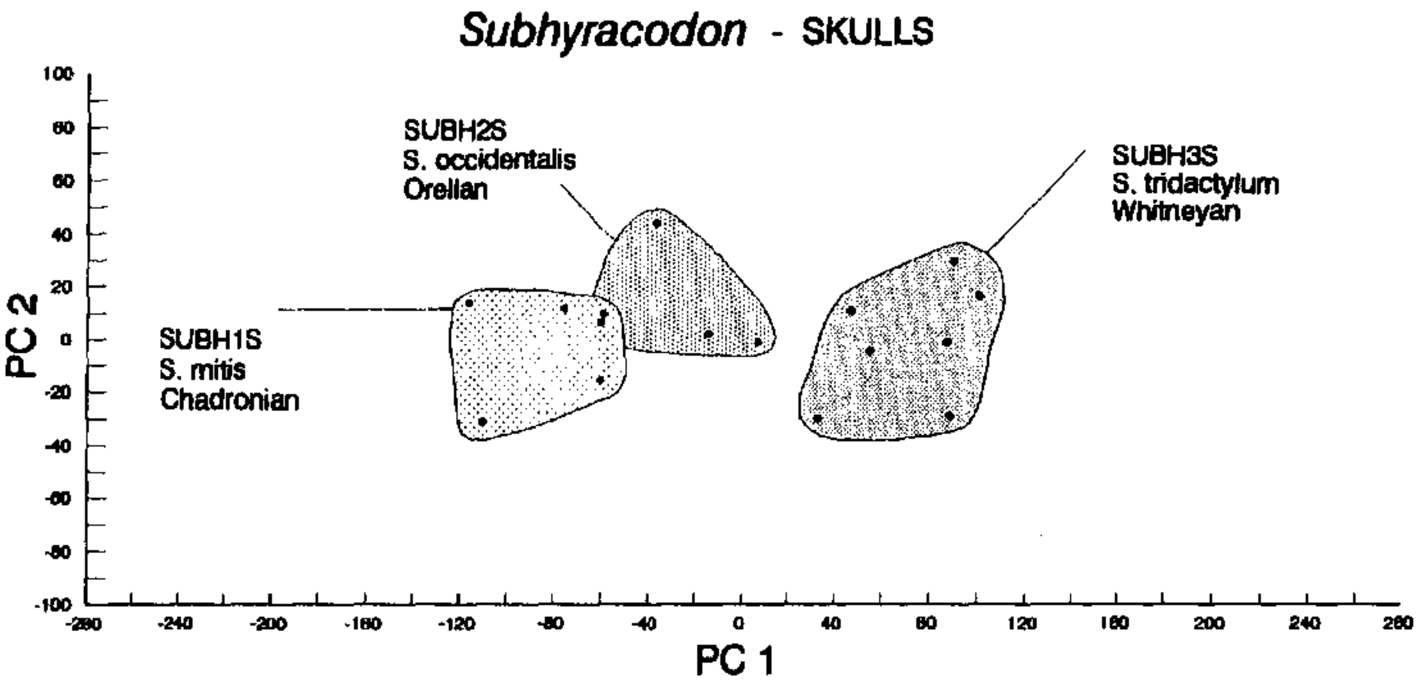
Peraceras - MANDIBLES
PERA1M
New Mexico
Barstovian
PERA2M
P. superciliosum
New Mexico
Barstovian
P. hessei
P. profectum
PC 2
40
30
20
10
0
-10
-20
-30
-40
-100
-80
-60
-40
-20
0
20
40
60
80
100
PC 1

Subhyracodon

Subhyracodon is a primitive rhinocerotid genus which evolved in the late Eocene of North America, probably from *Trigonias* or a similar form, and was a dominant group across the High Plains during the early Oligocene. It disappeared by the late Oligocene and was probably ancestral to *Diceratherium*. Among the largest rhinos of its time, *Subhyracodon* reached a medium, horse size, exceeded only by *Amphicaenopus* (not included in this study). Paleoecologically, *Subhyracodon* fossils are associated with forested areas near streams where they lived as relatively unspecialized hornless browsers. Craniodental features of this genus include a generally flat dorsal skull profile, narrow pointed nasal bones, a low, broad sagittal crest, flaring lambdoid crests, incipient (i.e., inconstant) loss of upper canines, and broad, flat, nearly horizontal mandibular condyles. (Prothero, 1987, in press; Prothero, et al., 1986, 1989; Russell, 1982; Wood, 1929).

Skull (Figure 45) -- Total and PC1 variation (Table 5) are intermediate with respect to the living taxa. *Diceros* and *Ceratotherium* are less variable, *Rhinoceros* is more variable. This generic variation pattern does not by itself support a hypothesis that the sample consists of more than one subgeneric group. Further, the data is well-constrained geographically (South Dakota and Wyoming) which is consistent with a single group (but not

FIGURE 45. Principal components plot of *Subhyracodon* skulls with specimens identified by species and age. Shaded areas include all specimens in the same subgeneric group.



Subhyracodon - SKULLS
SUBH2S
S. occidentalis
Orellan
SUBH3S
S. tridactylum
Whitneyan
SUBH1S
S. mitis
Chadronian
PC 2
PC 1

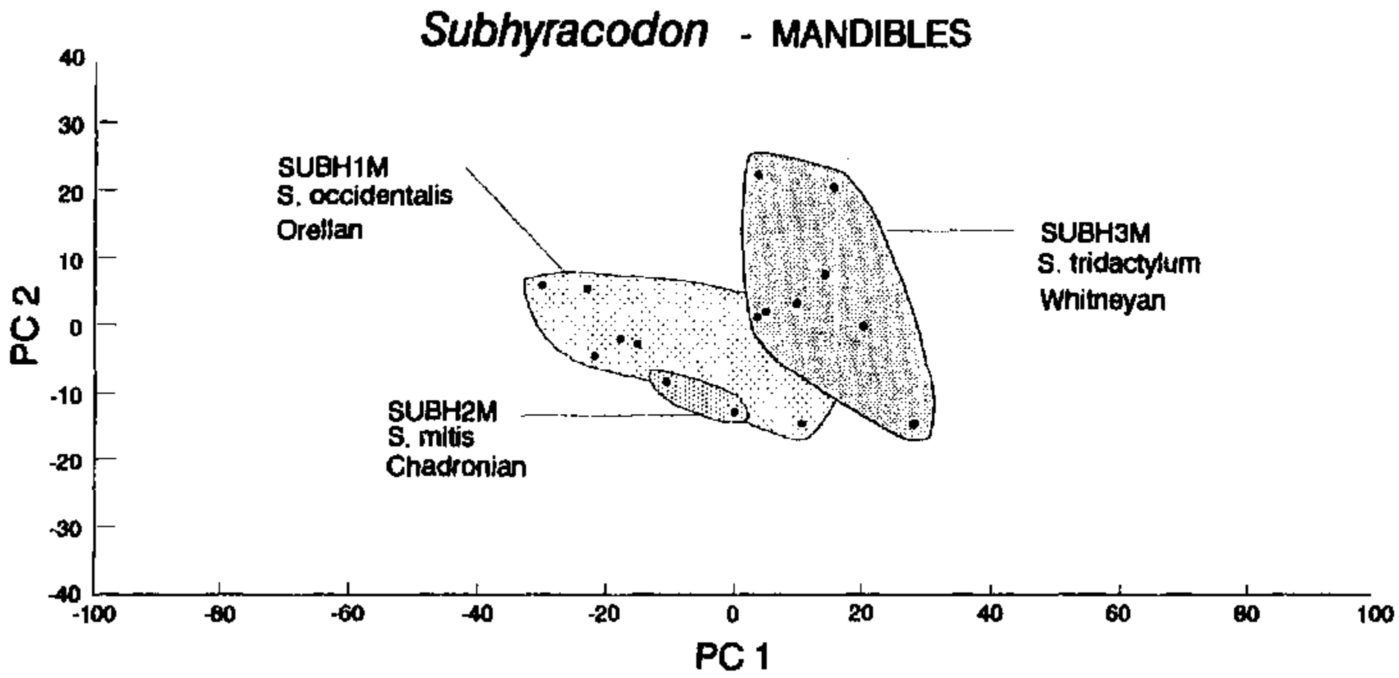
inconsistent with multiple groups). However, most of the specimens of *Subhyracodon* are identified to species and represent localities temporally spread across the early Oligocene (Chadronian, Orellan, Whitneyan). The Whitneyan *Subhyracodon* are considered by some to be *Diceratherium* (Prothero, personal communication). Because these specimens are well defined morphometrically and show a clear temporal sequence of size increase with the other *Subhyracodon* species they are retained within *Subhyracodon* for the purposes of this discussion. Further, canonical variates results (see Chapter 4) show that *Diceratherium* and *Subhyracodon* are very similar morphometrically. *Subhyracodon* might therefore be an intermediate transitional form between the two genera. Dissection of the variation based on the taxonomic and temporal data produced three nearly nonoverlapping subgeneric groups in the morphometric space. SUBH1S consists of all the Chadronian specimens attributable to *S. mitis*, including two specimens labelled *S. trigonodum*. SUBH2S includes all Orellan *S. occidentalis* specimens. SUBH3S comprises the Whitneyan *S. tridactylum* specimens. The morphometric uniqueness of the three time-taxonomic groups, illustrated by non-overlapping boundaries, supports the subgeneric groupings. The variation in each of the subgroups is relatively low compared with the black and white rhinos. Sampling problems notwithstanding, *Subhyracodon* may have maintained lower than average variation in its populations. SUBH1S, SUBH2S, and SUBH3S are temporally sequenced from left to right (earlier to later) indicating evolution of larger size with time.

Mandible (Figure 46) -- Total and PC1 variation is slightly larger than that of the black or white rhinos (Table 5). The specimens form a cloud of variation approximately equal to that of the white rhino but represent the same three time taxonomic groups as determined for the skull data. They were thus subdivided into analagous subgeneric groups (SUBH1M, SUBH2M and SUBH3M) on the same basis. However, overlap is significant here with *S. mitis* entirely within the size range of *S. occidentalis* such that the temporal pattern seen in the skulls is seen here only between *S. occidentalis* and *S. tridactylum*.

Teleoceras

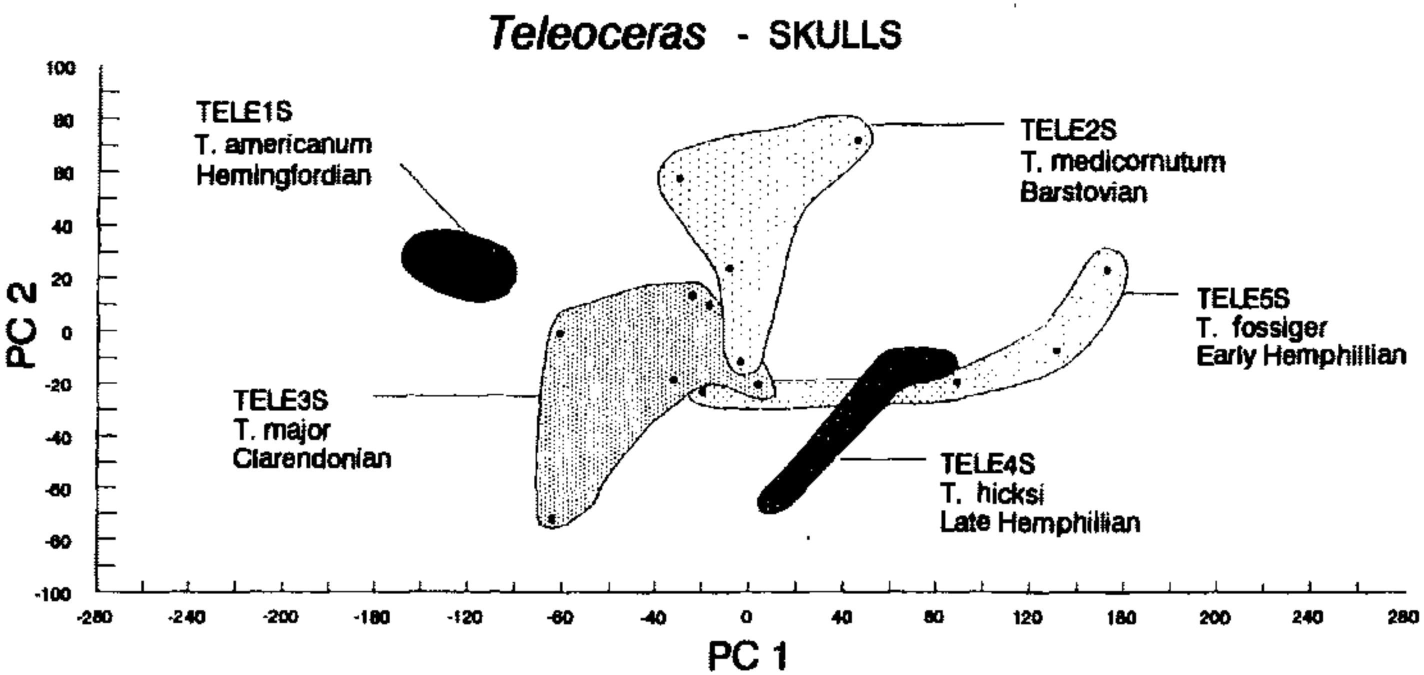
Teleoceras is a common mid-to-late Miocene genus which probably immigrated to North America from Eurasia. Abundant fossils are found in many localities, especially those of the northern Great Plains. These localities are usually interpreted as river channel deposits, suggesting that *Teleoceras* frequented riparian habitats and perhaps was significantly aquatic in its behavior. Body proportions similar to those of the living hippopotamus (i.e. barrel-like trunk and stumpy limbs) have been cited as aquatic adaptations. However, there are no unusual

FIGURE 46. Principal components plot of *Subhyracodon* mandibles with specimens identified by species and age. Shaded areas include all specimens of the same subgeneric group.


Subhyracodon - MANDIBLES
SUBH1M
S. occidentalis
Orellan
SUBH2M
S. mitis
Chadronian
SUBH3M
S. tridactylum
Whitneyan
PC 2
PC 1
40
30
20
10
0
-10
-20
-30
-40
-100
-80
-60
-40
-20
0
20
40
60
80
100

adaptations of the *Teleoceras* skull which might correlate with an aquatic lifestyle (in contrast, the hippopotamus has dorsally shifted orbits, nares, and auditory meati). Among Miocene rhinoceroses, *Teleoceras* has hypsodont (high-crowned) teeth, a character traditionally associated with grazing and cursorial habits. *Teleoceras* is thus paradoxical vis-a-vis the hypsodonty-cursoriality correlation. A further convolution is the grazing analogy between *Teleoceras* and the hippopotamus, since the hippopotamus is a brachydont (low-crowned) grazer. The same localities which yield *Teleoceras* usually also contain a brachydont, browsing rhinoceros which is typically *Aphelops* or a related form (these browsers have not been hypothesized as aquatic). Size changes in *Teleoceras* were irregular such that later forms were not the largest. At least one small form may have been a dwarfed lineage. Diagnostic features of the *Teleoceras* skull include: brachycephaly, hypsodonty, broad lambdoid crests and zygomatic arches, fused and laterally downturned nasal bones, shallow nasal incision, reduced premolars, and retained upper incisors. Most, but not all, *Teleoceras* had a small terminal rugosity on the nasal tip indicating the presence of a single, median horn (Osborn, 1904; Prothero, 1987; Prothero et al., 1986, 1989; Prothero and Manning, 1987; Prothero and Sereno, 1982; Hooijer, 1978; Voorhies and Thomasson, 1979; .

FIGURE 47. Principal components plot of *Teleoceras* skulls with specimens identified by species and age. Shaded areas include all specimens in the same subgeneric group.


Teleoceras - SKULLS
TELE1S
T. americanum
Hemingfordian
TELE2S
T. medicornutum
Barstovian
TELE3S
T. major
Clarendonian
TELE4S
T. hicksi
Late Hemphillian
TELE5S
T. fossiger
Early Hemphillian
PC 2
PC 1

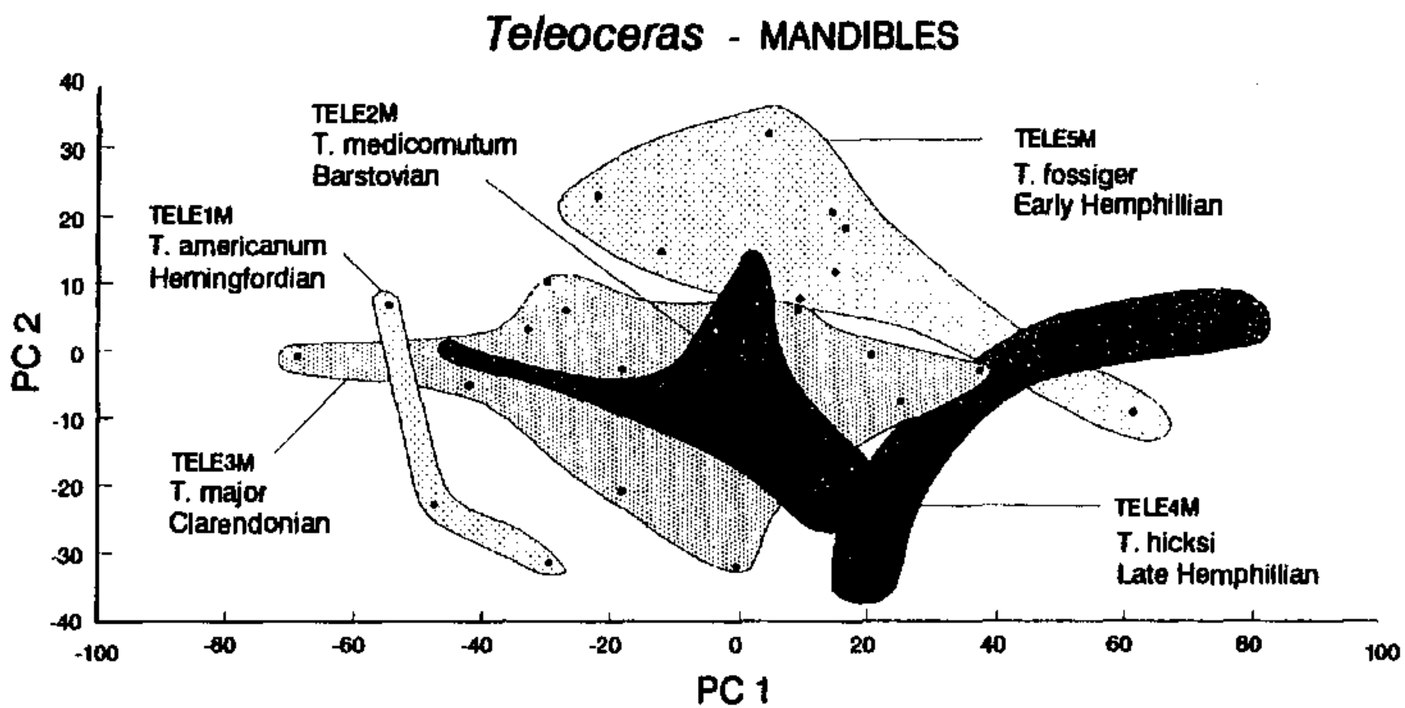
<u>Skull</u> (Figure 47) -- Total PC variation is greater than in *Rhinoceros* and similar to *Diceratherium* among the fossils. PC1 variation is slightly less than in *Rhinoceros*. Taking both PC axes into account, *Teleoceras* has one of the largest scatter of points among all the genera. Dissection of this variation resulted in five subgeneric groups, principally distinguished by age and taxonomy. Geographically, the sample is from plains states (see Table 2), and none of the subgeneric groups represent large or complex ranges, especially when compared with the range of the black rhino. TELE1S comprises two morphologically similar Hemingfordian specimens (*T. americanum*). The association of these smallest specimens with the earliest time interval is similar to the patterns of size evolution observed in other rhinocerotoid genera. TELE2S unites Barstovian specimens from Nebraska classified as *T. medicornutum* (including one specimen labeled as *T. thompsoni*). The dispersion of this group is similar to other subgroups in other genera based on the same types of information. In comparison with living rhinos, no more than single-species variation is indicated. TELE3S represents *T. major* from the Clarendonian of Nebraska. Dispersion size and minimal overlap with other groups suggest that TELE3S is a morphometrically distinct group, different from other *Teleoceras* at other times, and probably a single species. TELE4S comprises late Hemphillian group of *T. hicksi*. It is morphometrically distinct from TELE3S and TELE4S and

its dispersion is consistent with those groups. TELE5S is a time-taxonomic group representing early Hemphillian *T. fossiger*. This is a problematic group because of the morphometric overlap with TELE4S and its odd dispersion. In such cases of overlap, morphometric distinctiveness might be revealed by analyses of variation along higher axes.

Because the five subgeneric groups represent five consecutive land mammal ages, some tentative statements about size-shape evolution in *Teleoceras* may be attempted. This assumes that the groups (populations) at any one time are derived from the previous group (or very similar, but unknown, group). Because there is no temporal unidirectionality among the *Teleoceras* groups in terms of size and shape change, the subgeneric pattern may be analysed pairwise with the following results. *Teleoceras* increased in size from the Hemingfordian to the Barstovian (TELE1S to TELE2S). From the Barstovian to the Clarendonian (TELE2S to TELE3S), there appears to have been some significant shape change since these two groups are separated along the second PC axis by as much as any two groups in this study. It also appears that a size decrease may have acompanied this change. From the Clarendonian to the early Hemphillian (TELE3S to TELE5S), size increased but without any apparent change in average shape. The youngest group, TELE4S (late Hemphillian), appears to be slightly smaller than TELE5S (but not smaller than *T. hicksi* within TELE4S). The temporal (and evolutionary?) pattern of the subgeneric groups is consistent with earlier observations by Prothero and Sereno (1987) that *Teleoceras* does not simply follow a gradient of gradual increase in size through time. A statement by the same authors that *T. fossiger* is unusually large is not supported by the skull results presented here. Lastly, it should be noted that some specimens from three of the groups (TELE2S, TELE3S, and TELE5S) are clustered near the center of the plot and are morphometrically similar.

Mandible (Figure 48) -- The total PC variation associated with the *Teleoceras* mandibles is intermediate (somewhat less than *Rhinoceros*). This amount of variation, not by itself indicative of multiple species, is associated with the largest PC1-PC2 scatter of any genus (skull or mandible) in the study. Accordingly, the variation in this sample was the most difficult to analyse of all the genera (skull or mandible) and produced the least satisfactory results. Generally, the subgeneric groups have more "irregular" and larger dispersions, and exhibit more morphometric overlap, than any other sample. As with the skull sample, the *Teleoceras* mandible variation was grossly reducible by grouping specimens to age and age-associated taxonomies; dispersion and geoegraphy were not helpful. Five subgeneric groups were determined. TELE1M represents the earliest specimens and are among the smallest in the sample (Hemingfordian *T. americanum*). TELE2M is a Barstovian group of *T. medicornutum* (which includes two specimens labeled as *T.*

FIGURE 48. Principal components plot of *Teleoceras* mandibles with specimens identified by species and age. Shaded areas include all specimens in the same subgeneric group.



Teleoceras - MANDIBLES
TELE2M
T. medicornutum
Barstovian
TELE5M
T. fossiger
Early Hemphillian
TELE1M
T. americanum
Hemingfordian
TELE3M
T. major
Clarendonian
TELE4M
T. hicksi
Late Hemphillian
PC 2
PC 1
40
30
20
10
0
-10
-20
-30
-40
-100
-80
-60
-40
-20
0
20
40
60
80
100

thomsoni as in the skull analysis). This group significantly a overlaps the Clarendonian group (TELE3M), which was not the case with the skulls (i.e., Barstovian and Clarendonian mandibles appear to be more similar in size and shape than are the skulls). TELE3M unites Clarendonian specimens of *T. major*, but as is typical in this genus, it has a large dispersion indicative of polyspecific variation. As previously stated, the significant overlap with specimens from the Barstovian (TELE2M) was not observed in the skulls. Specimens from the Hemphillian were subdivided into early (TELE5M - *T. fossiger*) and late (TELE4M - *T. hicksi*) groups. TELE5M is fairly distinct from TELE3M (Clarendonian) along the second axis, reflecting morphometric shape differences, but they overlap greatly in size. If the large outlier in TELE5M were removed from this group, the remaining dispersion would be very consistent with single species variation as shown by the living analogues and well-defined fossil groups. TELE4M is problematic because of its small sample size and odd dispersion. Little can be said except that it overlaps in both shape and size with three other groups. Temporally, the only obvious evolutionary change observed is a shape change between the earlier *T. major* and the later *T. fossiger* assuming they are more or less linked in a lineage. These unsatisfactory results for *Teleoceras* mandibles, given good results elsewhere, suggest either that their classifications and stratigraphy are less accurate, or that they are evolving in more mosaic, less patterned ways.

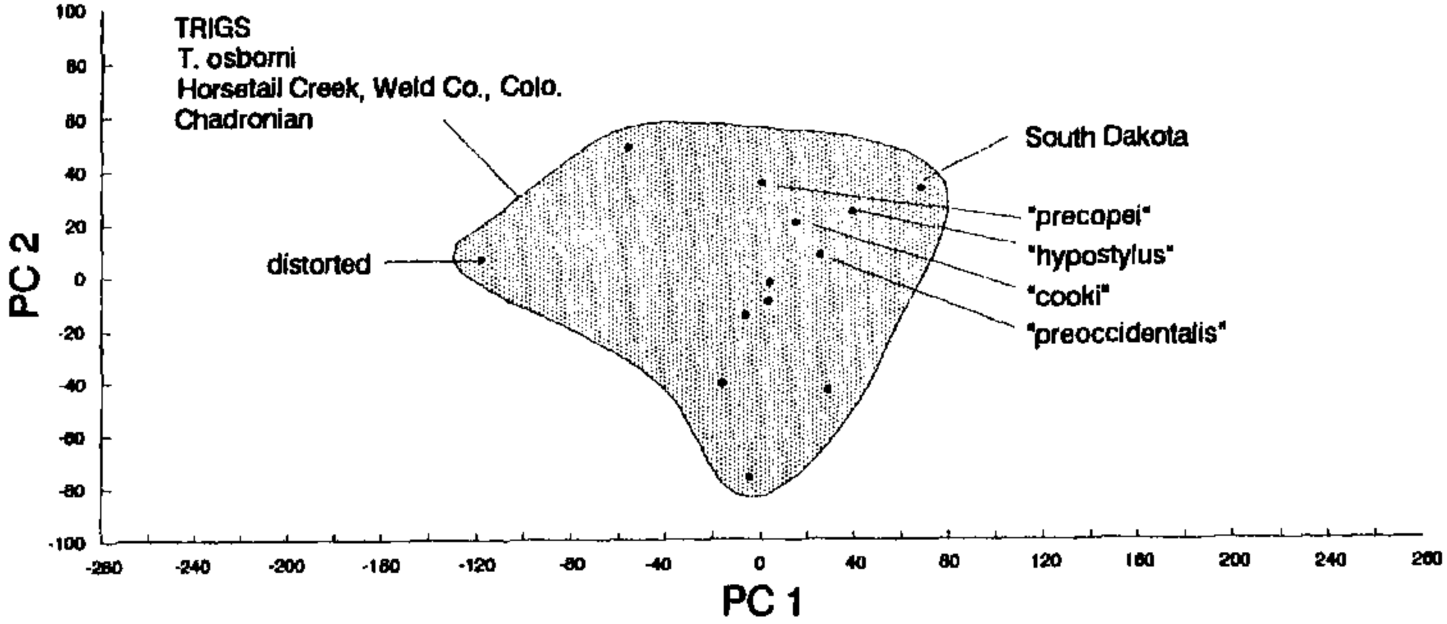
Trigonias

Trigonias is the most primitive genus among the rhinocerotids, or true rhinoceroses, and probably evolved in North America within a lineage leading back to *Hyrachyus* and including *Teletaceras* and *Penetrigonias*. By the early Oligocene, *Trigonias* was distributed over the High Plains and is best known from abundant quarry samples in Colorado. *Trigonias* was a medium-sized rhinoceros with a relatively long, narrow skull (dolichocephalic), a concave or saddle-shaped dorsal skull profile, an extended occiput with flared lambdoid crests, low broad sagittal crests, long nasal bones, retained canines, and a dorsally convex, medially tilted mandibular condyle with straight anterior and posterior borders. Highly variable premolars among the specimens within quarry samples led to typological taxonomic splitting by early paleontologist (Matthew, 1931; Prothero in press a; Prothero et al., 1989; Russell, 1982; Wood, 1931).

Skull (Figure 49) -- Total variation is intermediate to low among the fossil genera and is interemediate between *Diceros* and *Rhinoceros* among the living analogues (Table 5). All of the specimens are late Eocene (Chadronian) in age, and all but one are from Weld County, Colorado. Neither taxonomic nor morphometric

FIGURE 49. Principal components plot of *Trigonias* skulls with specimens identified by taxonomy, locality, and/or geologic age. Shaded areas include all specimens in the same subgeneric group.

Trigonias - SKULLS



evidence suggests any distinct subgeneric groups. Therefore, the sample was united as a single subgroup (TRIGS). The most outlying specimen was noted as being particulary distorted. Exclusion of this specimen would result in a more satisfactory dispersion for a single subgeneric group. However, most of the specimens are probably at least somewhat distorted. Because distortion is difficult to judge objectively, the specimen was not arbitrarily excluded. Additionally, varying degrees of distortion can be expected to contribute to the "normal" variation within most fossil samples and should be considered. The second most outlying specimen, labeled as "Type", may also be distorted. The significance of the "Type" label is undetermined, but probably refers to an invalid species. The remaining specimens are fairly uniform in size and more consistent with living species in terms of overall dispersion. The small morphometric cluster of labeled specimens are individuals originally given species status based on small differences in premolar tooth morphology (this was quickly corrected by other investigators, but the specimens still retain their original labels). It would not be unreasonable, within the context of this study, to hypothesize that those specimens represent a single sex of one species from a single microgeographic locality and preserved within a short time span.

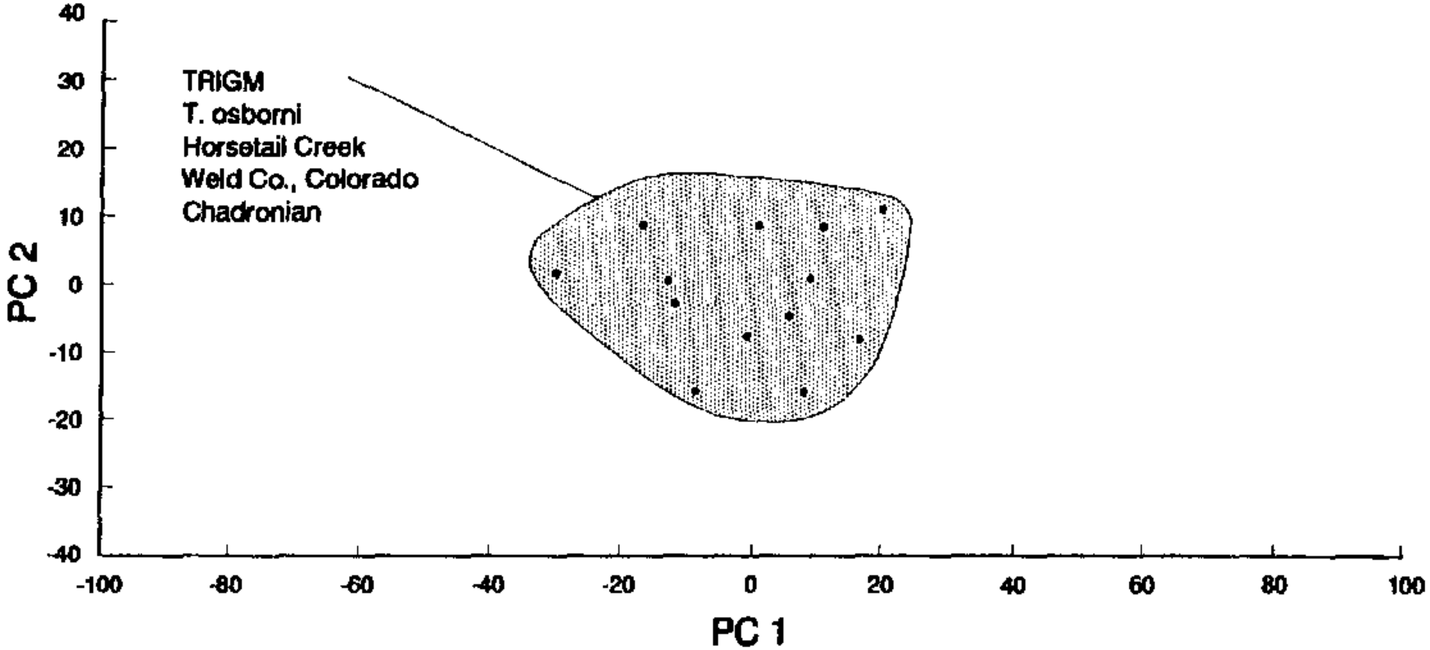
Mandible (Figure 50) -- Total variation is less than that for any of the extant rhinoceroses and suggests that the multivariate variation of the sample is consistent with that found in single species. This is supported by the size and shape of the dispersion in the principal components space (compare with *Diceros* and *Menoceras*, Figures 9 and 41). Additionally, the sample is geographically and temporally constrained with no taxonomic differentiation indicated. Thus, there is no combination of evidence to suggest that more than one distinct subgeneric group exists. All of the *Trigonias* mandibles were therefore retained as a group (TRIGM) for subsequent among-groups analyses. At least one of the two specimens classified to species is invalid because there is no evidence that they represent different populations. Complete morphometric overlap of mandibles labelled only "Weld, Co." with those from Horsetail Creek suggests that they represent the same populational-variational unit, contrary to the result seen in the skulls. However, the five "Weld" specimens are fairly well clustered in a pattern that would perhaps suggest some locality differentiation.

Zaisanamynodon

Zaisanamynodon is the only representative in this study of the more derived genera of the atypical family Amynodontidae. It

FIGURE 50. Principal components plot of *Trigonias* mandibles with specimens identified by taxonomy, locality, and/or geologic age. Shaded areas include all specimens in the same subgeneric group.

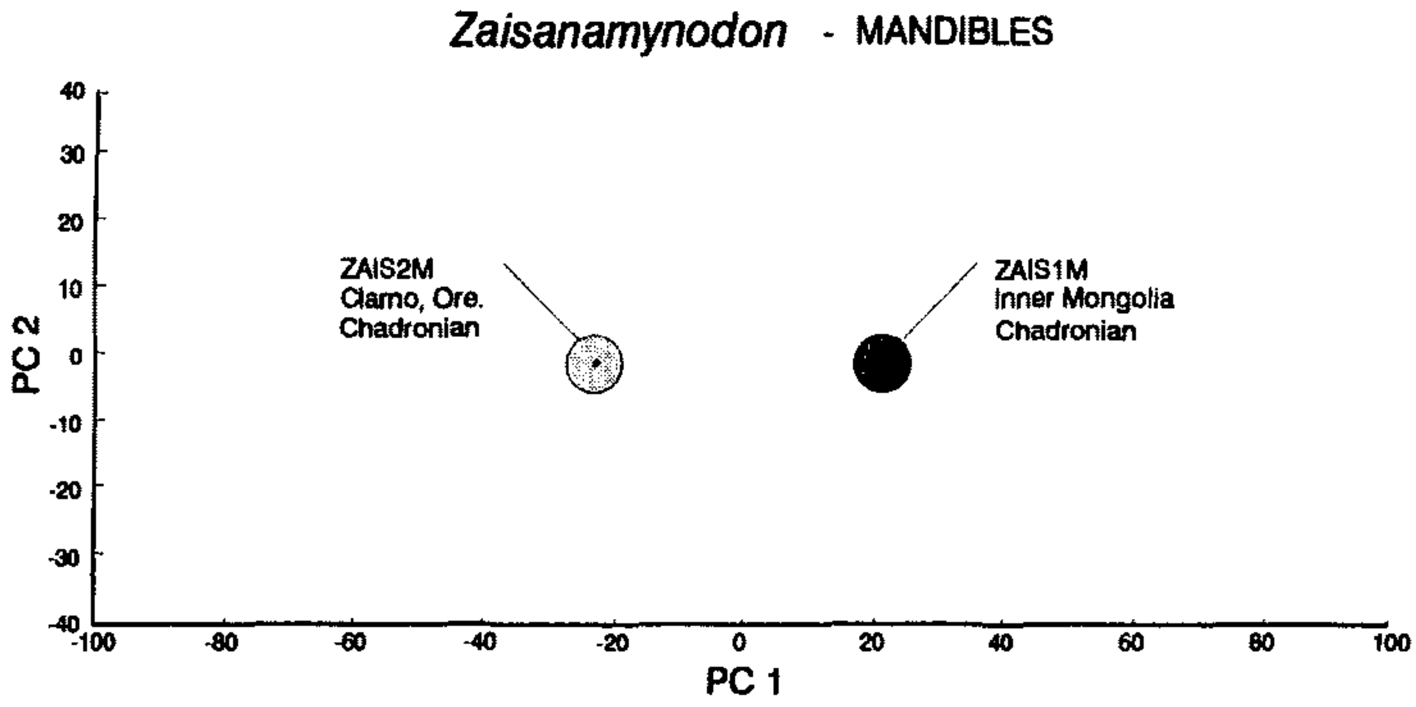
Trigonias - MANDIBLES



is found in the late Eocene of both Inner Mongolia (Sannoisian) and North America (Chadronian) indicating a successful dispersal of one or more species across the Bering Land Bridge route. Little is known about *Zaisanamynodon*; more is known about its close relative *Metamynodon*, a large, stocky form known from river-channel sandstone deposits. Like *Teleoceras*, its sedimentary setting and hippopotamus-like body shape have led to interpretations of an aquatic lifestyle. The same interpretation may apply to *Zaisanamynodon*. Craniomandibular characteristics of the *Zaisanamynodon* skull include brachycephaly, reduced preorbital region, small preorbital fossae present, thickened lower jaws and zygomatic arches, orbit high on skull, shortened nasal bones, enlargement of canines, high-crowned but narrow cheek-teeth, and concave palate (Prothero et al., 1986; Wall, 1989). No skulls and only two mandibles of *Zaisanamynodon* were available for analysis.

Mandible (Figure 51) -- Morphometrically, the separation of the two *Zaisanamynodon* mandibles is within, but near, the limits of a single-species dispersion. However, the specimens were divided (ZAIS1M, ZAIS2M) on the basis of their large geographic difference.

FIGURE 51. Principal components plot of *Zaisanamynodon* mandibles with specimens identified by taxonomy, locality, and/or geologic age. Shaded areas include all specimens in the same subgeneric group.


Zaisanamynodon - MANDIBLES
ZAIS2M
Clarno, Ore.
Chadronian
ZAIS1M
Inner Mongolia
Chadronian
PC 2
PC 1
40
30
20
10
0
-10
-20
-30
-40
-100
-80
-60
-40
-20
0
20
40
60
80
100

GENERIC AND SUBGENERIC POOLED WITHIN-GROUP DISPERSIONS

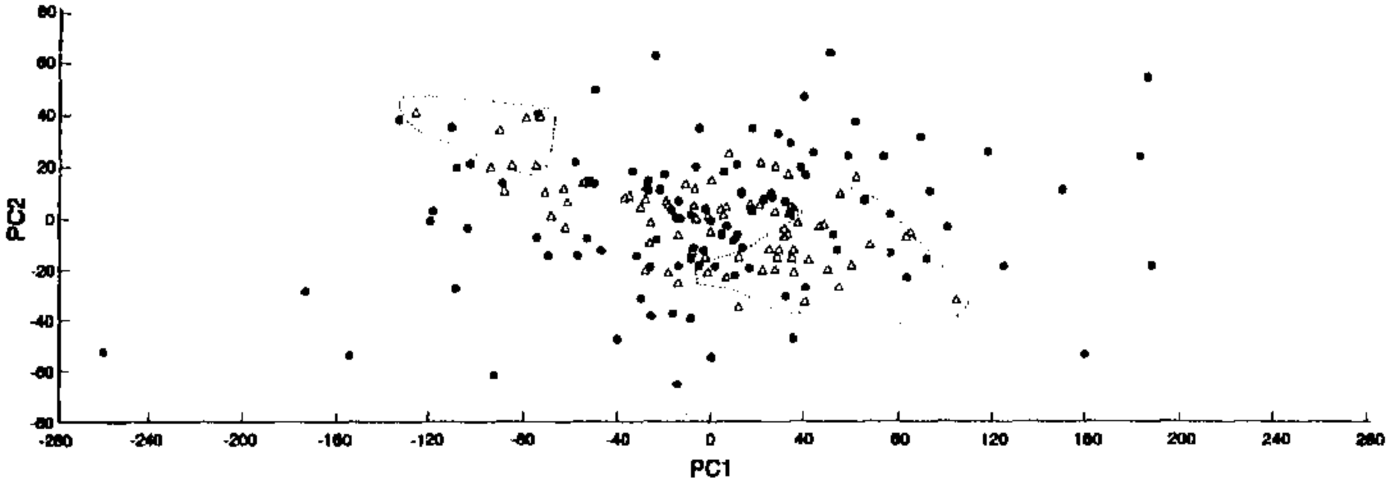
The subgeneric groups determined in the preceding analyses will be used in the among-groups analyses of Chapter 4 to derive a pooled within-group dispersion. This dispersion is used as a standard by which to judge among-groups variation in the canonical variates analyses. Here, the pooled generic and pooled subgeneric dispersions for both skull and mandible are presented. They graphically show the effect of dissecting the generic variation into subgeneric groups.

Skull

Pooled Genera (Figure 52) -- This figure shows a principal components analysis of pooled skull data for all living and fossil genera. The data set is derived from Figure 7 by centering the mean of each genus at the origin such that all the genera are superimposed. The greater variation in the fossils is consistent with the variances of Table 5 and provides *a posteriori* support for the dissection of the genera into subgeneric groups. Especially significant in Figure 52 are the positions of the *Rhinoceros* specimens. The four specimens of the Javan rhino (dotted outline, upper left) and many of the specimens of the Indian rhino (dotted outline, lower right) are on the periphery of the main cloud. Because *Rhinoceros* is the only multi-species genus among the living

FIGURE 52. Principal components plot of all living and fossil skull specimens, pooled by mean-centered genera. Axes are the same as for Figure 53. Fossil - dark circles. Living - open triangles. Specimens of the Javan rhinoceros (upper left) and Indian rhinoceros (lower right) are indicated by dotted lines.

POOLED GENERA - SKULLS LIVING (△) FOSSIL (•)

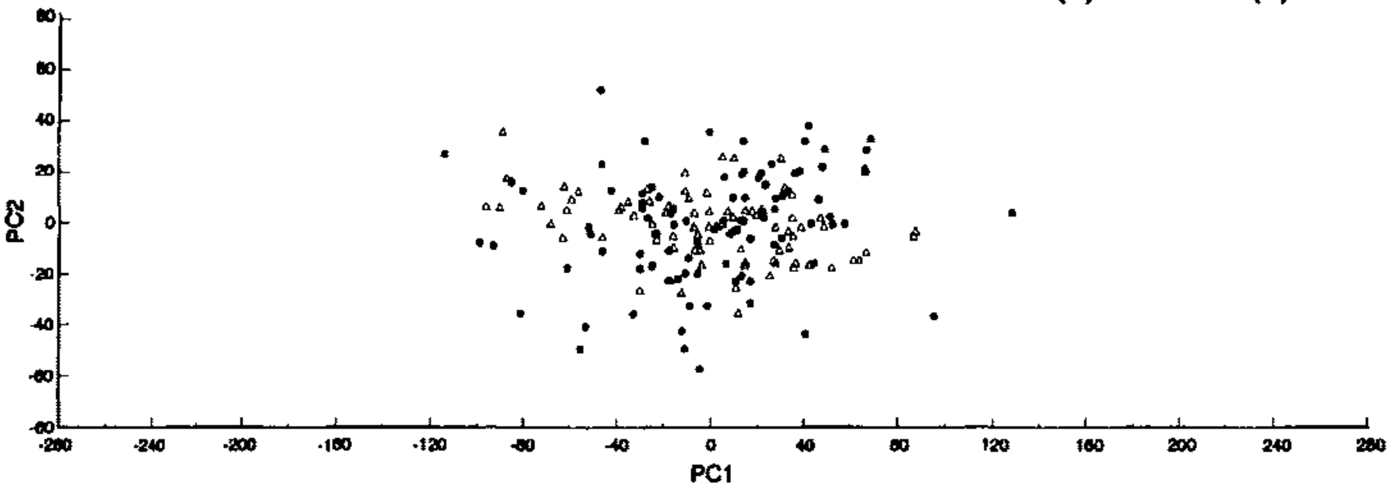


analogues, the pooled pattern suggests that much of the size and shape variation of the fossil genera is equal to or less than that found in *Rhinoceros*. The small number of very outlying specimens (far left and far right) belong to only a few of the more variable fossil genera (*Teleoceras*, *Diceratherium*, and *Peraceras*).

Pooled Subgeneric Groups (Figure 53) -- All of the subgeneric groups identified in Chapter 3 were superimposed by centering their means (centroids) on the origin. This plot dramatically shows the effect of controlling for biological and geological factors such as stratigraphy, time, geography, and character-based taxonomy when investigating morphometric variation. When this is done, the overall variation in the pooled fossil rhinoceros subgroups becomes relatively homogenous and similar in degree to that of the living species. The limits of the pooled variation are still determined by fossils (i.e, *Teleoceras* distributed cicumferentially and *Diceratherium* on left and right extremes). This is reasonable because at least some the fossil subgroups are probably still polytypic, but undivided due to lack of data. Additionally, the variation of the living rhinos most likely does not represent a maximum or minimum. Given the diversity of fossil rhinos, different groups would be expected to have more or less variation. In summary, the variation in the

FIGURE 53. Principal components plot of all living and fossil skull specimens, pooled by mean-centered subgeneric groups. Axes are the same as for Figure 52. Fossil - dark circles. Living - open triangles.

POOLED SUBGENERIC GROUPS - SKULLS LIVING (▵) FOSSIL (•)



analogues is a reasonable measure of species/population level variation in rhinocerotoids generally. When fossil genera are dissected into hypothesized population or species level subgeneric groups, the overall fossil variation conforms well to that of the living analogues. Therefore, the pooled subgeneric data set provides a good estimate of within-group variation by which to maximize variation among those groups.

Mandible

Pooled Genera (Figure 54) -- In general, the results for mandibles are similar to that for skulls (discussed above). That is, variation in most of the fossils is not much greater than that of the living forms (some living specimens are peripheral). The more extreme outlying specimens belong to a few of the more variable fossil genera. Most of the circumferential fossils are *Teleoceras* specimens, but unlike the pooled skull dispersion, the extreme left and right outlying mandibles are *Aphelops*.

Pooled Subgeneric Groups (Figure 55) -- As in the skull analysis, when the genera are subdivided based on known correlates of population or species level variation, the pooled dispersion becomes more homogenous and suggests that the living analogues are good measures of species level variation in rhinocerotoids generally.

FIGURE 54. Principal components plot of all living and fossil mandible specimens, pooled by mean-centered genera. Axes are the same as for Figure 55. Fossil - dark circles. Living - open triangles. Specimens of the Javan rhinoceros (left) and Indian rhinoceros (right) are indicated by dotted lines.

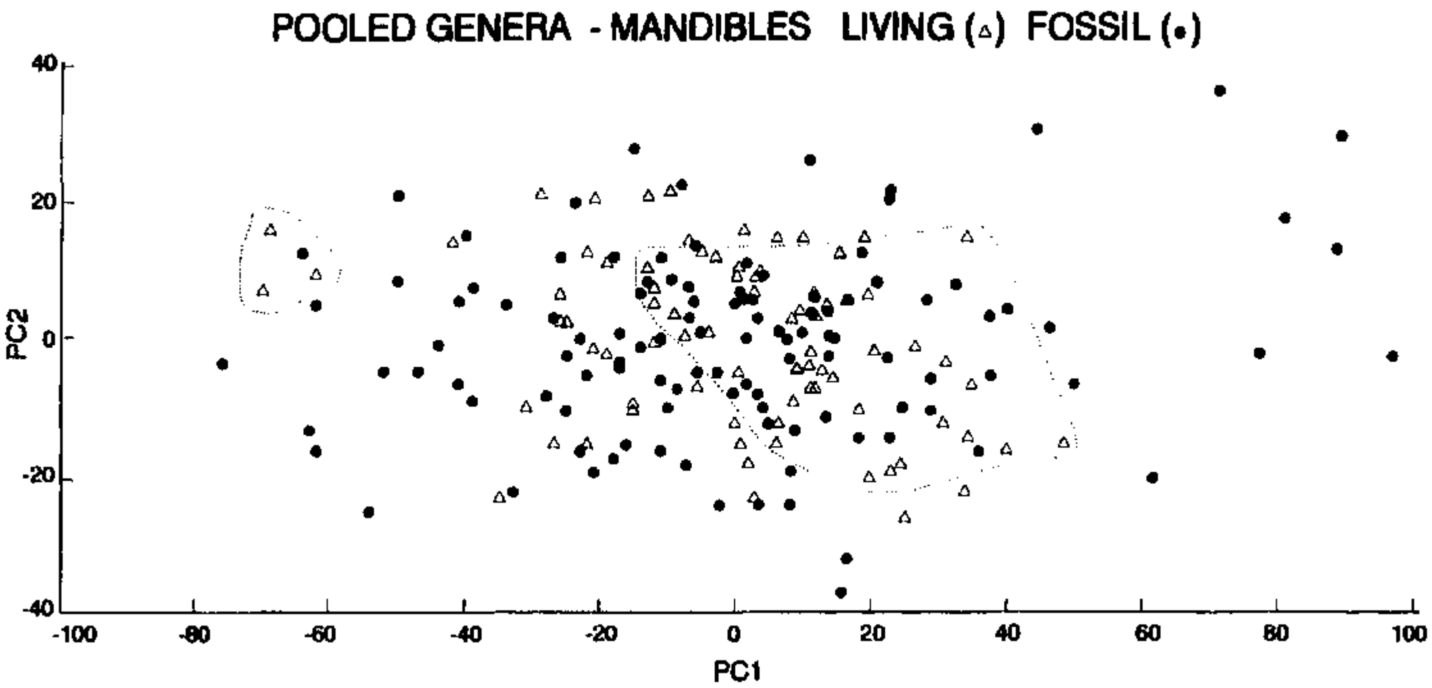
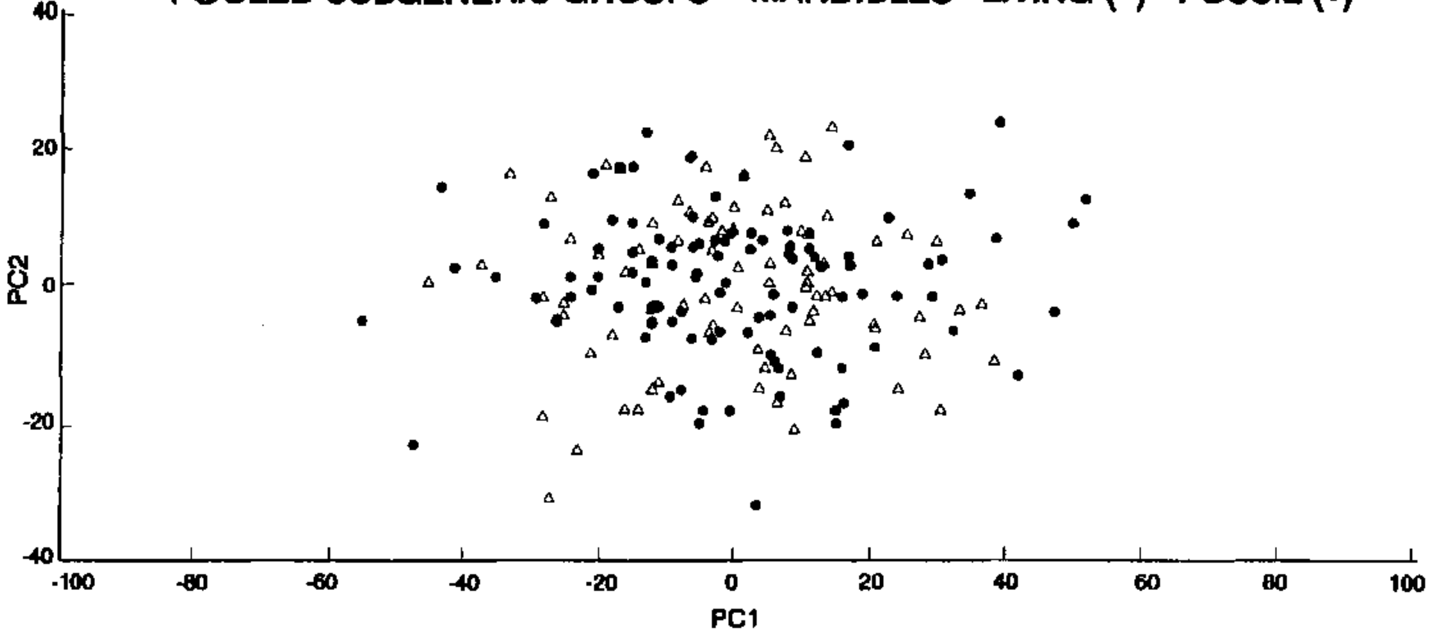

POOLED GENERA - MANDIBLES LIVING (△) FOSSIL (•)
PC2
PC1
40
20
0
-20
-40
-100
-80
-60
-40
-20
0
20
40
60
80
100

FIGURE 55. Principal components plot of all living and fossil mandible specimens, pooled by mean-centered subgeneric. Axes are the same as for Figure 54. Fossil - dark circles. Living - open triangles.

POOLED SUBGENERIC GROUPS - MANDIBLES LIVING (△) FOSSIL (•)



CHAPTER 4.

AMONG-GROUPS RELATIONSHIPS - CANONICAL VARIATES ANALYSES

MULTIVARIATE VARIATION AND CANONICAL VARIATES ANALYSIS

Each of the subgeneric groups determined in the previous chapter may be represented by its multivariate mean (centroid). The resulting set of group means may then be treated as data points analogous to the specimens in principal components analysis. Similarly, the variation among the group means can be partitioned among a new set of mutually orthogonal, variance-maximizing axes (Campbell and Atchley, 1981; Albrecht, 1980, 1992). However, canonical variates analysis (CV) is not simply a principal components analysis of group means. Two features distinguish CV from PC: (1) CV maximizes the proportion of among-groups variation relative to within-group variation (hence, the emphasis on within-group variation in Chapter 3); and (2) the CV axes are scaled such that they represent equivalent units of within-group variation, effectively eliminating within-group correlations. The overall effect of CV is to maximally separate groups along each respective axis. Because the new CV axes define a morphospace (as do the PC axes), means reflecting similar morphologies plot more closely together, while means reflecting different morphologies plot more distantly from each other.

STRATEGY AND SIGNIFICANCE OF CANONICAL VARIATES RESULTS

The strategy in Chapter 3 of dissecting the variation of living and fossil genera resulted in subgroups whose variation approximates the range of individual differences at the population or species level. The relative homogeneity of the living and fossil subgroups provides the basis for pooling of these presumably similar groups. The pooled within-group dispersion is a better estimate of within-group variation across all rhinoceros genera. Canonical variates (CV) analysis uses this pooled within-group estimate to maximize among-groups variation in the multivariate morphospace.

Canonical variates are usually presented as a plot of the means (centroids) of the groups being considered. Individual specimens may be plotted by finding their scores (projections) on the axes which are determined by the variation among the means. In both cases, the group means are ordinated so as to maximize their separation relative to a pooled-within group dispersion (as discussed above). In the following section, the canonical variates ordination is first presented with individuals identified by genus (Figures 56 and 57). This is followed by plotting of subgroup means with 90% concentration ellipses around each mean (Figures 58 and 59). These two set of plots indicate the significance of the pooled-within group dispersion determined in Chapter 3.

Once the pattern of group relationships is established in the CV morphospace, the morphological affinities of groups can be interpreted in terms of various biological correlates. This analysis of among-groups variation is analogous to the dissection of the specimens in the principal components analyses. In the following section, the morphological relationships in CV space are analysed in three major ways. First, the multivariate morphology is observed relative to more traditional, character-based taxonomic investigations (including postcranial and non-morphological characters). Taxonomic correlations are analyzed with respect to genera, families and subfamilies, and cladistic character states. Second, the multivariate morphology is observed relative to two structural-functional aspects of rhinoceros skull biology, in particular, horn arrangement and feeding strategy. Third, temporal patterns of morphological change are analysed with respect to intergeneric and intrageneric variation.

INTERPRETATION OF CANONICAL VARIATES RESULTS

For each data set (skull or mandible), one CV analysis was done, based on the appropriate pooled within-group dispersion. Each CV analysis resulted in an ordination of the subgeneric means along a new set of variance-maximizing axes. Within skulls or mandibles, the same equally scaled-CV axes are used for all plots. Figures 58-73 are based on the same fundamental canonical variates result where the means of the subgeneric groups are shown in the plane of the first two canonical axes. The subgroups correspond to those in Table 2 (skull) and Table 3 (mandible).

Eigenvalues (variances) of the canonical variate axes are summarized in Table 6. The first two canonical axes include much of the total variation for both skulls and mandibles (82% and 86%, respectively). The first CV axis, like the first PC axis, is a size axis (discussed below). The canonical variate means of subgroups are given in Tables 7 (skull) and 8 (mandible) for all CV axes on which there is among-groups variation. These means represent the scores of the group centroids on the respective axes. The range of mean values for a given axis decreases from lower to higher axes, as indicated by the decreasing eigenvalues of Table 6.

Because the group means exist within a multidimensional hyperspace, the separation of the means in the plane of two CV axes may not always accurately reflect the true distances between them. The more the first two axes account for the total variation, the more the distances will reflect the true distances. One measure of the distances between means in the multidimensioanl space is the generalized distance (GD), D^2. Generalized distances are given in Table 9 (skull) and Table 10 (mandible). For those genera with subgroups, inter-subgroup distances are summarized in Table 11.

TABLE 6. Summary of eigenvalues, percent of total variance, and cumulative percent of total variance for skull and mandible canonical variates.

SKULL

CV	Eigenvalues	% of Total	Cumulative %
CV1	93.4	61.7	61.7
CV2	33.3	21.8	83.1
CV3	6.3	4.1	87.2
CV4	4.6	3.0	90.2
CV5	3.0	2.0	92.2
CV6	2.9	1.9	94.2
CV7	1.7	1.1	95.3
CV8	1.7	1.1	96.4
CV9	1.2	0.8	97.3
CV10	0.8	0.6	97.8
CV11	0.7	0.5	98.3
CV12	0.7	0.5	98.8
CV13	0.5	0.4	99.2
CV14	0.5	0.3	99.5
CV15	0.3	0.2	99.7
CV16	0.2	0.1	99.8
CV17	0.1	0.1	99.9
CV18	0.1	0.1	99.9
CV19	0.1	0.1	100.0

MANDIBLE

CV	Eigenvalues	% of Total	Cumulative %
CV1	69.9	77.3	77.3
CV2	10.5	11.1	88.4
CV3	3.8	4.2	92.7
CV4	2.4	2.7	95.4
CV5	1.2	1.3	96.8
CV6	1.1	1.2	98.7
CV7	0.5	0.6	98.7
CV8	0.5	0.5	99.5
CV9	0.2	0.3	99.5
CV10	0.2	0.2	99.8
CV11	0.1	0.2	100.0

TABLE 7. Canonical variate means for skull subgroups. Genera and subgroups are listed in the same order as in Table 2. Eigenvalues (EIGEN) and percentages of total among-subgroup variance (%) are given at the bottom.

SUBGROUP	CV1	CV2	CV3	CV4	CV5	CV6	CV7	CV8	CV9	CV10	CV11	CV12	CV13	CV14	CV15	CV16	CV17	CV18	CV19
CERAS	9.8	-0.6	2.3	-7.4	-1.0	-2.1	-1.4	-1.2	-0.2	-0.2	-0.8	-0.7	-0.1	0.5	-0.0	0.1	0.2	0.0	0.0
SUMAS	-2.9	1.6	4.9	-1.0	-1.0	3.7	0.6	3.2	0.5	0.3	1.2	0.4	0.3	-0.3	-0.3	0.0	-0.2	-0.2	-0.1
BICOS	4.8	1.1	2.2	-1.6	1.6	-0.3	-1.8	-1.2	-1.5	0.7	-1.2	1.2	-8.1	-0.1	-0.0	-0.5	-0.2	-0.0	8.1
UNICS	7.3	6.9	2.7	0.9	-0.3	-1.7	-0.3	-0.3	0.4	-1.2	-0.4	-0.6	-8.2	1.2	-0.3	-0.2	0.9	-0.1	-0.1
JAVAS	3.5	6.2	2.6	6.3	-0.1	-0.3	-3.3	-0.6	-2.1	0.1	-0.3	-0.1	-0.5	-0.0	0.2	-0.1	-0.2	-0.1	0.0
ACER1S	4.0	1.7	0.3	1.2	-1.0	-3.6	1.0	-3.6	0.2	1.1	-0.2	0.1	0.4	-0.6	0.0	-0.1	-0.3	-0.1	0.1
ACER2S	6.3	-1.3	8.5	1.1	-0.8	2.4	3.5	-0.2	-1.0	8.8	1.2	0.1	-0.1	0.0	0.0	0.3	0.1	0.3	0.0
AMYHS	-5.3	-5.9	-0.9	0.3	-2.5	0.7	0.0	-0.9	0.6	0.7	0.4	3.1	0.0	0.2	0.2	0.5	0.0	-0.2	-8.1
APHE1S	-0.9	-0.8	-0.4	-1.8	-2.0	4.1	0.3	8.7	0.2	1.3	-2.0	-0.9	0.2	0.7	-0.3	0.3	-0.5	0.3	0.1
APHE2S	2.7	2.4	1.1	-2.0	1.2	2.5	-1.8	-1.1	1.5	0.9	1.3	-0.3	-0.5	0.6	0.0	0.2	0.3	-0.5	-0.6
DICE1S	-5.8	-2.3	-0.2	1.0	0.9	2.8	0.3	0.1	-0.3	-1.6	-2.0	-0.2	0.2	0.5	0.1	0.5	0.3	0.4	-0.3
DICE2S	-3.1	-3.2	-1.3	-0.4	0.5	0.4	0.3	0.9	-0.1	0.6	-1.3	-0.2	-1.0	-0.6	0.0	-0.1	0.2	-0.4	0.3
DICE3S	0.1	-3.3	-2.9	-0.5	3.8	1.6	-0.6	-1.5	-0.3	1.0	0.2	0.6	1.1	1.1	0.3	-0.5	0.6	0.2	0.5
FORSS	-5.2	-4.1	-0.4	-2.1	1.5	1.8	0.1	-0.2	-2.3	-1.4	1.0	0.3	-0.2	-1.3	-0.8	-0.1	-0.2	0.2	-0.3
HYRA1S	-16.0	-3.4	-0.0	0.8	-1.1	-0.7	-1.8	1.1	0.4	-0.0	0.1	-0.6	-0.2	-0.1	-0.2	0.4	-0.3	0.1	0.1
HYRA2S	-13.0	-3.0	-0.4	0.4	-2.0	-0.8	-8.7	0.9	-0.0	-1.0	-0.1	0.3	0.9	-0.0	-8.3	-0.0	0.3	-0.1	-0.4
HYCOS	-13.0	-5.4	0.5	0.6	-1.5	-1.2	0.2	0.0	0.3	-0.6	0.9	-1.2	-0.9	0.9	0.5	-0.4	-0.5	8.2	0.4
INDRS	37.7	-18.0	-1.8	2.1	-0.4	-0.5	-0.6	1.0	0.4	-0.4	0.0	-0.3	0.3	-0.0	0.0	-0.1	-0.1	-8.1	-0.0
MENOS	-7.7	-0.3	-8.1	0.3	1.1	0.9	-0.2	0.0	0.3	0.5	0.9	-1.0	1.2	-0.7	0.6	-0.1	-0.3	-0.4	0.2
PERA1S	-1.8	2.7	0.1	-1.0	-1.8	-1.4	0.0	-0.5	0.5	-0.7	-0.2	-0.1	1.5	0.1	-0.9	-0.8	-0.5	-0.5	-0.2
PERA2S	7.8	8.0	2.0	0.6	-0.0	2.5	-0.5	-1.0	2.5	-2.4	-0.0	0.8	-0.5	-1.0	0.3	-0.2	-0.3	0.3	0.4
SUBH1S	-6.3	-2.0	-0.9	-0.2	-0.5	-0.3	0.7	0.3	-0.4	0.8	-0.1	-0.5	-0.7	-0.9	0.8	-0.8	0.6	-0.2	-0.2
SUBH2S	-4.2	-2.6	-0.5	-0.4	-0.6	-0.1	0.6	-0.8	0.2	-0.1	-0.1	-0.7	0.7	-1.0	0.1	1.0	0.6	-0.4	0.3
SUBH3S	-3.1	-2.0	-1.9	-0.1	2.1	0.1	0.4	0.4	0.8	0.9	-0.2	0.2	-0.8	-0.2	0.7	-0.7	0.2	0.5	-0.5

SUBGROUP	CV1	CV2	CV3	CV4	CV5	CV6	CV7	CV8	CV9	CV10	CV11	CV12	CV13	CV14	CV15	CV16	CV17	CV18	CV19
TELE1S	-0.0	5.9	-1.2	1.5	2.9	0.7	-0.1	-0.9	-0.1	-0.0	0.9	-0.0	1.2	0.8	0.1	-0.0	-0.1	0.6	-0.2
TELE2S	5.6	8.6	-3.7	2.6	0.3	-0.4	2.2	0.3	-0.0	0.7	0.3	-0.6	-0.9	0.2	-0.6	0.2	-0.3	-0.5	-0.4
TELE3S	4.7	6.9	-3.7	-0.0	-1.8	-1.1	-0.2	1.5	0.3	1.0	0.4	0.1	0.1	-0.9	-1.3	-0.2	0.6	0.5	0.5
TELE4S	6.5	9.3	-2.4	-2.7	-1.3	-1.4	-1.1	1.0	0.0	0.4	-0.1	-0.3	0.7	-0.7	1.0	0.6	-0.3	0.7	-0.4
TELE5S	7.8	8.9	-3.4	-0.8	-0.3	-0.3	1.3	1.4	-1.5	-1.2	0.1	0.8	-0.1	0.8	0.8	0.3	-0.1	-0.6	0.3
TRIGS	-4.0	-3.0	-1.6	-0.6	-0.5	-0.6	2.2	-0.6	-0.0	-0.4	0.2	0.3	-0.1	0.8	-0.4	-0.2	-0.4	0.0	0.1
EIGEN.	93.4	33.3	6.3	4.6	3.0	2.9	1.7	1.7	1.2	0.8	0.7	0.7	0.5	0.5	0.3	0.2	0.1	0.1	0.1
%	61.2	21.8	4.1	3.0	2.0	1.9	1.1	1.1	0.8	0.5	0.3	0.5	0.4	0.3	0.2	0.1	0.1	0.1	0.1

TABLE 8. Canonical variate means for mandible subgroups. Genera and subgroups are listed in the same order as in Table 3. Eigenvalues (EIGEN) and percentages of total among-subgroups variance are given at the bottom.

SUBGROUP	CV1	CV2	CV3	CV4	CV5	CV6	CV7	CV8	CV9	CV10	CV11
CERAM	7.6	-5.9	0.5	2.2	0.5	0.8	-1.9	2.0	-1.0	-0.4	0.2
SUMAM	1.6	-7.9	1.2	-0.9	-5.8	0.5	1.3	0.1	-0.2	0.8	-0.3
BICOM	3.8	-4.8	1.4	-0.2	0.3	1.9	-0.2	0.3	1.2	-0.3	0.3
UNICM	5.8	-2.5	2.1	0.9	-2.0	-2.2	-0.4	-1.2	-0.5	-0.4	0.1
JAVAM	0.1	-1.6	2.2	0.7	0.5	0.0	0.6	0.0	1.0	-0.5	0.2
ACER1M	2.5	-0.3	0.0	0.1	-0.3	0.2	0.3	0.3	-0.1	-0.1	-0.1
ACER2M	1.1	-0.2	2.0	1.8	-2.7	0.2	0.1	0.5	0.1	0.6	-0.4
APHE1M	0.6	-1.3	-1.6	1.1	-0.9	0.7	0.4	-0.6	-0.7	-0.1	-0.2
APHE2M	1.7	-0.7	0.1	0.7	-1.7	-0.2	-0.4	0.6	-0.2	-0.5	-0.2
APHE3M	7.7	-0.7	-1.2	1.2	-0.7	0.7	1.0	-0.0	0.2	0.3	-0.4
APHE4M	10.6	-1.1	-3.6	-0.6	-1.0	-0.2	1.7	0.9	1.0	1.0	-0.0
OICE1M	-0.7	1.5	-1.1	-3.3	0.2	-0.3	1.0	0.5	0.8	-0.6	-0.3
OICE2M	-7.8	-0.7	4.9	-0.9	0.0	-1.1	-1.6	0.2	-0.6	-0.0	0.1
FORS1M	-5.1	4.3	1.2	-1.7	0.8	0.9	0.1	1.2	-0.6	-0.2	-0.2
FORS2M	-9.7	1.9	-0.5	0.2	0.1	1.0	0.4	0.4	0.0	-0.5	-0.3
HYRA1M	-17.0	-0.1	0.5	0.8	0.8	0.5	0.1	0.2	0.4	-0.0	-0.2
HYRA2M	-13.2	1.6	-0.2	0.6	0.7	-0.1	-0.1	0.8	0.2	0.6	-0.0
HYCOM	-14.0	0.3	-1.0	1.6	-0.3	0.6	-0.2	-0.3	0.5	0.3	-0.2
INORM	23.2	3.2	4.9	0.0	0.8	0.8	1.6	0.2	0.2	0.5	0.1
MENO1M	-7.8	-0.2	3.9	-0.9	0.0	-0.9	-1.5	-0.7	0.5	0.3	0.2
MENO2M	-3.7	-2.2	1.0	-1.3	-0.1	-1.7	-0.5	-1.9	0.2	0.3	-0.2
PENE1M	-11.0	-1.6	-0.9	-0.7	-0.8	-0.1	1.3	-0.5	-0.1	0.7	0.2
PERA1M	0.6	-1.8	-2.3	-1.2	0.0	0.8	1.3	-0.5	-0.1	0.7	0.2
PERA2M	6.6	-1.1	-2.2	-0.1	1.4	0.3	1.5	-0.5	-0.7	0.1	0.0

SUBGROUP	CV1	CV2	CV3	CV4	CV5	CV6	CV7	CV8	CV9	CV10	CV11
SUBH1M	-6.4	0.2	-0.4	-0.5	0.1	0.2	0.4	-0.3	-0.2	-0.3	0.2
SUBH2M	-6.8	0.7	-1.4	0.7	0.1	0.2	-0.0	0.2	0.0	0.4	0.6
SUBH3M	-4.4	0.9	-0.3	-0.1	1.4	1.5	0.5	-0.3	0.0	-0.2	0.2
TELE1M	2.5	-0.1	-0.9	-0.8	1.5	-0.1	1.2	0.3	-0.2	-0.4	-0.2
TELE2M	5.4	-0.5	-1.1	-0.1	-0.1	0.1	-0.1	-0.6	-0.4	0.5	0.4
TELE3M	4.7	-1.8	-1.2	-1.2	0.3	0.0	0.1	-0.5	0.1	-1.1	-0.1
TELE4M	7.5	-2.9	-0.0	-8.5	-1.1	-0.4	-0.1	-0.4	0.5	-1.1	8.2
TELE5M	7.7	-2.1	-1.9	-0.6	-0.8	0.8	-1.0	-1.1	-0.2	0.1	-0.2
TRIGM	-4.1	0.3	-1.4	-0.1	0.2	-0.0	0.4	-0.1	-0.4	0.0	0.8
ZAIS1M	5.3	8.2	-0.8	5.3	1.9	2.2	-1.0	-1.0	0.2	-0.0	-0.0
ZAIS2M	7.1	11.1	-0.5	-2.7	-1.8	-1.9	-0.6	0.2	-0.2	-0.3	0.2
EIGEN.	69.9	10.5	3.8	2.4	1.2	1.1	0.5	0.4	0.2	0.2	0.1
%	77.3	11.1	4.2	2.7	1.3	1.2	0.6	0.5	0.2	0.2	0.2

TABLE 9. Generalized distances ($\sqrt{D^2}$) for skull CV means. D^2 matrix is shown in two panels (left and right halves). Subgroup symbols correspond to those in Figure 58 and are listed below.

A1 - ACER1S *Aceratherium*
A2 - ACER2S *Aceratherium*
AM - AMYNS *Amynodon*
BI - BICOS *Diceros* (black rhino)
CE - CERAS *Ceratotherium* (white rhino)
D1 - DICE1S *Diceratherium*
D2 - DICE2S *Diceratherium*
D3 - DICE3S *Diceratherium*
FO - FORSS *Forstercooperia*
HY - HYCOS *Hyracodon*
IN - INDRS *Indricotherium*
JV - JAVAS *Rhinoceros* (Javan rhino)
L1 - APHE1S *Aphelops*
L1 - APHE2S *Aphelops*
ME - MENOS *Menoceras*
P1 - PERA1S *Peraceras*
P2 - PERA2S *Peraceras*
S1 - SUBH1S *Subhyracodon*
S2 - SUBH2S *Subhyracodon*
S3 - SUBH3S *Subhyracodon*
SU - SUMAS *Dicerorhinus* (Sumatran rhino)
T1 - TELE1S *Teleoceras*
T2 - TELE2S *Teleoceras*
T3 - TELE3S *Teleoceras*
T4 - TELE4S *Teleoceras*
T5 - TELE5S *Teleoceras*
TR - TRIGS *Teleoceras*
UN - UNICS *Rhinoceros* (Indian rhino)
Y1 - HYRA1S *Hyrachyus*
Y2 - HYRA2S *Hyrachyus*

	A1	A2	AN	BI	CE	D1	D2	D3	FO	HY	IN	JV	L1	L2	ME	P1	P2
A1		12.4	14.3	7.9	12.1	13.2	11.7	11.4	14.6	19.4	40.0	10.6	12.0	9.4	14.2	9.5	11.8
A2	12.4		16.6	10.4	13.1	16.1	14.7	14.9	16.2	21.9	37.7	13.6	13.0	11.7	17.3	13.5	13.3
AN	14.3	16.6		14.2	18.9	7.6	6.7	9.6	7.5	9.4	45.2	17.6	9.3	13.4	8.6	10.4	20.2
BI	7.9	10.4	14.2		9.0	12.4	11.0	9.4	12.7	19.9	38.9	10.1	9.7	5.8	13.9	9.0	10.1
CE	12.1	13.1	18.9	9.0		18.8	16.5	14.8	17.6	24.7	34.9	16.9	14.5	11.2	19.9	14.7	13.8
D1	13.2	16.1	7.6	12.4	18.8		4.3	8.0	5.7	9.3	46.6	15.1	8.8	11.6	4.1	8.4	18.1
D2	11.7	14.7	6.7	11.0	16.5	4.3		6.2	6.8	11.0	43.8	14.6	6.7	10.2	6.7	7.6	17.0
D3	11.4	14.9	9.6	9.4	14.8	8.0	6.2		8.3	15.4	41.1	14.8	8.6	8.7	10.0	9.6	16.1
FO	14.6	16.2	7.5	12.7	17.6	5.7	6.8	8.3		10.3	45.8	17.2	8.8	11.9	6.7	9.4	19.0
HY	19.4	21.9	9.4	19.9	24.7	9.3	11.0	15.4	10.3		52.4	21.6	14.6	18.6	8.5	14.4	25.4
IN	40.0	37.7	45.2	38.9	34.9	46.6	43.8	41.1	45.8	52.4		42.8	43.1	41.4	49.1	45.2	40.4
JV	10.6	13.6	17.6	10.1	16.9	15.1	14.6	14.8	17.2	21.6	42.8		14.0	10.7	15.5	11.5	10.0
L1	12.0	13.0	9.3	9.7	14.5	8.8	6.7	8.6	8.8	14.6	43.1	14.0		8.0	9.4	6.2	14.4
L2	9.4	11.7	13.4	5.8	11.2	11.6	10.2	8.7	11.9	18.6	41.4	10.7	8.0		11.9	7.1	9.4
ME	14.2	17.3	8.6	13.9	19.9	4.1	6.7	10.0	6.7	8.5	49.1	15.5	9.4	11.9		8.0	18.5
P1	9.5	13.5	10.4	9.0	14.7	8.4	7.6	9.6	9.4	14.4	45.2	11.5	6.2	7.1	8.0		12.2
P2	11.8	13.3	20.2	10.1	13.8	18.1	17.0	16.1	19.0	25.4	40.4	10.0	14.4	9.4	18.5	12.2	
S1	12.8	16.5	6.4	13.0	18.4	4.3	5.1	9.3	5.7	8.2	47.2	15.8	8.3	11.8	4.2	7.7	18.3
S2	11.6	14.8	5.5	11.2	16.6	4.7	3.6	7.8	6.0	9.7	45.0	14.8	6.6	10.1	5.6	7.0	17.0
S3	11.0	15.4	7.6	10.3	16.1	5.0	4.6	5.5	6.0	11.6	44.2	14.1	7.7	9.0	6.5	7.6	16.1
SU	12.8	14.3	13.7	11.0	16.5	9.7	10.5	12.5	11.9	15.1	46.3	13.9	12.5	11.4	10.2	10.3	15.8
T1	9.9	15.0	14.7	9.3	16.2	10.4	10.4	10.1	12.7	18.1	45.1	9.0	10.6	7.5	10.5	7.0	10.4
T2	10.7	16.3	19.4	11.8	16.3	16.8	15.5	14.8	18.4	23.9	42.2	10.0	14.2	11.0	17.0	11.7	8.8
T3	9.7	15.8	17.1	10.1	13.7	15.6	13.8	13.3	16.5	22.2	41.8	10.4	12.2	9.6	15.7	9.7	9.3
T4	12.1	16.9	20.3	11.1	13.2	18.2	16.8	16.2	19.0	25.0	42.2	12.2	14.6	10.9	18.3	12.2	8.7
T5	11.8	16.6	20.7	11.2	13.8	18.5	17.0	15.7	19.4	25.8	40.8	11.8	14.8	11.3	18.9	12.7	8.1
TR	11.4	15.4	6.6	11.7	16.7	4.7	4.1	7.2	5.7	10.2	44.8	15.8	8.0	11.0	6.4	7.6	17.6
UN	9.6	11.7	19.0	8.6	12.0	17.0	15.4	15.4	18.3	23.8	40.0	8.1	13.4	9.1	17.6	11.1	5.6
Y1	22.0	24.8	12.0	22.1	27.5	11.4	13.6	17.7	12.6	4.9	55.8	22.9	16.7	20.5	9.7	16.1	27.1
Y2	18.7	21.6	9.1	19.0	24.3	8.4	10.7	15.2	9.9	4.3	52.8	20.3	13.7	17.7	7.2	12.7	23.8

	S1	S2	S3	SU	T1	T2	T3	T4	T5	TR	UN	Y1	Y2
A1	12.8	11.6	11.0	12.8	9.9	10.7	9.7	12.1	11.8	11.4	9.6	22.0	18.7
A2	16.5	14.8	15.4	14.3	15.0	16.3	15.8	16.9	16.6	15.4	11.7	24.8	21.6
AM	6.4	5.5	7.6	13.7	14.7	19.4	17.1	20.3	20.7	6.6	19.0	12.0	9.1
BI	13.0	11.2	10.3	11.0	9.3	11.8	10.1	11.1	11.2	11.7	8.6	22.1	19.0
CE	18.4	16.6	16.1	16.5	16.2	16.3	13.7	13.2	13.8	16.7	12.0	27.5	24.3
D1	4.3	4.7	5.0	9.7	10.4	16.8	15.6	18.2	18.5	4.7	17.0	11.4	8.4
D2	5.1	3.6	4.6	10.5	10.4	15.5	13.8	16.8	17.0	4.1	15.4	13.6	10.7
D3	9.3	7.8	5.5	12.5	10.1	14.8	13.3	16.2	15.7	7.2	15.4	17.7	15.2
FO	5.7	6.0	6.0	11.9	12.7	18.4	16.5	19.0	19.4	5.7	18.3	12.6	9.9
HY	8.2	9.7	11.6	15.1	18.1	23.9	22.2	25.0	25.8	10.2	23.8	4.9	4.3
IN	47.2	45.0	44.2	46.3	45.1	42.2	41.8	42.2	40.8	44.8	40.0	55.8	52.8
JV	15.8	14.8	14.1	13.9	9.0	10.0	10.4	12.2	11.8	15.8	8.1	22.9	20.3
L1	8.3	6.6	7.7	12.5	10.6	14.2	12.2	14.6	14.8	8.0	13.4	16.7	13.7
L2	11.8	10.1	9.0	11.4	7.5	11.0	9.6	10.9	11.3	11.0	9.1	20.5	17.7
ME	4.2	5.6	6.5	10.2	10.5	17.0	15.7	18.3	18.9	6.4	17.6	9.7	7.2
P1	7.7	7.0	7.6	10.3	7.0	11.7	9.7	12.2	12.7	7.6	11.1	16.1	12.7
P2	18.3	17.0	16.1	15.8	10.4	8.8	9.3	8.7	8.1	17.6	5.6	27.1	23.8
S1		3.1	5.3	10.6	11.4	16.7	14.9	17.8	18.4	4.2	17.1	10.6	7.5
S2	3.1		4.4	9.9	10.8	15.8	13.9	16.6	17.3	3.6	15.7	12.3	9.3
S3	5.3	4.4		10.3	9.3	14.6	13.1	16.2	16.2	4.0	15.2	13.9	11.3
SU	10.6	9.9	10.3		10.8	15.9	14.7	15.9	17.0	10.5	14.2	16.6	14.0
T1	11.4	10.8	9.3	10.8		8.1	8.4	10.4	10.2	10.8	10.0	19.3	16.6
T2	16.7	15.8	14.6	15.9	8.1		5.2	7.4	5.3	15.7	8.2	25.5	22.6
T3	14.9	13.9	13.1	14.7	8.4	5.2		5.6	5.6	14.2	7.8	23.7	20.7
T4	17.8	16.6	16.2	15.9	10.4	7.4	5.6		4.9	17.2	8.0	26.4	23.4
T5	18.4	17.3	16.2	17.0	10.2	5.3	5.6	4.9		17.2	7.7	27.4	24.3
TR	4.2	3.6	4.0	10.5	10.8	15.7	14.2	17.2	17.2		16.2	13.2	10.0
UN	17.1	15.7	15.2	14.2	10.0	8.2	7.8	8.0	7.7	16.2		25.8	22.5
Y1	10.6	12.3	13.9	16.6	19.3	25.5	23.7	26.4	27.4	13.2	25.8		4.5
Y2	7.5	9.3	11.3	14.0	16.6	22.6	20.7	23.4	24.3	10.0	22.5	4.5	

TABLE 10. Generalized distances ($\sqrt{D^2}$) for mandible canonical means. D^2 matrix is shown in two panels (left and right halves). Subgroup symbols correspond to those in Figure 59 and are listed below.

A1 - ACER1M *Aceratherium*
A2 - ACER2M *Aceratherium*
BI - BICOM *Diceros* (black rhino)
CE - CERAM *Ceratotherium* (white rhino)
D1 - DICE1M *Diceratherium*
D2 - DICE2M *Diceratherium*
F1 - FORS1M *Forstercooperia*
F2 - FORS2M *Forstercooperia*
HY - HYCOM *Hyracodon*
IN - INDRM *Indricotherium*
JV - JAVAM *Rhinoceros* (Javan rhino)
L1 - APHE1M *Aphelops*
L2 - APHE2M *Aphelops*
L3 - APHE3M *Aphelops*
L4 - APHE4M *Aphelops*
M1 - MENO1M *Menoceras*
M2 - MENO2M *Menoceras*
PE - PENE1M *Penetrigonias*
P1 - PERA1M *Peraceras*
P2 - PERA2M *Peraceras*
S1 - SUBH1M *Subhyracodon*
S2 - SUBH2M *Subhyracodon*
S3 - SUBH3H *Subhyracodon*
SU - SUMAM *Dicerorhinus* (Sumatran rhino)
T1 - TELE1M *Teleoceras*
T2 - TELE2M *Teleoceras*
T3 - TELE3M *Teleoceras*
T4 - TELE4M *Teleoceras*
T5 - TELE5M *Teleoceras*
TR - TRIGM *Teleoceras*
UN - UNICM *Rhinoceros* (Indian rhino)
Y1 - HYRA1M *Hyrachyus*
Y2 - HYRA2M *Hyrachyus*
Z1 - ZAIS1M *Zaisanamynodon*
Z2 - ZAIS2M *Zaisanamynodon*

	A1	A2	BI	CE	D1	D2	F1	F2	HY	IN	JV	L1	L2	L3	L4	M1	M2	PE
A1		3.8	5.7	8.5	5.4	11.4	9.5	12.3	16.5	21.2	4.5	3.2	1.8	5.6	9.3	11.1	7.3	13.9
A2	3.8		7.6	9.9	7.1	10.4	9.6	11.9	15.8	22.2	4.3	4.7	2.8	7.5	11.5	10.2	7.6	13.3
BI	5.7	7.6		5.9	9.1	12.9	13.2	15.3	18.9	21.2	5.7	7.0	6.4	7.3	10.2	12.9	8.7	15.9
CE	8.5	9.9	5.9		13.0	17.2	17.1	19.4	22.9	18.8	9.9	9.7	8.7	6.9	7.9	17.4	13.2	20.0
D1	5.4	7.1	9.1	13.0		9.8	6.4	9.4	13.9	24.9	6.4	6.0	5.8	10.1	13.0	9.2	6.4	11.3
D2	11.2	10.4	12.9	17.2	9.8		7.2	6.9	9.3	30.8	8.9	11.1	10.9	16.9	20.4	1.9	6.3	7.4
F1	9.5	9.6	13.2	17.1	6.4	7.2		5.8	10.6	28.2	9.2	9.5	9.5	14.6	17.8	6.7	7.9	9.4
F2	12.3	11.9	15.3	19.4	9.4	6.9	5.8		5.0	32.7	11.0	10.9	11.9	17.5	20.8	6.0	8.4	4.4
HY	16.5	15.8	18.9	22.9	13.9	9.3	10.6	5.0		37.1	14.7	14.7	15.9	21.6	24.8	8.5	11.5	4.0
IN	21.2	22.2	21.2	18.8	24.9	30.8	28.2	32.7	37.1		23.8	23.5	22.1	16.9	15.8	30.8	27.6	34.8
JV	4.5	4.3	5.7	9.9	6.4	8.9	9.2	11.0	14.7	23.8		5.3	4.4	8.9	12.9	8.7	5.7	11.9
L1	3.2	4.7	7.0	9.7	6.0	11.1	9.5	10.9	14.7	23.5	5.3		2.9	7.2	10.6	10.6	6.5	12.0
L2	1.8	2.8	6.4	8.7	5.8	10.9	9.5	11.9	15.9	22.1	4.4	2.9		6.4	9.9	10.7	7.0	13.2
L3	5.6	7.5	7.3	6.9	10.1	16.9	14.6	17.5	21.6	16.9	8.9	7.2	6.4		4.8	16.5	12.4	19.0
L4	9.3	11.5	10.2	7.9	13.0	20.4	17.8	20.8	24.8	15.8	12.9	10.6	9.9	4.8		20.0	15.5	22.3
M1	11.1	10.2	12.9	17.4	9.2	1.9	6.7	6.0	8.5	30.8	8.7	10.6	10.7	16.5	20.0		5.6	6.7
M2	7.3	7.6	8.7	13.2	6.4	6.3	7.9	8.4	11.5	27.6	5.7	6.5	7.0	12.4	15.5	5.6		8.5
PE	13.9	13.3	15.9	20.0	11.3	7.4	9.4	4.4	4.0	34.8	11.9	12.0	13.2	19.0	22.3	6.7	8.5	
P1	3.9	6.3	6.6	10.2	4.9	11.3	9.5	11.2	15.0	23.9	5.8	3.0	4.5	7.8	10.8	10.8	6.2	12.0
P2	5.0	8.1	6.4	7.1	8.8	16.0	13.6	16.4	20.6	18.5	8.4	6.4	6.4	3.3	6.0	15.7	11.2	17.8
S1	9.0	8.9	11.7	15.9	6.5	5.9	5.3	4.0	7.9	29.7	7.6	7.7	8.6	14.3	17.6	5.0	5.1	5.4
S2	9.6	9.5	12.5	16.4	7.5	7.1	6.0	3.8	7.3	30.3	8.5	8.1	9.2	14.6	17.8	6.1	6.2	5.5
S3	7.3	7.9	10.4	14.6	5.4	7.0	4.5	5.4	9.8	27.6	6.6	6.3	7.3	12.5	15.9	6.2	5.1	7.8
SU	10.1	11.0	7.7	10.2	11.3	14.1	15.6	16.6	19.4	25.6	8.4	10.7	10.3	12.0	14.4	14.1	10.3	16.0
T1	2.5	5.8	5.8	9.1	4.7	11.9	9.3	12.3	16.6	21.7	5.0	4.2	4.0	6.3	9.7	11.5	7.6	13.9
T2	3.5	6.5	6.1	7.6	7.4	14.3	12.0	15.1	19.3	19.1	7.4	5.3	4.7	3.9	6.6	13.9	9.5	16.6
T3	3.3	6.6	4.9	7.0	7.0	13.8	12.1	14.7	18.8	20.1	6.5	5.0	4.4	4.5	7.4	13.5	8.9	15.9
T4	5.9	7.7	6.0	5.8	10.3	16.2	14.8	17.5	21.5	17.7	8.7	7.4	6.3	3.8	6.2	16.0	11.8	16.6
T5	6.4	9.4	6.6	6.9	9.7	16.9	14.9	17.8	21.9	18.1	9.6	7.9	7.4	4.4	5.1	16.6	11.7	19.0
TR	7.0	7.5	10.3	14.1	5.1	7.5	5.7	5.9	9.9	27.9	6.5	5.6	6.8	12.2	15.4	6.8	4.8	7.4
UN	5.2	5.5	5.8	6.4	10.0	14.2	13.9	16.4	20.2	18.8	6.7	6.7	5.2	5.0	8.6	14.1	10.1	17.3
Y1	19.1	18.3	21.0	25.2	16.3	10.3	12.5	7.4	3.4	39.5	16.9	17.5	18.5	24.3	27.7	9.9	13.6	6.1
Y2	15.6	14.8	18.2	22.3	12.7	8.2	8.7	3.6	2.4	35.9	13.9	14.1	15.0	20.8	24.0	7.5	10.9	4.4
Z1	11.1	11.8	14.7	15.2	13.0	18.1	13.9	17.3	21.3	20.3	12.8	12.1	11.6	11.0	12.8	17.6	15.7	20.3
Z2	12.5	13.4	16.9	17.7	12.4	19.3	14.2	18.9	23.5	19.8	15.2	14.4	13.1	12.7	13.6	18.8	17.1	22.0

	P1	P2	S1	S2	S3	SU	T1	T2	T3	T4	T5	TR	UN	Y1	Y2	Z1	Z2
A1	3.9	5.0	9.0	9.6	7.3	10.1	2.5	3.5	3.3	5.9	6.4	7.0	5.2	19.1	15.6	11.1	12.5
A2	6.3	8.1	8.9	9.5	7.9	11.0	5.8	6.5	6.6	7.7	9.4	7.5	5.5	18.3	14.8	11.8	13.4
B1	6.6	6.4	11.7	12.5	10.4	7.7	5.8	6.1	4.9	6.0	6.6	10.3	5.8	21.0	18.2	14.7	16.9
CE	10.2	7.1	15.9	16.4	14.6	10.2	9.1	7.6	7.0	5.8	6.9	14.1	6.4	25.2	22.3	15.2	17.7
D1	4.9	8.8	6.5	7.5	5.4	11.3	4.7	7.4	7.0	10.3	9.7	5.1	10.0	16.3	12.7	13.0	12.4
D2	11.3	16.0	5.9	7.1	7.0	14.1	11.9	14.3	13.8	16.2	16.9	7.5	14.2	10.3	8.2	18.1	19.3
F1	9.5	13.6	5.3	6.0	4.5	15.6	9.3	12.0	12.1	14.8	14.9	5.7	13.9	12.5	8.7	13.9	14.2
F2	11.2	16.4	4.0	3.8	5.4	16.6	12.3	15.1	14.7	17.5	17.8	5.9	16.4	7.4	3.6	17.3	18.9
HY	15.0	20.6	7.9	7.3	9.8	19.4	16.6	19.3	18.8	21.5	21.9	9.9	20.2	3.4	2.4	21.3	23.5
IN	23.9	18.5	29.7	30.3	27.6	25.6	21.7	19.1	20.1	17.7	18.1	27.9	18.8	39.5	35.9	20.3	19.8
JV	5.8	8.4	7.6	8.5	6.6	8.4	5.0	7.4	6.5	8.7	9.6	6.5	6.7	16.9	13.9	12.8	15.2
L1	3.0	6.4	7.7	8.1	6.3	10.7	4.2	5.3	5.0	7.4	7.9	5.6	6.7	17.5	14.1	12.1	14.4
L2	4.5	6.4	8.6	9.2	7.3	10.3	4.0	4.7	4.4	6.3	7.4	6.8	5.2	18.5	15.0	11.6	13.1
L3	7.8	3.3	14.3	14.6	12.5	12.0	6.3	3.9	4.5	3.8	4.4	12.2	5.0	24.3	20.8	11.0	12.7
L4	10.8	6.0	17.6	17.8	15.9	14.4	9.7	6.6	7.4	6.2	5.1	15.4	8.6	27.7	24.0	12.8	13.6
M1	10.8	15.7	5.0	6.1	6.2	14.1	11.5	13.9	13.5	16.0	16.6	6.8	14.1	9.9	7.5	17.6	18.8
M2	6.2	11.2	5.1	6.2	5.1	10.3	7.6	9.5	8.9	11.8	11.7	4.8	10.1	13.6	10.9	15.7	17.1
PE	12.0	17.8	5.4	5.5	7.8	16.0	13.9	16.6	15.9	18.6	19.0	7.4	17.3	6.1	4.4	20.3	22.0
P1		6.2	7.6	8.2	6.4	9.8	3.7	5.2	4.7	7.7	7.4	5.7	7.8	17.6	14.2	13.5	14.7
P2	6.2		13.1	13.5	11.2	10.7	4.6	3.0	3.3	5.0	3.5	10.9	6.1	23.2	19.8	11.4	13.1
S1	7.6	13.1		2.0	2.8	13.0	8.9	11.7	11.3	14.1	14.4	2.5	13.0	10.3	6.9	15.7	17.2
S2	8.2	13.5	2.0		3.5	14.0	9.6	12.3	12.0	14.7	15.0	2.9	13.7	10.1	6.5	15.3	17.4
S3	6.4	11.2	2.8	3.5		13.0	7.1	10.0	9.7	12.6	12.7	2.2	11.7	12.3	8.8	13.6	15.6
SU	9.8	10.7	13.0	14.0	13.0		9.5	10.9	9.5	11.8	11.1	12.1	10.1	21.2	19.0	18.1	19.7
T1	3.7	4.6	8.9	9.6	7.1	9.5		4.1	3.5	7.0	6.3	7.0	6.8	19.1	15.6	11.1	12.6
T2	5.2	3.0	11.7	12.3	10.0	10.9	4.1		2.4	4.3	3.7	9.7	5.0	21.9	18.4	11.4	12.2
T3	4.7	3.3	11.3	12.0	9.7	9.5	3.5	2.4		4.4	3.4	9.3	4.9	21.4	18.0	12.3	13.4
T4	7.7	5.0	14.1	14.7	12.6	11.8	7.0	4.3	4.4		4.5	12.2	4.5	24.0	20.7	13.6	14.6
T5	7.4	3.5	14.4	15.0	12.7	11.1	6.3	3.7	3.4	4.5		12.4	6.3	24.5	21.1	13.2	13.7
TR	5.7	10.9	2.5	2.9	2.2	12.1	7.0	9.7	9.3	12.2	12.4		11.3	12.6	9.0	13.8	15.6
UN	7.8	6.1	13.0	13.7	11.7	10.1	6.8	5.0	4.9	4.5	6.3	11.3		22.6	19.5	12.8	14.4
Y1	17.6	23.2	10.3	10.1	12.3	21.2	19.1	21.9	21.4	24.0	24.5	12.6	22.6		4.3	24.0	26.0
Y2	14.2	19.8	6.9	6.5	8.8	19.0	15.6	18.4	18.0	20.7	21.1	9.0	19.5	4.3		20.3	21.9
Z1	13.5	11.4	15.7	15.3	13.6	18.1	11.1	11.4	12.3	13.6	13.2	13.8	12.8	24.0	20.3		9.2
Z2	14.7	13.1	17.2	17.4	15.6	19.7	12.6	12.2	13.4	14.6	13.7	15.6	14.4	26.0	21.9	9.2	

TABLE 11. Summary of skull and mandible inter-subgroup generalized distances in genera with more than one subgroup. For genera with more than two subgroups, values in the table represent means. The living genus *Rhinoceros* (Asian one-horned rhino) is given first, followed by fossil genera listed alphabetically.

GENUS (Subgroups)	SKULL	MANDIBLE
Rhinoceros (UN, JV)	8.1	6.7
Aceratherium (A1-A2)	12.4	3.8
Aphelops (L1-L2), (L1-L4)	8.0	7.0
Diceratherium (D1-D3), (D1-D2)	6.2	9.8
Forstercooperia (F1-F2)	---	5.8
Hyrachyus (Y1-Y2)	4.5	4.3
Peraceras (P1-P2)	12.2	6.2
Subhyracodon (S1-S3)	4.3	2.8
Teleoceras (T1-T5)	7.1	4.3
Zaisanamynodon (Z1-Z2)	---	9.2

Ordination - Specimens Plotted By Genus

Figure 56 (skull) and Figure 57 (mandible) show the individual specimens plotted about their respective subgroup means (not shown). However, because the specimens are identified only by genus, direct comparisons may only be made between monotypic genera (whose generic and subgroup means are identical). These plots nicely show the amount of generic differentiation in morphology. Several features are common to the plots of skulls and mandibles. In both plots, *Hyrachyus* and *Indricotherium*, which represent the size extremes among the Rhinocerotoidea, are the extreme left and right specimens. Several analyses (not shown) confirmed that the size axis is approximately parallel to CV1. This is more obvious in the mandible plot than in the skull plot where a line through *Hyrachyus* and *Indricotherium* would be oblique to CV1. Also shown in both plots is the effect of the CV method on within group correlations. For example, comparison of the CV and PC (Figure 8) for the monotypic black rhino dispersions shows how the within-group variation has been made circular by the CV. The same effect occurs for each of the subgroups, but is only observable here in the monotypic genera. The skull and mandible CV clouds of black rhinos approximate the pooled within-group dispersions used for those respective analyses. The dispersions also approximate the size of the concentration ellipses in Figures 58 and 59 of the following section. Finally, it should be noted again that

FIGURE 56. Canonical variates plot of living and fossil skull specimens. Differences between number of symbols plotted and sample sizes (Table 2 are due to overstrikes. Specimens are identified to genus as indicated below.

Key to symbols (listed alphabetically):

A - *Amynodon*
B - *Diceros* (black rhino)
C - *Ceratotherium* (white rhino)
D - *Diceratherium*
F - *Forstercooperia*
H - *Hyracodon*
I - *Indricotherium*
J - *Rhinoceros* (Javan rhino)
L - *Aphelops*
M - *Menoceras*
P - *Peraceras*
Q - *Aceratherium*
R - *Trigonias*
S - *Subhyracodon*
T - *Teleoceras*
U - *Rhinoceros* (Indian rhino)
Y - *Hyrachyus*
Z - *Dicerorhinus* (Sumatran rhino)

CANONICAL VARIATES - INDIVIDUAL SKULL SPECIMENS

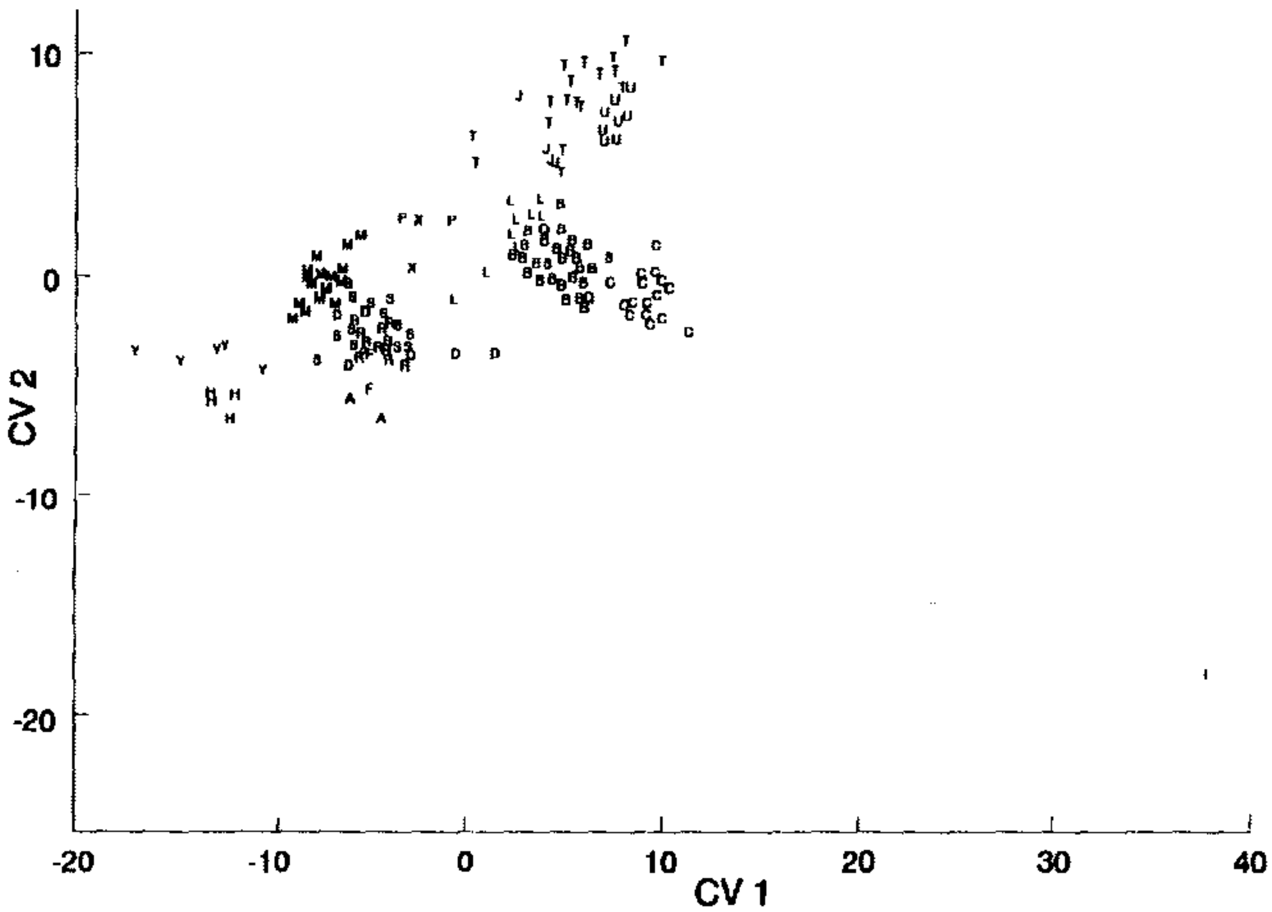
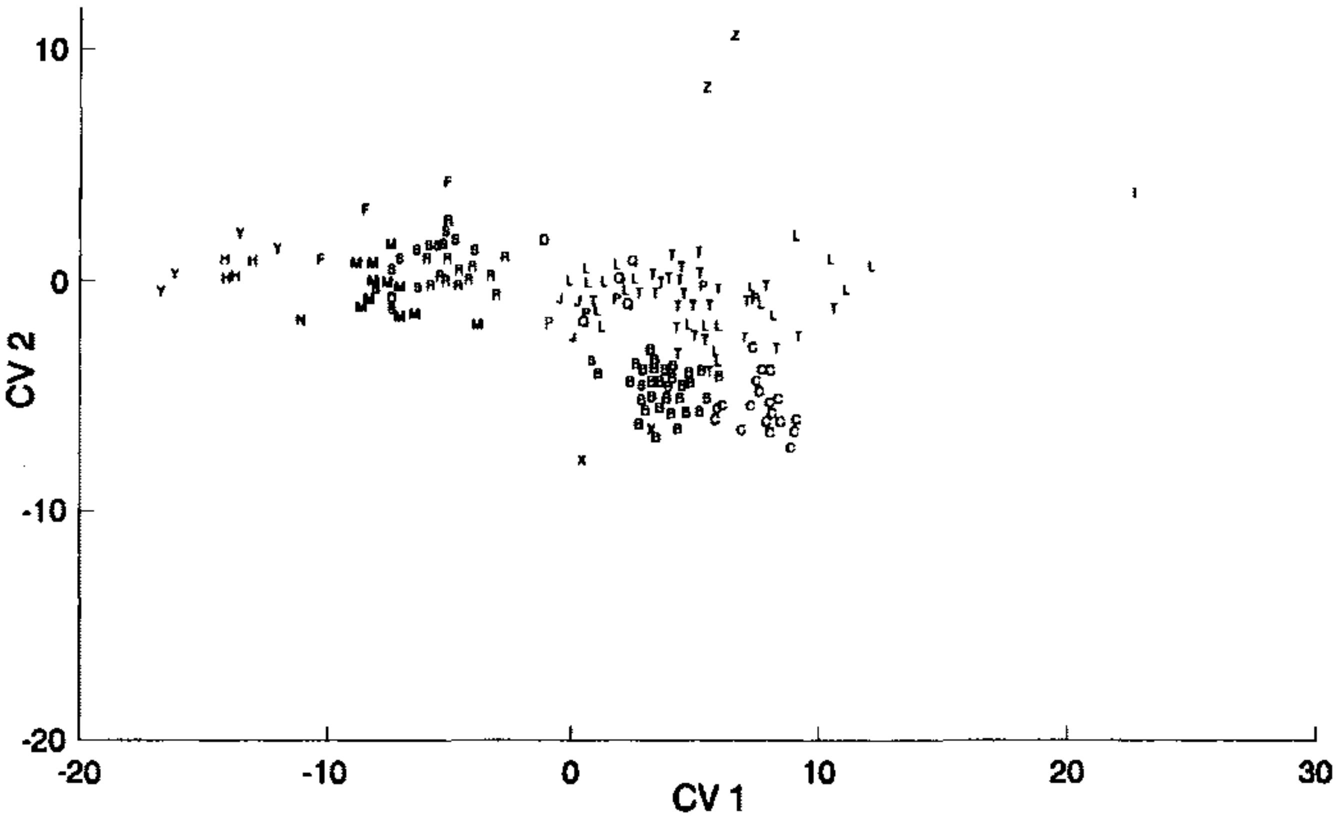


FIGURE 57. Canonical variates plot of living and fossil mandible specimens. Differences between number of symbols plotted and sample sizes (Table 3) are due to overstrikes. Specimens are identified to genus as indicated below.

Key to symbols (listed alphabetically):

B - *Diceros* (black rhino)
C - *Ceratotherium* (white rhino)
D - *Diceratherium*
F - *Forstercooperia*
H - *Hyracodon*
I - *Indricotherium*
J - *Rhinoceros* (Javan rhino)
L - *Aphelops*
M - *Menoceras*
N - *Penetrigonias*
P - *Peraceras*
Q - *Aceratherium*
R - *Trigonias*
S - *Subhyracodon*
T - *Teleoceras*
U - *Rhinoceros* (Indian rhino)
Y - *Hyrachyus*
X - *Dicerorhinus* (Sumatran rhino)
Z - *Zaisanamynodon*

CANONICAL VARIATES - INDIVIDUAL MANDIBLE SPECIMENS



morphologically similar specimens cluster together in the multivariate CV morphospace. This is clearly observed for the specimens of the black and white rhinoceroses in Figures 56 and 57, and is also true for the subgroup means in the following plots.

Ordination - Subgroup Means With Concentration Ellipses

This section presents the ordination of the subgroups with 90% concentration ellipses (circles) around each group. Statistically, each ellipse theoretically includes 90% of all individuals from its group within its boundary. The ellipses are standardized and uniform in both skull and mandible plots such that the radii are equivalent to 2.15 standard deviations. The apparent size difference of the ellipses between skull and mandible plots is due to the difference in scales. Because the ellipse is based on the pooled within-group dispersion, it represents the best estimate of the variation around a given mean. Some authors (e.g., Neff and Marcus, 1980) argue that groups with smaller sample sizes should have correspondingly larger confidence (or concentration) limits because of greater uncertainty about the position of the mean. However, the philosophy taken here is that the mean of the specimens available (even if a single specimen) represents the best estimate of the true mean, and that therefore the best estimate of group variation over all groups should apply to that mean. Finally, it should be noted that the ellipses are not meant to imply any kind of statistical test for differences between means.

In most cases, it is already known on biological grounds that the groups are different (for example, the Javan and Indian rhinos). The degree of overlap then reflects the degree of morphological similarity between groups known to be different in other ways.

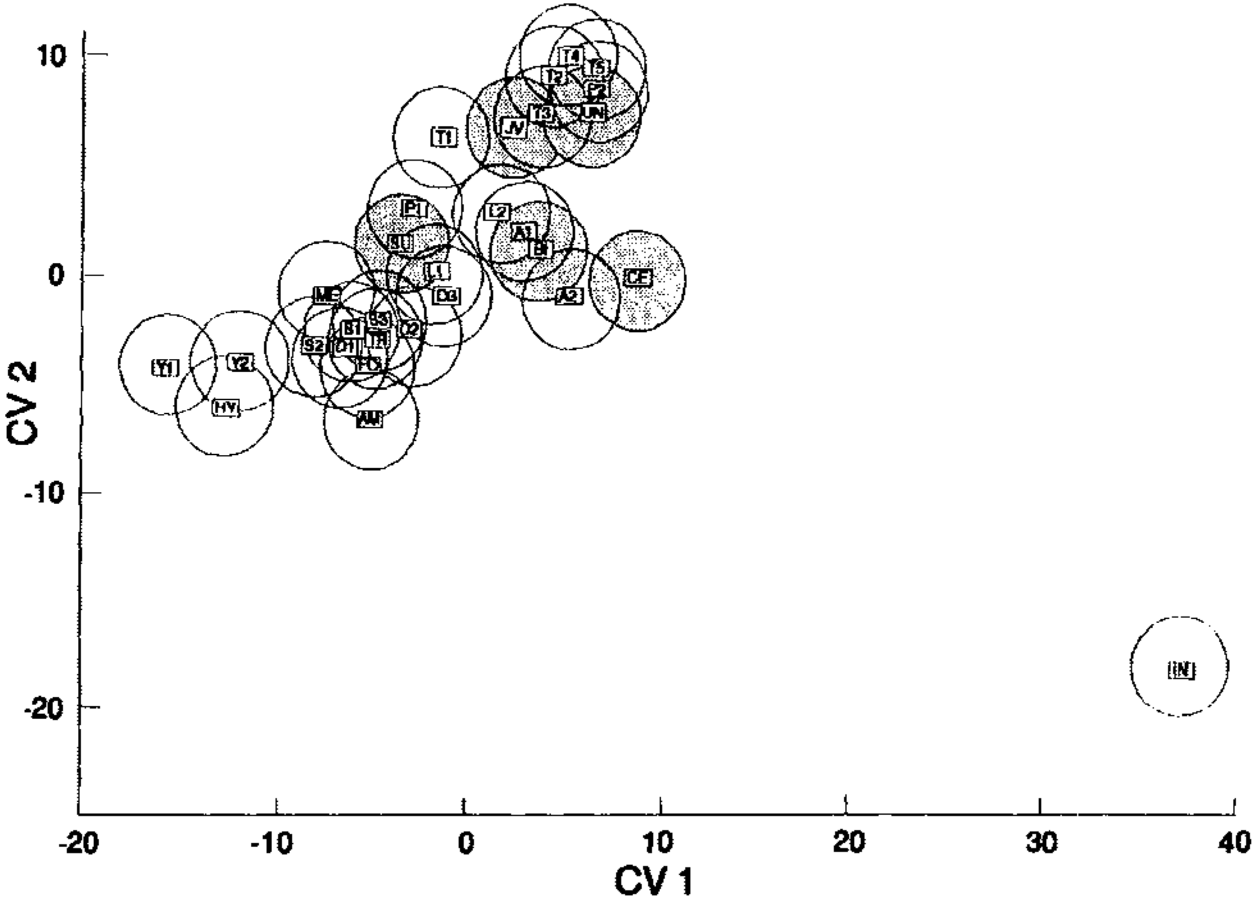
Skull (Figure 58) -- The most obvious feature of this plot is the outlying position of *Indricotherium* (IN in Figure 58) which, both on the first axis (size) and second axis (shape), is many standard deviations away from the closest genus (*Ceratotherium*). *Ceratotherium* (CE) is also closest to *Indricotherium* in the total morphological space (GD = 32, Table 9), which suggests that CV1-CV2 is reflecting the multivariate relationships well. In contrast to the outlying position of *Indricotherium*, another striking feature of this plot is the continuum of morphometric variation formed by the other genera. If *Indricotherium* represents the end-point of a lineage with a similar kind of continuous morphometric evolution, then there must be many undiscovered fossils which would fall in the morphospace between *Indricotherium* and the primitive rhinocerotoids. Among the remaining rhinoceroses, the densest cluster of morphometrically similar groups is formed by members of all three families: *Amynodon* (AM), *Forstercooperia* (FO), and the early rhinocerotids *Subhyracodon* (S1-S4), *Trigonias* (TR), *Diceratherium* (D1-D3), and *Menoceras* (ME). All but two of the pairwise generalized distances (Table 9) are smaller than the

FIGURE 58. Canonical variates plot of living and fossil subgroup means for skulls showing 90% concentration ellipses. Subgroups correspond to those in Table 2. Circles are 90% concentration ellipses (radius = 2.15) based on the pooled within-group dispersion for skulls. Shaded circles indicate living groups.

Key to symbols (listed alphabetically):

A1 - ACER1S *Aceratherium*
A2 - ACER2S *Aceratherium*
AM - AMYNS *Amynodon*
BI - BICOS *Diceros* (black rhino)
CE - CERAS *Ceratotherium* (white rhino)
D1 - DICE1S *Diceratherium*
D2 - DICE2S *Diceratherium*
D3 - DICE3S *Diceratherium*
FO - FORSS *Forstercooperia*
HY - HYCOS *Hyracodon*
IN - INDRS *Indricotherium*
JV - JAVAS *Rhinoceros* (Javan rhino)
L1 - APHE1S *Aphelops*
L1 - APHE2S *Aphelops*
ME - MENOS *Menoceras*
P1 - PERA1S *Peraceras*
P2 - PERA2S *Peraceras*
S1 - SUBH1S *Subhyracodon*
S2 - SUBH2S *Subhyracodon*
S3 - SUBH3S *Subhyracodon*
SU - SUMAS *Dicerorhinus* (Sumatran rhino)
T1 - TELE1S *Teleoceras*
T2 - TELE2S *Teleoceras*
T3 - TELE3S *Teleoceras*
T4 - TELE4S *Teleoceras*
T5 - TELE5S *Teleoceras*
TR - TRIGS *Teleoceras*
UN - UNICS *Rhinoceros* (Indian rhino)
Y1 - HYRA1S *Hyrachyus*
Y2 - HYRA2S *Hyrachyus*

CANONICAL VARIATE MEANS - SKULL SUBGROUPS - 90% CONCENTRATION ELLIPSES



average intersubgroup GD (Table 11). Among the larger, later rhinos there is more morphological differentiation. *Teleoceras* (T1-T5) and *Rhinoceros*(UN-Indian and JV-Javan rhinos) with *Peraceras* (P2) form a cluster separate from *Diceros* (BI), *Ceratotherium* (CE), and *Aceratherium* (A1-A2). GD's show that A2 is further from CE, and JV is further from T3 than is indicated in the plot. Also, T1 is closer to T2-T5 than is shown. These two clusters seem to form branches which separate out along CV2. *Dicerorhinus* (SU-Sumatran rhino) appears to be morphometrically primitive and in fact, is closest to S3 based on generalized distance.

Generic distinctions are clearly greater among the later rhinos. For example, among the living forms, the four genera do not overlap but the two species of *Rhinoceros* (UN, JV) do overlap. This morphometric result is consistent with the currently accepted taxonomy for the living analogues. Superficially, it appears that the Sumatran rhino could be ancestral to the other living rhinos. However, when the morphometric affinities with fossils are considered the picture becomes problematic. The Sumatran rhino is phylogenetically younger than *Teleoceras* and *Aceratherium*, and is not believed to be anceetral to them. The consequences of this are, one, that the *Sumatran* rhino is very conservative (static), and two, that the affinities of the other living genera with the fossils represent convergences or parallelisms. Alternatively, if the morphometric affinities represent common phylogenies, then

Diceros, *Ceratotherium*, and *Rhinoceros* may have evolved from a group much older than *Dicerorhinus*.

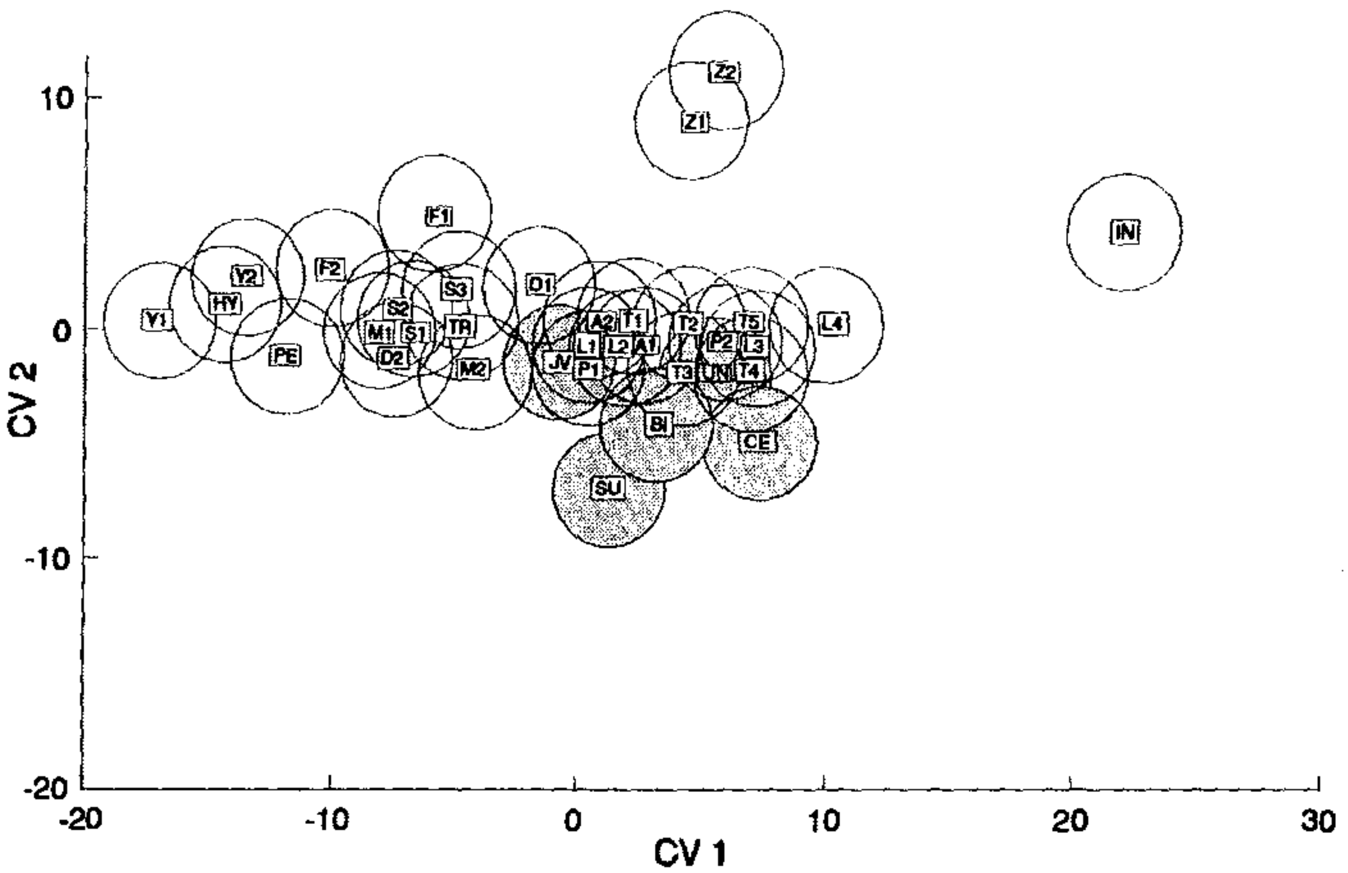
Mandible (Figure 59) -- The mandible CV plot is similar to the skull plot in that *Indricotherium* (IN) is a size outlier, and most of the remaining living and fossil groups form a continuous cloud of variation. This again suggests that there are missing fossils morphometrically uniting *Indricotherium* (IN) with its ancestors (unless saltatory evolution occurred). Differences with the skull plot include less relative size difference (about 10, rather than 20, standard deviations from its nearest neighbor along the first axis), and less second axis difference from the other genera. These latter two features of the mandible plot suggest that *Indricotherium* (IN) had a relatively small, conservative mandible for its size. Generalized distances (Table 11) agree well with the apparent distances to its nearest neighbors in the plane of CV1-CV2.

Another difference with the skull plot is the addition of the *Zaisanamynodon* (Z1-Z2) subgroups as outliers from the main continuum of genera, separated primarily along the second axis. They differ most from *Diceros* (BI), *Dicerorhinus* (SU), and *Ceratotherium* (CE) which are all on the opposite side of the continuum. That all of the living groups are on one side is interesting, but *Rhinoceros* (JV, UN) may also be interpreted as being part of the main group.

FIGURE 59. Canonical variates plot of living and fossil subgroup means for mandibles showing 90% concentration ellipses. Subgroups correspond to those in Table 3. Circles are 90% concentration ellipses (radius = 2.15) based on the pooled within-group dispersion for mandibles. Shaded circles indicate living groups. Key to symbols (listed alphabetically):

A1 - ACER1M *Aceratherium*
A2 - ACER2M *Aceratherium*
BI - BICOM *Diceros* (black rhino)
CE - CERAM *Ceratotherium* (white rhino)
D1 - DICE1M *Diceratherium*
D2 - DICE2M *Diceratherium*
F1 - FORS1M *Forstercooperia*
F2 - FORS2M *Forstercooperia*
HY - HYCOM *Hyracodon*
IN - INDRM *Indricotherium*
JV - JAVAM *Rhinoceros* (Javan rhino)
L1 - APHE1M *Aphelops*
L2 - APHE2M *Aphelops*
L3 - APHE3M *Aphelops*
L4 - APHE4M *Aphelops*
M1 - MENO1M *Menoceras*
M2 - MENO2M *Mneoceras*
PE - PENE1M *Penetrigonias*
P1 - PERA1M *Peraceras*
P2 - PERA2M *Peraceras*
S1 - SUBH1M *Subhyracodon*
S2 - SUBH2M *Subhyracodon*
S3 - SUBH3M *Subhyracodon*
SU - SUMAM *Dicerorhinus* (Sumatran rhino)
T1 - TELE1M *Teleoceras*
T2 - TELE2M *Teleoceras*
T3 - TELE3M *Teleoceras*
T4 - TELE4M *Teleoceras*
T5 - TELE5M *Teleoceras*
TR - TRIGM *Teleoceras*
UN - UNICM *Rhinoceros* (Indian rhino)
Y1 - HYRA1M *Hyrachyus*
Y2 - HYRA2M *Hyrachyus*
Z1 - ZAIS1M *Zaisanamynodon*
Z2 - ZAIS2M *Zaisanamynodon*

CANONICAL VARIATE MEANS - MANDIBLE SUBGROUPS - 90% CONCENTRATION ELLIPSES



The morphometric continuity of the majority of groups is striking. There is less differentiation and distinction of the later, larger groups than was evident in the skulls. *Diceros* (BI) and *Ceratotherium* (CE) are somewhat distinct but are not associated with *Aceratherium* (A1-A2). The latter genus is mixed in with other fossils. The Indian rhino mandibles (UN) are associated with *Teleocaras* (T3,T4), as in the skull analysis, but the Javan rhino (JV) mandible is less so. The Indian and Javan rhinos are separated by as much as are the other genera of living rhinos. Here, it is the Javan rhino which is the most primitive among the living analogues. The Sumatran (SU) rhino is an outlier, in distinct contrast to the case for skulls where it was the most primitive. In general, all of the rhinocerotid groups appear to be more conservative in terms of shape differentiation. Differences in morphometric affinities and differentiation between the skull and mandible CV plots suggest that there has been some evolutionary mosaicism between these two regions of the rhinoceros head.

Taxonomic Patterns - Relationships of Genera

It is of interest to observe whether the morphometric relationships of the subgroup means correspond to the taxonomies based on whole organism biology. Such taxonomies include information about morphological characters (cranial and postcranial, soft and hard tissues), molecular data, behavior and ecology, biogeography, and other relevant features of an organisms' biology. In this section, means are labelled and grouped according to genera. Comparisons are made with respect to relative morphometric span of each genus, and to overlap/non-overlap relationships.

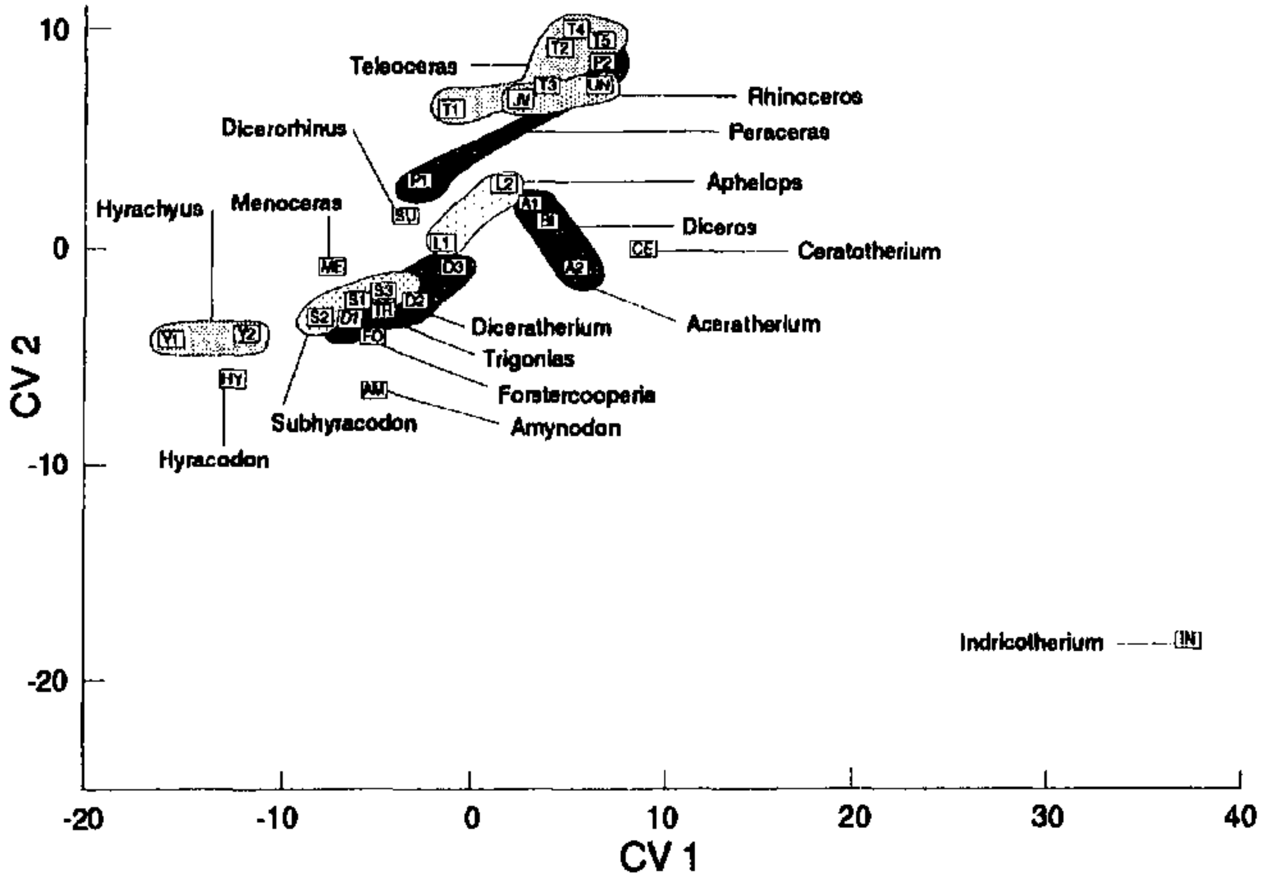
Skull (Figure 60) -- Of the eight genera comprised of more than one subgeneric group, four occupy non-overlapping parts of the morphometric space. These are *Hyrachyus* (Y1-Y2), *Aceratherium* (A1-A2), *Aphelops* (L1-L2), and *Teleoceras* (T1-T5). The remaining four genera form two sets of overlapping genera; *Subhyracodon* (S1-S2)-*Diceratherium* (D1-D2) and *Rhinoceros* (JV,UN)-*Peraceras* (P1-P2). All of the polytypic genera except *Teleoceras* and *Peraceras* appear to have approximately similar ranges of CV1-CV2 subgroup separation. However, generalized distances (Tables 9 and 11) indicate a more diverse range. If *Rhinoceros* (JV, UN) is taken as a standard (GD = 8.2), *Aceratherium* (A1-A2) has a greater intersubgroup distance, while the rest have smaller distances. The A1-A2 distance is in fact similar to the P1-P2 distance and both distances are greater than JV-UN or BI-CE distances. This suggests that A1-A2 and P1-P2 each represent species level variation at a minimum, but may indicate generic level also. If P1 and P2 are distinct generically, then the overlap of *Peraceras* and *Rhinoceros* (JV, UN) is not meaningful. Among the other polytypic genera, the smaller distances suggest that their subgroups represent species level or lesser amounts of variation. Within *Teleoceras* (T1-T5),

FIGURE 60. Canonical variates plot of living and fossil subgroup means for skulls with subgroups shown by genus. Means are labeled by genus. Shaded areas include all subgroups of the same genus.

Key to symbols (listed alphabetically):

A1 - ACER1S *Aceratherium*
A2 - ACER2S *Aceratherium*
AM - AMYNS *Amynodon*
BI - BICOS *Diceros* (black rhino)
CE - CERAS *Ceratotherium* (white rhino)
D1 - DICE1S *Diceratherium*
D2 - DICE2S *Diceratherium*
D3 - DICE3S *Diceratherium*
FO - FORSS *Forstercooperia*
HY - HYCOS *Hyracodon*
IN - INDRS *Indricotherium*
JV - JAVAS *Rhinoceros* (Javan rhino)
L1 - APHE1S *Aphelops*
L1 - APHE2S *Aphelops*
ME - MENOS *Menoceras*
P1 - PERA1S *Peraceras*
P2 - PERA2S *Peraceras*
S1 - SUBH1S *Subhyracodon*
S2 - SUBH2S *Subhyracodon*
S3 - SUBH3S *Subhyracodon*
SU - SUMAS *Dicerorhinus* (Sumatran rhino)
T1 - TELE1S *Teleoceras*
T2 - TELE2S *Teleoceras*
T3 - TELE3S *Teleoceras*
T4 - TELE4S *Teleoceras*
T5 - TELE5S *Teleoceras*
TR - TRIGS *Teleoceras*
UN - UNICS *Rhinoceros* (Indian rhino)
Y1 - HYRA1S *Hyrachyus*
Y2 - HYRA2S *Hyrachyus*

CANONICAL VARIATE MEANS - SKULL SUBGROUPS - BY GENUS



subgroups (including T1) are separated by distances which are on average slightly less than that between JV and UN. Overall, most the fossil genera appear to be morphometrically coherent when compared against living analogue differences and, in general, the morphometric relationships are fairly consistent with generic level taxonomies.

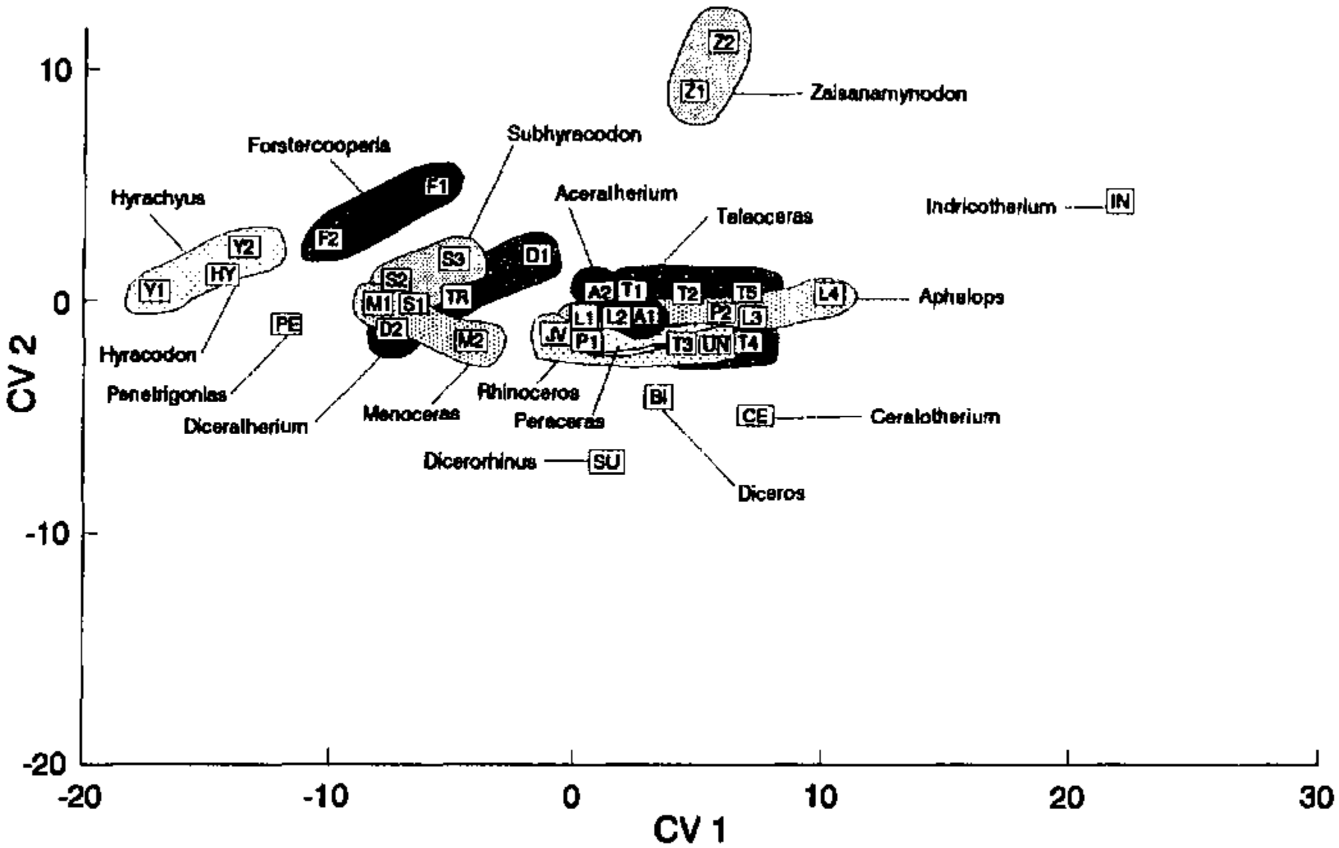
Mandible (Figure 61) -- Eleven of the sixteen genera are represented by means for more than one subgroup. Of these genera, three are morphometrically distinct: *Hyrachyus* (Y1-Y2), *Forstercooperia* (F1-F2), and *Zaisanamynodon* (Z1-Z2), among which *Hyrachyus* is overlapped by the monotypic genus *Hyracodon* (HY). The remaining polytypic genera are arranged in two clusters of overlapping genera. One cluster consists of the smaller forms *Subhyracodon* (S1-S3), *Menoceras* (M1-M2), *Diceratherium* (D1-D4). The other cluster consists of the larger forms *Aceratherium* (A1-A2), *Teleoceras* (T1-T5), *Aphelops* (L1-L3), *Peraceras* (P1-P3), and *Rhinoceros* (JV, UN). Within these two groups there is significant overlap of the genera. As with the skulls, intersubgroup morphometric distances are more accurately reflected by the generalized distances (Tables 10 and 11). Analysis of the generalized distances shows that *Aphelops* (L1-L4), *Hyrachyus* (Y1-Y2), and *Zaisanamynodon* (Z1-Z2) have average intersubgroup distances greater than that between the Indian (UN) and Javan (JV) rhinos (GD = 6.7). This suggests species level or greater variation. In fact, the distance between UN and JV is greater

FIGURE 61. Canonical variates plot of living and fossil subgroup means for mandible data with subgroups shown by genus. Means are labeled by genus. Shaded areas include all subgroups of the same genus.

Key to symbols (listed alphabetically):

A1 - ACER1M *Aceratherium*
A2 - ACER2M *Aceratherium*
BI - BICOM *Diceros* (black rhino)
CE - CERAM *Ceratotherium* (white rhino)
D1 - DICE1M *Diceratherium*
D2 - DICE2M *Diceratherium*
F1 - FORS1M *Forstercooperia*
F2 - FORS2M *Forstercooperia*
HY - HYCOM *Hyracodon*
IN - INDRM *Indricotherium*
JV - JAVAM *Rhinoceros* (Javan rhino)
L1 - APHE1M *Aphelops*
L2 - APHE2M *Aphelops*
L3 - APHE3M *Aphelops*
L4 - APHE4M *Aphelops*
M1 - MENO1M *Menoceras*
M2 - MENO2M *Menoceras*
PE - PENE1M *Penetrigonias*
P1 - PERA1M *Peraceras*
P2 - PERA2M *Peraceras*
S1 - SUBH1M *Subhyracodon*
S2 - SUBH2M *Subhyracodon*
S3 - SUBH3M *Subhyracodon*
SU - SUMAM *Dicerorhinus* (Sumatran rhino)
T1 - TELE1M *Teleoceras*
T2 - TELE2M *Teleoceras*
T3 - TELE3M *Teleoceras*
T4 - TELE4M *Teleoceras*
T5 - TELE5M *Teleoceras*
TR - TRIGM *Teleoceras*
UN - UNICM *Rhinoceros* (Indian rhino)
Y1 - HYRA1M *Hyrachyus*
Y2 - HYRA2M *Hyrachyus*
Z1 - ZAIS1M *Zaisanamynodon*
Z2 - ZAIS2M *Zaisanamynodon*

CANONICAL VARIATE MEANS - MANDIBLE SUBGROUPS - BY GENUS



than that between the black (BI) and white (CE) rhinos. That mandibles within *Rhinoceros* are more different than mandibles between *Diceros* and *Ceratotherium* further suggests some degree of mosaicism in rhinoceros skull evolution. Overall, there is less correspondence between morphometric uniqueness and generic level taxonomy for mandibles than for skulls.

Taxonomic Patterns - Family and Subfamily Relationships

In addition to the generic and subgeneric levels, it is also of interest to compare morphometric patterns at higher levels of the taxonomic hierarchy. In this section, the genera are identified by family and sometimes by subfamily. Although more subfamilies have been defined in the taxonomic literature, only those two subfamilies which include the higher rhinocerotids are investigated here. The three rhinocerotoid families vary in the number and diversity of skulls available for use in this study. It has already been stated that there is a large gap in fossil representation of relatively complete hyracodontid skulls and mandibles (between *Forstercooperia* [FO] and *Indricotherium* [IN]). Amynodontidae are also poorly represented (here only *Amynodon* [AM] for the skulls and *Zaisanamynodon* [Z1-Z2] for the mandibles). Accordingly, the following discussions are primarily concerned with the Rhinocerotidae and its two subfamilies, Aceratheriinae and Rhinocerotinae.

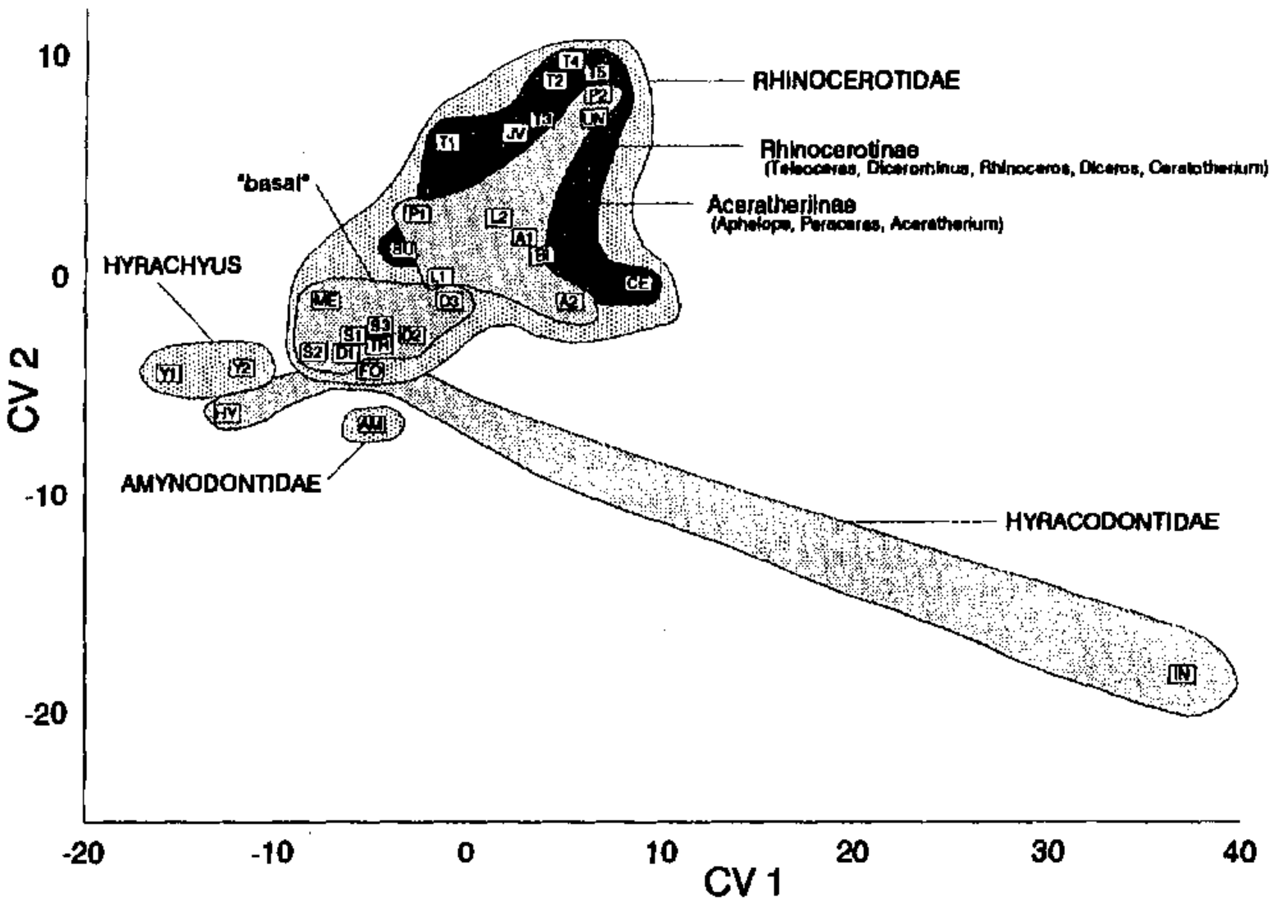
__Skull__ (Figure 62) -- Little can be said about the morphometric relationships of the non-rhinocerotid families because of the small number of taxa represented. *Hyrachyus* is distinct as a genus and probably also as an ancestral family. It is not known what kind of morphometric diversity is represented by the *Amynodon* skull, but the amynodontid mandibles (see below) suggest that this family is distinct. The amynodontid skull has affinities with both primitive rhinocerotids and hyracodontids. The Hyracodontidae is undoubtedly distinct at the family level given the position of *Indricotherium*. The shading which unites *Forstercooperia* (FO) and *Indricotherium* does not necessarily represent the part of the morphometric space that would be occupied by the "missing" hyracodontids. The diversity of genera included within Rhinocerotidae forms two distinct morphometric groups. A basal group unites *Menoceras* (ME), *Subhyracodon* (S1-S4), *Diceratherium* (D1-D3), and *Trigonias* (TR). Subfamilies have been proposed for these genera (see Prothero et al., 1986), but there is not enough morphometric diversity to analyze them at the higher level. A more advanced group consists of the remaining rhinocerotid genera, classified in two subfamilies, Rhinocerotinae and Aceratheriinae. Morphometrically, the subfamilies are completely overlapping. Thus, at the subfamily level, there are no morphological differences detected by the measurements used. Both subfamilies

FIGURE 62. Canonical variates plot of living and fossil subgroup means for skull data with subgroups shown by family and subfamily. Means are grouped by family and subfamily classifications after Prothero et al. (1986).

Key to symbols (listed alphabetically):

A1 - ACER1S *Aceratherium*
A2 - ACER2S *Aceratherium*
AM - AMYNS *Amynodon*
BI - BICOS *Diceros* (black rhino)
CE - CERAS *Ceratotherium* (white rhino)
D1 - DICE1S *Diceratherium*
D2 - DICE2S *Diceratherium*
D3 - DICE3S *Diceratherium*
FO - FORSS *Forstercooperia*
HY - HYCOS *Hyracodon*
IN - INDRS *Indricotherium*
JV - JAVAS *Rhinoceros* (Javan rhino)
L1 - APHE1S *Aphelops*
L1 - APHE2S *Aphelops*
ME - MENOS *Menoceras*
P1 - PERA1S *Peraceras*
P2 - PERA2S *Peraceras*
S1 - SUBH1S *Subhyracodon*
S2 - SUBH2S *Subhyracodon*
S3 - SUBH3S *Subhyracodon*
SU - SUMAS *Dicerorhinus* (Sumatran rhino)
T1 - TELE1S *Teleoceras*
T2 - TELE2S *Teleoceras*
T3 - TELE3S *Teleoceras*
T4 - TELE4S *Teleoceras*
T5 - TELE5S *Teleoceras*
TR - TRIGS *Teleoceras*
UN - UNICS *Rhinoceros* (Indian rhino)
Y1 - HYRA1S *Hyrachyus*
Y2 - HYRA2S *Hyrachyus*

CANONICAL VARIATE MEANS - SKULL SUBGROUPS - FAMILY & SUBFAMILY GROUPS



appear to confound the groupings suggested by morphology. For example, P2 is morphologically similar to T4, but they are in different subfamilies. Likewise, A2 and CE are similar but in different subfamilies.

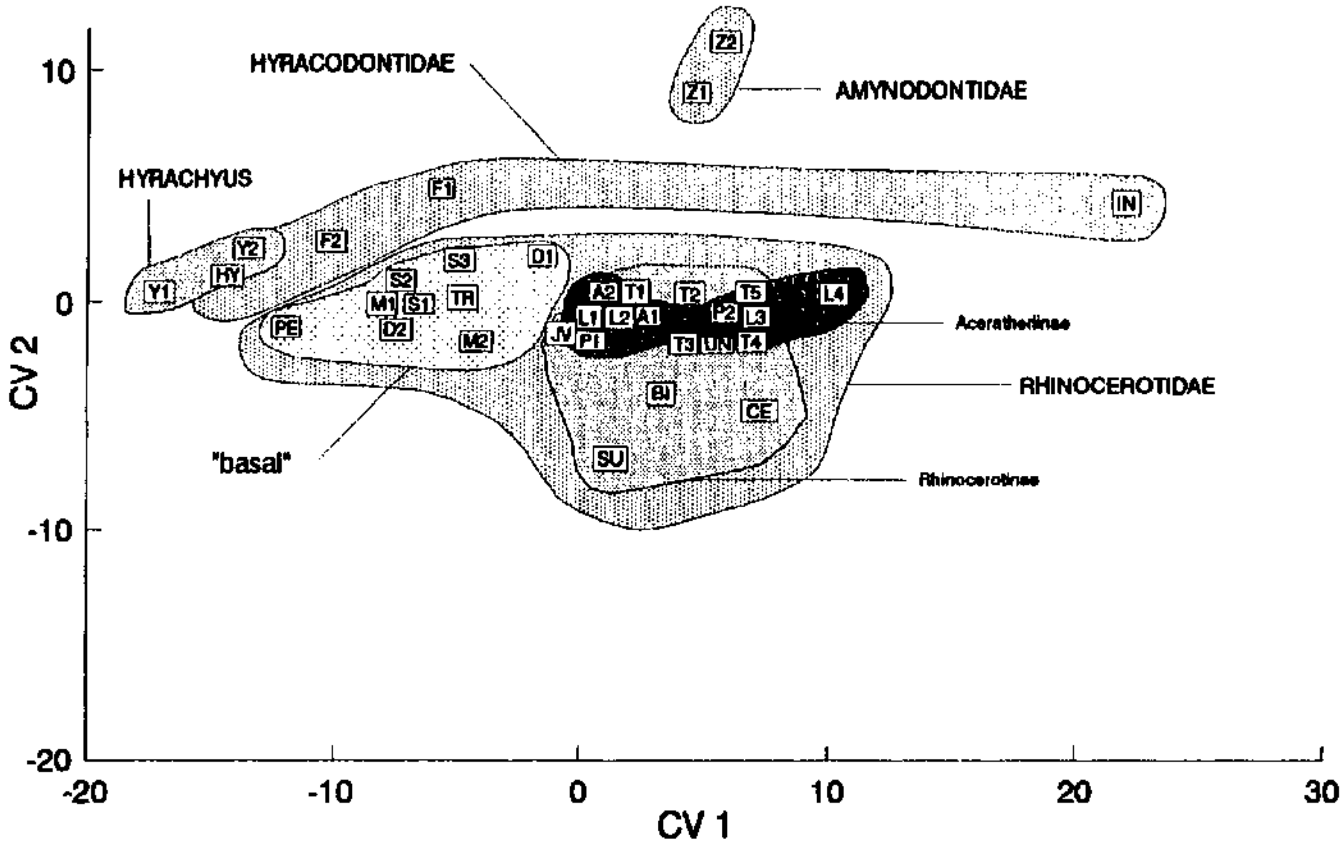
Mandible (Figure 63) -- Small sample sizes (few genera) for Amynodontidae and Hyracodontidae limit the interpretations that can be made at the family level. The outlying position of *Zaisanamynodon* (Z1-Z2) suggests that this family is morphometrically unique. The intermediate position of Hyracodontidae between Amynodontidae and Rhinocerotidae may or may not be indicative of the morphometric relations of this family. The Rhinocerotidae is morphometrically distinct from *Hyrachyus* (Y1-Y2), Amynodontidae, and Hyracodontidae. As with the skulls, there appears to be two rhinocerotid groupings; a basal group and a more advanced group. The basal group does not present any morphometric subgroupings which correspond to proposed subfamilies (see Prothero et al., 1986). The advanced genera are classified into two subfamilies, Aceratheriinae and Rhinocerotinae. Like the skulls, these overlap significantly but in a different way. *Diceros* (BI), *Ceratotherium* (CE), and *Dicerorhinus* (SU) mandibles are morphometrically distinct from other Rhinocerotinae. Conversely, the morphological affinites of *Teleoceras* (T1-T5) and *Rhinoceros* (JV, UN) with Aceratheriinae do not corrrespond to the subfamilial taxonomy. Reasons for this non-correspondence were suggested in the discussion of the skulls.

FIGURE 63. Canonical variates plot of living and fossil subgroup means for mandible data with subgroups shown by family and subfamily. Means are grouped by family and subfamily classifications after Prothero et al. (1986).

Key to symbols (listed alphabetically):

A1 - ACER1M *Aceratherium*
A2 - ACER2M *Aceratherium*
BI - BICOM *Diceros* (black rhino)
CE - CERAM *Ceratotherium* (white rhino)
D1 - DICE1M *Diceratherium*
D2 - DICE2M *Diceratherium*
F1 - FORS1M *Forstercooperia*
F2 - FORS2M *Forstercooperia*
HY - HYCOM *Hyracodon*
IN - INDRM *Indricotherium*
JV - JAVAM *Rhinoceros* (Javan rhino)
L1 - APHE1M *Aphelops*
L2 - APHE2M *Aphelops*
L3 - APHE3M *Aphelops*
L4 - APHE4M *Aphelops*
M1 - MENO1M *Menoceras*
M2 - MENO2M *Menoceras*
PE - PENE1M *Penetrigonias*
P1 - PERA1M *Peraceras*
P2 - PERA2M *Peraceras*
S1 - SUBH1M *Subhyracodon*
S2 - SUBH2M *Subhyracodon*
S3 - SUBH3M *Subhyracodon*
SU - SUMAM *Dicerorhinus* (Sumatran rhino)
T1 - TELE1M *Teleoceras*
T2 - TELE2M *Teleoceras*
T3 - TELE3M *Teleoceras*
T4 - TELE4M *Teleoceras*
T5 - TELE5M *Teleoceras*
TR - TRIGM *Teleoceras*
UN - UNICM *Rhinoceros* (Indian rhino)
Y1 - HYRA1M *Hyrachyus*
Y2 - HYRA2M *Hyrachyus*
Z1 - ZAIS1M *Zaisanamynodon*
Z2 - ZAIS2M *Zaisanamynodon*

CANONICAL VARIATE MEANS - MANDIBLE SUBGROUPS - FAMILY & SUBFAMILY GROUPS



Taxonomic Patterns - Phylogenetic Character States

The relationships between rhinoceros morphometry and classification were discussed in the previous two sections. Because classifications are usually based on a variety of characters, or character states, it is appropriate to investigate the relationships between the morphometric results and specific characters used in classification. The characters chosen for this analysis were selected from those used by Prothero et al. (1986) to formulate their phylogenetic hypotheses for the Rhinocerotoidea. Specifically, only those characters believed to directly or indirectly affect skull and/or mandible morphology were used. Currently, such taxonomic characters are most often presented in explicitly phylogenetic contexts under the umbrella of "cladistic analysis." Here, the question is being asked: are there any correlations between multivariate morphological affinities and qualitative morphological characters used in classification? Although some of the characters used are specific to the skull or mandible, the same set of characters was used for both skull and mandible. This was done for two reasons: (1) differences in the skull and mandible plots can be compared more directly, and (2) characters in one region having effects on the other region might be detected. That is, to some extent, the skull and mandible must coevolve (for example, matching of upper and lower teeth for efficient occlusion and mastication). In the following discussions of skull and mandible CV results, a list of eleven numbered characters is given for each plot. The characters were extracted from Table 1 of Prothero et al. (1986, page 349) and the numbers in that table correspond with those in the plots here. The numbers in the table likewise correspond to the numbered nodes in Figure 4 of Prothero et al. (1986). Not all of these characters define nodes by themselves; many are from lists including a variety of characters defining a particular node. The characters are dicussed in numerical sequence.

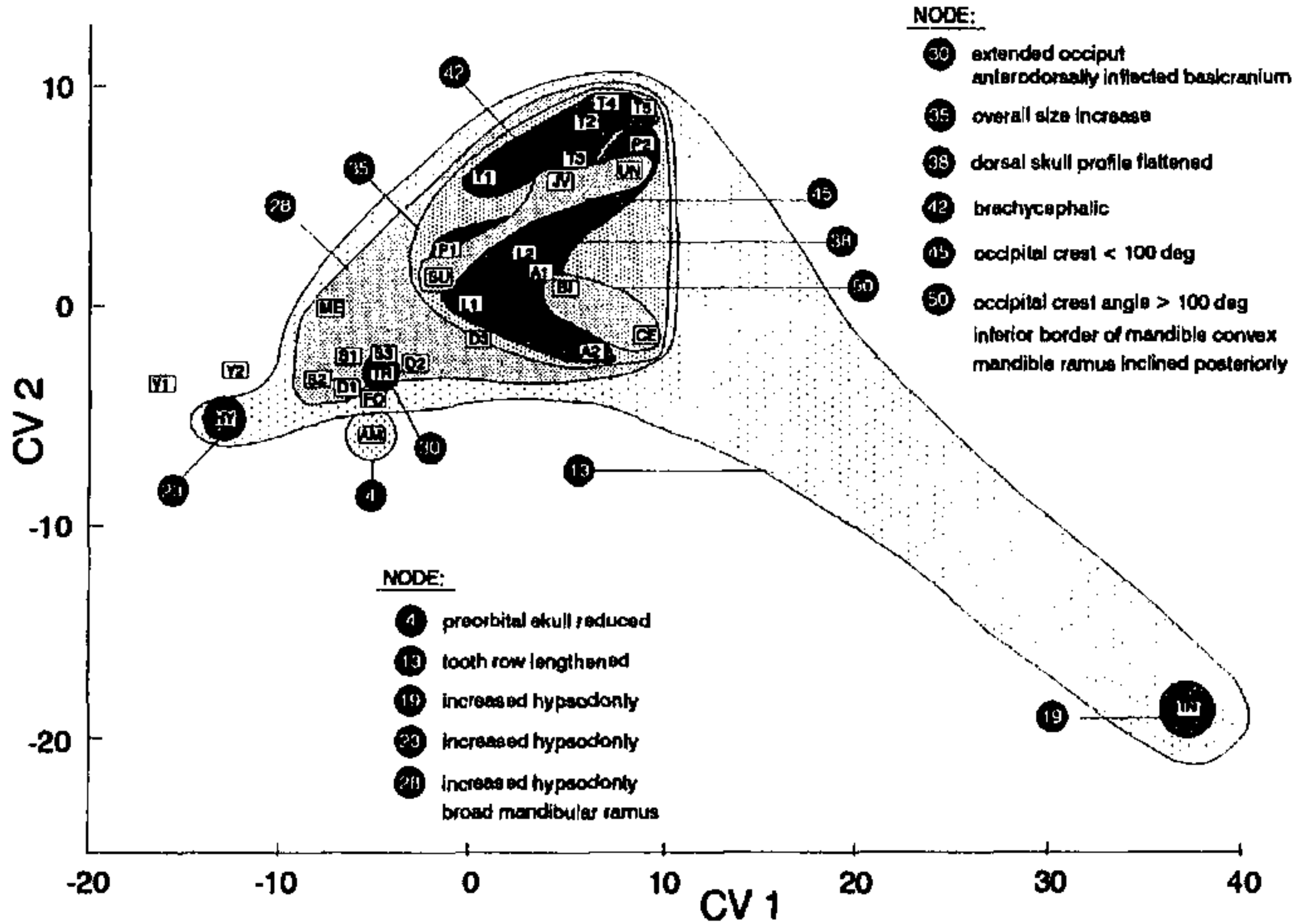
Skull (Figure 64) -- Reduction of the preorbital skull (NODE 4) is a derived feature of *Amynodon* (AM) (and *Zaisanamynodon*). Unfortunately, most of the original measurements in this region were not retained due to the prevalence of missing or broken premaxillae and nasal bones. Only AEP2 and OCP2 (see Figure 4) might directly detect such a change if the tooth row is correspondingly shortened or moved posteriorly. Because *Amynodon* (AM) is morphometrically similar to *Forstercooperia* (FO) and *Diceratherium* (D1-D3), which do not have reduced preorbital regions, it may be concluded that the reduction in *Amynodon* did not significantly affect other parts of the skull. Increased relative length of the cheek tooth row (NODE 13) characterizes hyracodontids and rhinocerotids. This character is general and does not appear to contribute to any morphometric separation of these two families.

FIGURE 64. Canonical variates plot of living and fossil subgroup means for skull data with subgroups shown by phylogenetic character states. Means are grouped by selected character states used for the phylogenetic hypotheses used in Prothero et al. (1986).

Key to symbols (listed alphabetically):

A1 - ACER1S *Aceratherium*
A2 - ACER2S *Aceratherium*
AM - AMYNS *Amynodon*
BI - BICOS *Diceros* (black rhino)
CE - CERAS *Ceratotherium* (white rhino)
D1 - DICE1S *Diceratherium*
D2 - DICE2S *Diceratherium*
D3 - DICE3S *Diceratherium*
FO - FORSS *Forstercooperia*
HY - HYCOS *Hyracodon*
IN - INDRS *Indricotherium*
JV - JAVAS *Rhinoceros* (Javan rhino)
L1 - APHE1S *Aphelops*
L1 - APHE2S *Aphelops*
ME - MENOS *Menoceras*
P1 - PERA1S *Peraceras*
P2 - PERA2S *Peraceras*
S1 - SUBH1S *Subhyracodon*
S2 - SUBH2S *Subhyracodon*
S3 - SUBH3S *Subhyracodon*
SU - SUMAS *Dicerorhinus* (Sumatran rhino)
T1 - TELE1S *Teleoceras*
T2 - TELE2S *Teleoceras*
T3 - TELE3S *Teleoceras*
T4 - TELE4S *Teleoceras*
T5 - TELE5S *Teleoceras*
TR - TRIGS *Teleoceras*
UN - UNICS *Rhinoceros* (Indian rhino)
Y1 - HYRA1S *Hyrachyus*
Y2 - HYRA2S *Hyrachyus*

CANONICAL VARIATE MEANS - SKULL SUBGROUPS - CHARACTER STATES



from the others. Increased relative hypsodonty (tooth height) is another general character (NODES 19, 23, and 28). It probably has more overall affect on the mandible (ramus height for example) than on the skull, but may affect face height since both maxillary and mandibular teeth must increase in height (equally or proportionally). There is no obvious morphometric correlation with this character, at least partly due to its non-exclusive use as a taxonomic character. Increased hypsodonty alone is not likely to account for the shape differences separating *Indricotherium* (IN) from the other rhinoceroses along the second CV axis. A broad mandibular ramus (NODE 28) distinguishes the rhinocerotids in this analysis from several genera not represented in the present morphometric study. It is therefore difficult to assess its contribution to the uniqueness of the skull morphology of the rhinocerotids used here. Two derived characters of *Trigonias* (TR), cited as distinguishing it from later rhinocerotids, are an extended occiput and an anterodorsally inflected basicranium (NODE 30). These characters would be expected to influence morphometry of the skull, especially measurements to the occiput. However, the *Trigonias* (TR) skulls are morphometrically very similar to the *Subhyracodon* (S1-S4) and *Diceratherium* (D1-D3) and thus do not reflect the changes morphometrically (given the measurements used). Roughly, as a group, the higher rhinocerotids (Aceratheriinae and Rhinocerotinae) are characterized by larger size (NODE 35).

However, significant size variation within this "group" reduces the importance which can be attached to this character in defining the group morphometrically. Flattening of the dorsal skull profile, (NODE 38) characteristic of *Aphelops* (L1-L2), *Peraceras* (P1-P2), and *Aceratherium* (A1-A2), is not associated with any morphometric uniqueness of these genera as a group. The *Teleoceras* (T1-T5) subgeneric groups are morphometrically unique from the remaining rhinocerotids. The taxonomic skull character associated with the genus is brachycephaly (NODE 42). Because *Teleoceras* skulls are among the largest of the rhinocerotids, the brachycephaly is only relative. This shape difference is reflected in the separation of *Teleoceras* (T1-T5) from other genera along the second axis. The last two characters (NODES 45 and 50) are polarized opposites of a character with a threshold value. If this character influences overall skull morphology, then it should be reflected morphometrically by two separate groups, as is the case. When *Dicerorhinus* (SU) and *Rhinoceros* (JV,UN) are united (NODE 45), they are distinct (non-overlapping) with the *Diceros* (BI)-*Ceratotherium* (CE) pair (NODE 50).

Mandible (Figure 65) -- The same characters are discussed in this section as were discussed for the skulls above. NODE 4 (reduced preorbital skull) and NODE 13 (lengthened tooth row) are associated with the separation of *Zaisanamynodon* (Z1-Z2) from the other genera. Secondary effects of preorbital changes in *Zaisanamynodon* on the tooth row may contribute to the morphometric

FIGURE 65. Canonical variates plot of living and fossil subgroup means for mandible data with subgroups shown by phylogenetic character states. Means are grouped by selected character states used for the phylogenetic hypotheses in Prothero et al., 1986.

Key to symbols (listed alphabetically):

A1 - ACER1M *Aceratherium*
A2 - ACER2M *Aceratherium*
BI - BICOM *Diceros* (black rhino)
CE - CERAM *Ceratotherium* (white rhino)
D1 - DICE1M *Diceratherium*
D2 - DICE2M *Diceratherium*
F1 - FORS1M *Forstercooperia*
F2 - FORS2M *Forstercooperia*
HY - HYCOM *Hyracodon*
IN - INDRM *Indricotherium*
JV - JAVAM *Rhinoceros* (Javan rhino)
L1 - APHE1M *Aphelops*
L2 - APHE2M *Aphelops*
L3 - APHE3M *Aphelops*
L4 - APHE4M *Aphelops*
M1 - MENO1M *Menoceras*
M2 - MENO2M *Menoceras*
PE - PENE1M *Penetrigonias*
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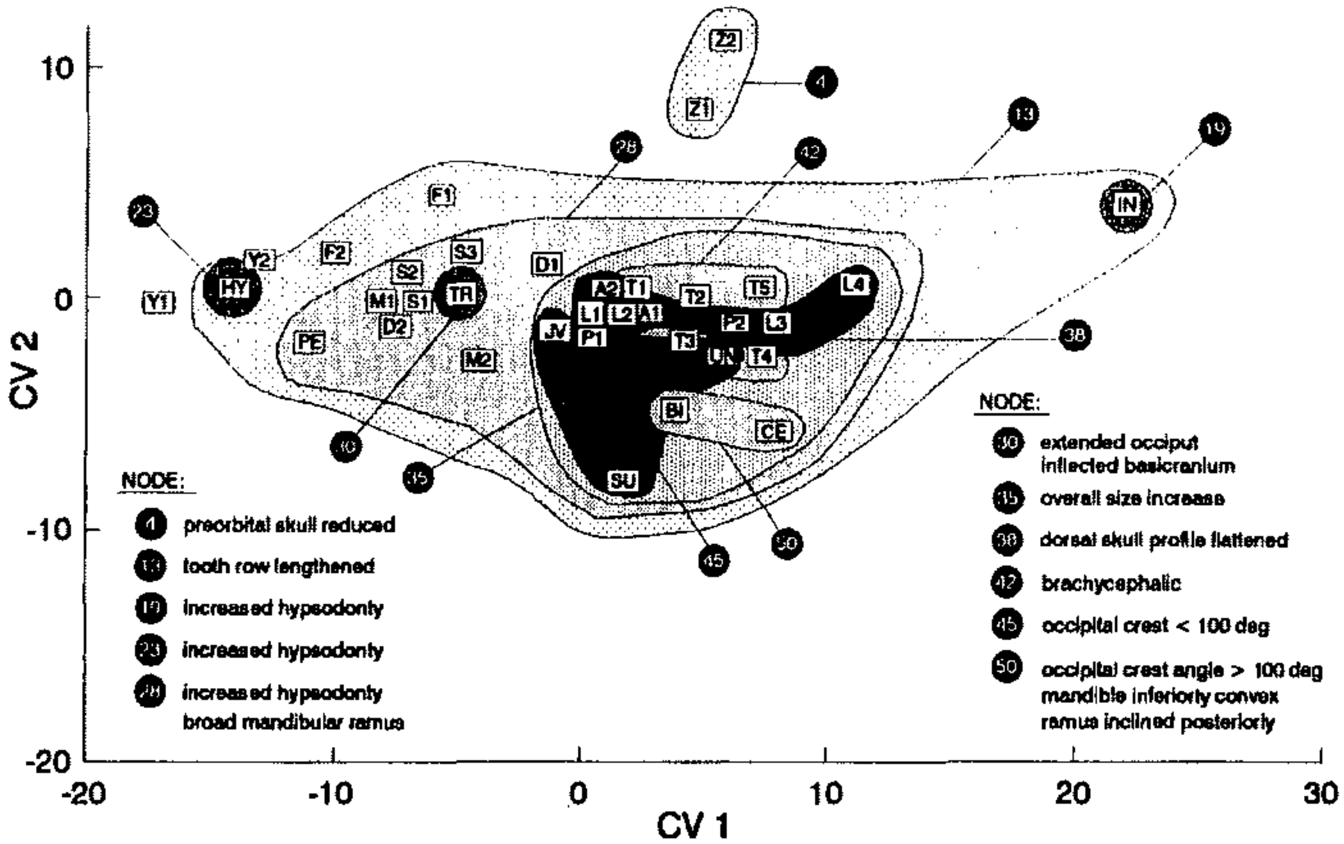
S1 - SUBH1M *Subhyracodon*
S2 - SUBH2M *Subhyracodon*
S3 - SUBH3M *Subhyracodon*
SU - SUMAM *Dicerorhinus* (Sumatran rhino)
T1 - TELE1M *Teleoceras*
T2 - TELE2M *Teleoceras*
T3 - TELE3M *Teleoceras*
T4 - TELE4M *Teleoceras*
T5 - TELE5M *Teleoceras*
TR - TRIGM *Teleoceras*
UN - UNICM *Rhinoceros* (Indian rhino)
Y1 - HYRA1M *Hyrachyus*
Y2 - HYRA2M *Hyrachyus*
Z1 - ZAIS1M *Zaisanamynodon*
Z2 - ZAIS2M *Zaisanamynodon*

CANONICAL VARIATE MEANS - MANDIBLE SUBGROUPS - CHARACTER STATES



difference between the two groups. As with the skulls, increased hypsodonty (NODES 19, 23, 28) is not correlated with any clear morphometric groups associated with the node individually. Taken altogether, the genera characterized by hypsodonty nearly correspond to the group defined by NODE 13 which is distinct from *Zaisanamynodon* (Z1-Z2). Likewise, a broad mandibular ramus (NODE 28) among the rhinocerotids may contribute to their difference from *Zaisanamynodon*. To the extent that the rhinocerotids are different from hyracodontids (see discussion for Figure 63), NODE 28 may contribute. The extended occiput and inflected basicranium do not morphometrically distinguish *Trigonias* (TR) from the basal rhinocerotids. The use of size increase as a taxonomic character (NODE 35) is probably weak and arbitrary given the size ranges within the two "size" groups formed and the continuous nature of the character. Unlike the skull plot, flattened dorsal skull profile (NODE 38) and brachycephaly (NODE 42) are associated with groups which completely overlap. Additionally, the groups defined by NODES 45 and 50 are not as clearly separate as in the skull plot. These last two facts provide further evidence that rhinoceros mandibles are more evolutionarily conservative (or at least, have been less affected by changes in other parts of the skull).

Functional Patterns - Horn Arrangement

Among the most obvious external features of the living rhinoceroses are the median sagittal horns located on the dorsal aspect of the skull. Although the horns are features of the head, they are not osteological features of the bony skull (in contrast to titanothere horns or bovid horn cores, for example). Rather, they are unique epidermal specializations that are fairly loosely attached to the underlying periosteum. Bony features related to horn presence vary from surface rugosity to elevated, rounded horn bosses. The horns therefore, probably have little direct influence on skull morphology, particularly from a mechanical veiw point. A *priori*, correlation between horn morphology and non-boss skull morphology could be attributed to developmental interactions and/or to shared phylogeny. Because of these potential relationships, it is of interest to compare horn morphologies (i.e., number and arrangement) with the morphometric patterns. In Figures 66 and 67, the living and fossil genera are grouped according to three types of recognized horn arrangement: paired nasal horns (side-by-side on the nasal bones); single nasal horns (single boss on the nasal bones in the median plane); and tandem horns (boss or rugosities in the median plane, anteriorly on the nasals and posteriorly on the frontals).

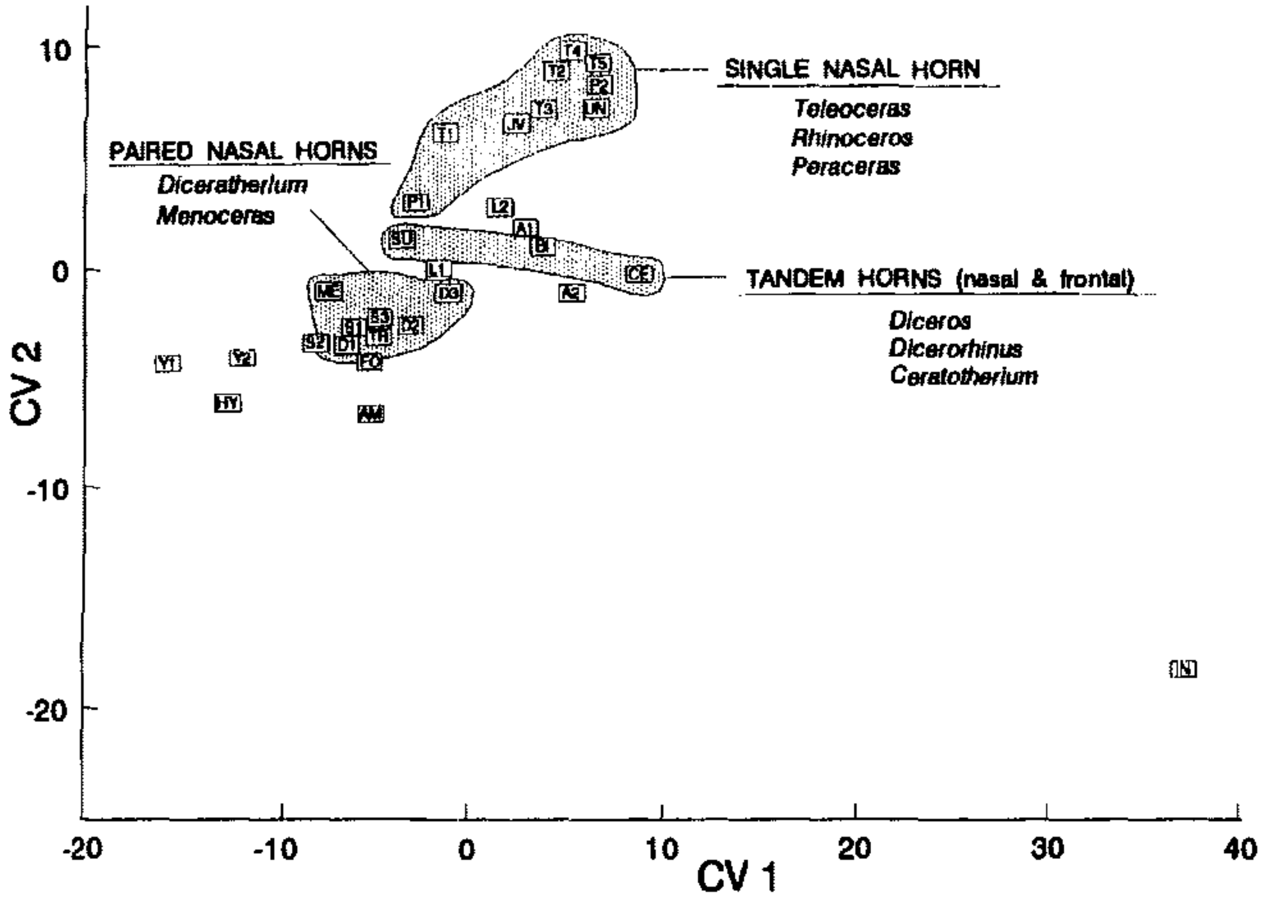
Skull (Figure 66) -- *Diceratherium* (D1-D3) and *Menoceras* (ME) have similar horn arrangements characterized by paired nasal

FIGURE 66. Canonical variates plot of living and fossil subgroup means for skull data with subgroups shown by horn arrangement. Means are grouped by qualitative arrangement of horns.

Key to symbols (listed alphabetically):

A1 - ACER1S *Aceratherium*
A2 - ACER2S *Aceratherium*
AM - AMYNS *Amynodon*
BI - BICOS *Diceros* (black rhino)
CE - CERAS *Ceratotherium* (white rhino)
D1 - DICE1S *Diceratherium*
D2 - DICE2S *Diceratherium*
D3 - DICE3S *Diceratherium*
FO - FORSS *Forstercooperia*
HY - HYCOS *Hyracodon*
IN - INDRS *Indricotherium*
JV - JAVAS *Rhinoceros* (Javan rhino)
L1 - APHE1S *Aphelops*
L1 - APHE2S *Aphelops*
ME - MENOS *Menoceras*
P1 - PERA1S *Peraceras*
P2 - PERA2S *Peraceras*
S1 - SUBH1S *Subhyracodon*
S2 - SUBH2S *Subhyracodon*
S3 - SUBH3S *Subhyracodon*
SU - SUMAS *Dicerorhinus* (Sumatran rhino)
T1 - TELE1S *Teleoceras*
T2 - TELE2S *Teleoceras*
T3 - TELE3S *Teleoceras*
T4 - TELE4S *Teleoceras*
T5 - TELE5S *Teleoceras*
TR - TRIGS *Teleoceras*
UN - UNICS *Rhinoceros* (Indian rhino)
Y1 - HYRA1S *Hyrachyus*
Y2 - HYRA2S *Hyrachyus*

CANONICAL VARIATE MEANS - SKULL SUBGROUPS - HORN TYPES



bosses. Although the bosses are different in detail and represent different lineages, here, the terminal side-by-side arrangement is the uniting factor. Morphometrically, these genera form a unique group. However, the presumably hornless *Subhyracodon* (S1-S4) and *Trigonias* (TR) are associated with them in a morphometric group of more primitive rhinoceroses. Thus, *Diceratherium* and *Menoceras* are probably similar more by virtue of primitiveness, less by virtue of common ancestry. Additionally, it may also be concluded that acquisition of paired horns did not significantly affect them morphometrically, relative to the other primitive rhinoceroses. Another morphometrically unique group united by horn arrangement comprises *Teleoceras* (T1-T5), *Peraceras* (P1-P2), and *Rhinoceros* (JV,UN). This grouping is significant because these three genera are not united by any of the taxonomic analyses above. The classification of *Peraceras* in a different subfamily (Aceratheriinae) implies a distant relationship with *Teleoceras* and *Rhinoceros* (Rhinocerotinae). If *Peraceras* (P1-P2) really represents a different lineage, then its morphometric affinity with some of the rhinocerotines may be explained by parallelism or convergence. However, for this to be true, it would have to be postulated that horn arrangement is constraining or "driving" skull morphology. The latter argument is weak (as discussed above) because of the epidermal nature of the horns. Alternatively, the morphometric result may indicate that these genera are more closely related than previously believed. Similarly, although in the same subfamily, *Dicerorhinus* (SU), *Diceros* (BI), and *Ceratotherium* (CE) are not united at lower taxonomic levels. *Dicerorhinus* (SU) and *Rhinoceros* (JV,UN) have been united at the subtribe level (Prothero et al., 1986, Table 4, NODE 44; this paper, Figure 64, NODE 45). The non-overlapping morphometric unity of tandem-horned rhinoceroses supports the view of a closer relationship than previously hypothesized.

Mandible (Figure 67) -- The morphometric distinctness of horn arrangement groups observed in the skulls is more evident with the mandibles. This is good evidence for the reality of these groups because in the previous analyses, mandibles have been less uniquely differentiated (more uniform) in morphology than the skulls. Further, if mechanical/developmental arguments were plausible, the mandible would be less directly affected by horn arrangement than the skull. Here also, *Dicerorhinus* (SU) has a clear affinity with *Diceros* (BI) and *Ceratotherium* (CE). Hence, morphometry of the mandible seems to have detected unique groups, correlated with horn arrangement, and most likely indicating common ancestries for those arrangements.

Functional Patterns - Herbivory Type

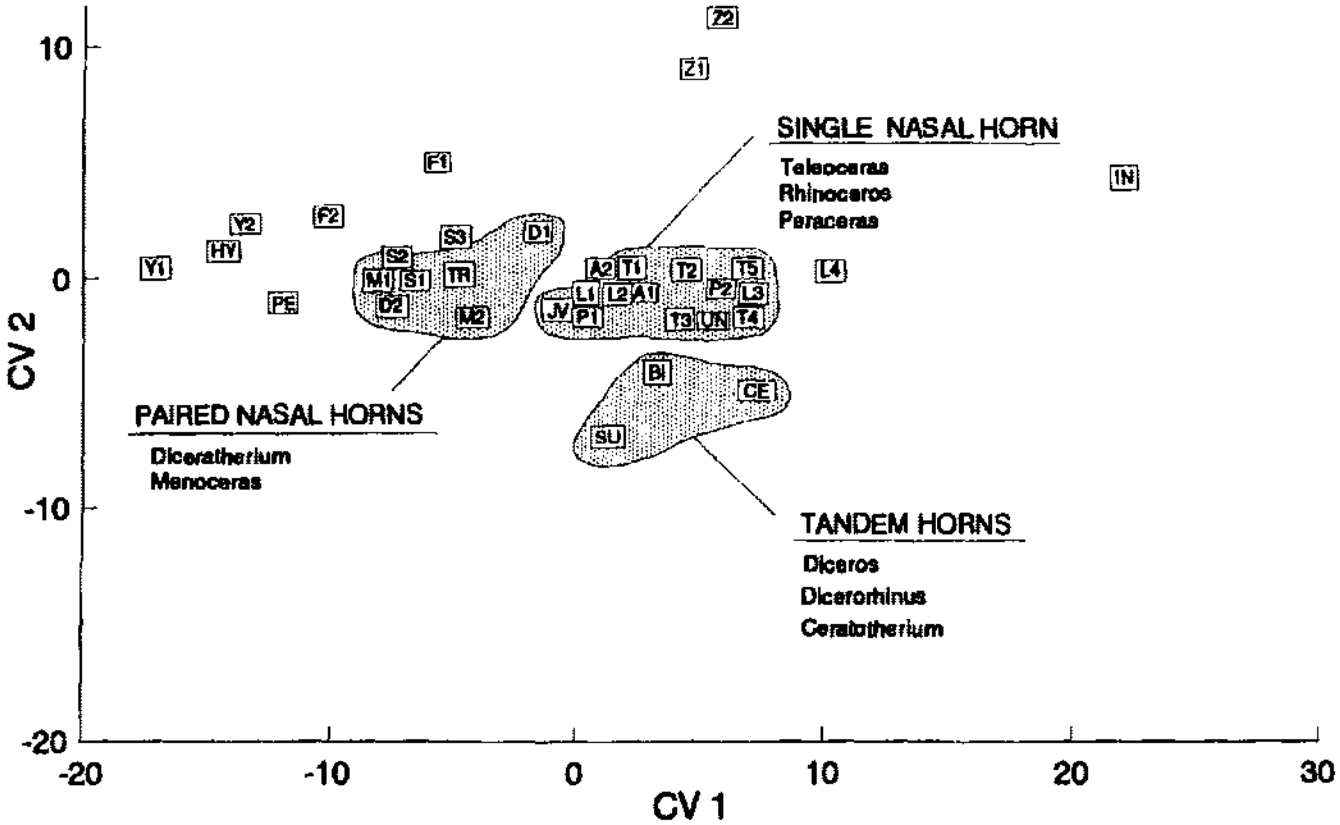
In the vertebrate fossil record, distinguishing herbivores from carnivores is trivial. Within herbivores, distinguishing dietary habits is more difficult. Primarily, herbivores are polarized around two types: grazing (on grasses) and browsing

FIGURE 67. Canonical variates plot of living and fossil subgroup means for mandible data with subgroups shown by horn arrangement. Means are grouped by qualitative arrangement of horns.

Key to symbols (listed alphabetically):

A1 - ACER1M *Aceratherium*
A2 - ACER2M *Aceratherium*
BI - BICOM *Diceros* (black rhino)
CE - CERAM *Ceratotherium* (white rhino)
D1 - DICE1M *Diceratherium*
D2 - DICE2M *Diceratherium*
F1 - FORS1M *Forstercooperia*
F2 - FORS2M *Forstercooperia*
HY - HYCOM *Hyracodon*
IN - INDRM *Indricotherium*
JV - JAVAM *Rhinoceros* (Javan rhino)
L1 - APHE1M *Aphelops*
L2 - APHE2M *Aphelops*
L3 - APHE3M *Aphelops*
L4 - APHE4M *Aphelops*
M1 - MENO1M *Menoceras*
M2 - MENO2M *Menoceras*
PE - PENE1M *Penetrigonias*
P1 - PERA1M *Peraceras*
P2 - PERA2M *Peraceras*
S1 - SUBH1M *Subhyracodon*
S2 - SUBH2M *Subhyracodon*
S3 - SUBH3M *Subhyracodon*
SU - SUMAM *Dicerorhinus* (Sumatran rhino)
T1 - TELE1M *Teleoceras*
T2 - TELE2M *Teleoceras*
T3 - TELE3M *Teleoceras*
T4 - TELE4M *Teleoceras*
T5 - TELE5M *Teleoceras*
TR - TRIGM *Teleoceras*
UN - UNICM *Rhinoceros* (Indian rhino)
Y1 - HYRA1M *Hyrachyus*
Y2 - HYRA2M *Hyrachyus*
Z1 - ZAIS1M *Zaisanamynodon*
Z2 - ZAIS2M *Zaisanamynodon*

CANONICAL VARIATE MEANS - MANDIBLE SUBGROUPS - HORN TYPES



(on herbs, shrubs, and trees). Typically, the browser-grazer spectrum has been correlated to one character, relative cheektooth height (low, or brachydont, for browsers; high, or hypsodont, for grazers). Other features primarily or secondarily related to diet include position of the occiput (related to head carriage) and position of the anterior dentition (related to procuring vegetation). Evolutionary changes of diet may therefore result in changes of mandible and skull morphology. Hence, it is of interest to investigate morphometric results in relation to hypothesized diet (herbivory type).

In Figures 68 and 69, genera or groups of genera are identified where possible by herbivory type. Classification is derived from previous authors' interpretations of diet based on both direct and indirect evidence. If these determinations are accurate and diet systematically influences morphology, then herbivory types should be detectable morphometrically. Primitively, there is little doubt that *Hyrachyus* (Y1-Y2) was a browser and that subsequent "grazing morphologies", therefore, evolved from the browsing condition. Here it is possible to hypothesize that dietary changes were related to the morphological changes. Conversely, morphological changes between a primitive browser and an advanced browser cannot directly be attributed to diet (at least at the resolution of this study).

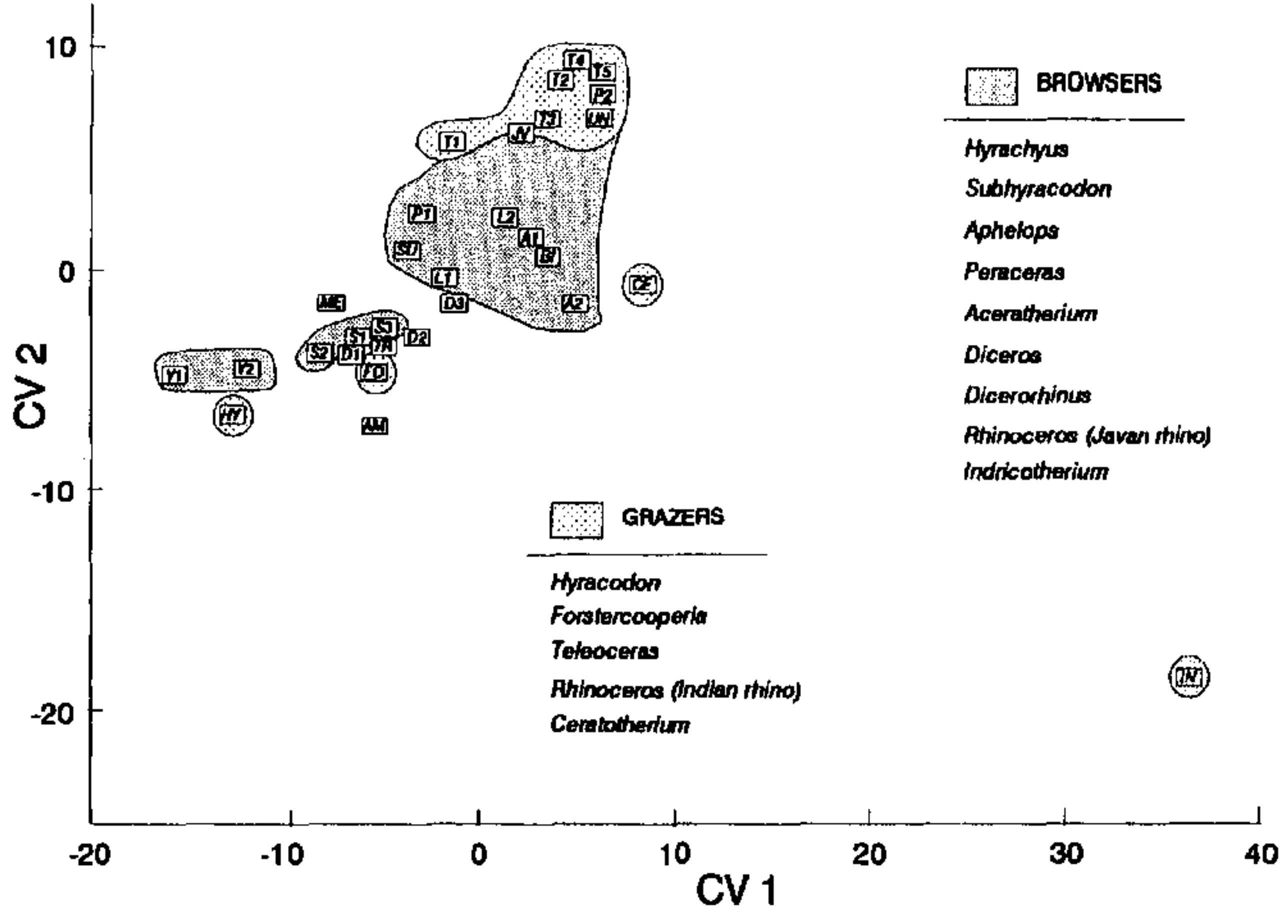
<u>Skull</u> (Figure 68) -- *Hyrachyus* (Y1-Y2) and *Hyracodon* (HY) are not obviously different despite increased hypsodonty and a

FIGURE 68. Canonical variates plot of living and fossil subgroup means for skull data with subgroups shown by herbivory type. Means are grouped by hypothesized type of herbivory.

Key to symbols (listed alphabetically):

A1 - ACER1S *Aceratherium*
A2 - ACER2S *Aceratherium*
AM - AMYNS *Amynodon*
BI - BICOS *Diceros* (black rhino)
CE - CERAS *Ceratotherium* (white rhino)
D1 - DICE1S *Diceratherium*
D2 - DICE2S *Diceratherium*
D3 - DICE3S *Diceratherium*
FO - FORSS *Forstercooperia*
HY - HYCOS *Hyracodon*
IN - INDRS *Indricotherium*
JV - JAVAS *Rhinoceros* (Javan rhino)
L1 - APHE1S *Aphelops*
L1 - APHE2S *Aphelops*
ME - MENOS *Menoceras*
P1 - PERA1S *Peraceras*
P2 - PERA2S *Peraceras*
S1 - SUBH1S *Subhyracodon*
S2 - SUBH2S *Subhyracodon*
S3 - SUBH3S *Subhyracodon*
SU - SUMAS *Dicerorhinus* (Sumatran rhino)
T1 - TELE1S *Teleoceras*
T2 - TELE2S *Teleoceras*
T3 - TELE3S *Teleoceras*
T4 - TELE4S *Teleoceras*
T5 - TELE5S *Teleoceras*
TR - TRIGS *Teleoceras*
UN - UNICS *Rhinoceros* (Indian rhino)
Y1 - HYRA1S *Hyrachyus*
Y2 - HYRA2S *Hyrachyus*

CANONICAL VARIATE MEANS - SKULL SUBGROUPS - HERBIVORY TYPES



presumed grazing habit in the latter (supported indirectly by postcranial adaptations for cursoriality associated with more open habitats). Similarly, *Forstercooperia* (FO) and *Subhyracodon* (S1-S4) have contrasting diets but are not different morphometrically. This result is conceptually like that for horn arrangement (Figure 66) where primitive groups were also not differentiated. In combination, these results imply that early evolution of teeth (or horns) did not significantly influence other aspects of morphology. The Hyracodontidae is somewhat problematic here for several reasons. If it is true that *Forstercooperia* (FO) is both a grazer and ancestral to *Indricotherium* (IN), then *Indricotherium* secondarily evolved the browsing condition. Further, *Indricotherium* (IN) provides an example of why dietary classifications based on tooth height are not absolute, and often speculative: it belongs to a lineage at least partly defined by increased hypsodonty (NODE 19, Figure 64). Of the remaining genera, *Teleoceras* (T1-T5), *Ceratotherium* (CE), and the Indian rhino (UN) are classed as grazers. *Teleoceras* and the Indian rhino are a distinct group well-separated from *Ceratotherium* (CE). This difference indicates that diet alone is not "driving" the morphometric results. Indeed, *Ceratotherium* is more closely related to the browsers *Diceros* (BI) and *Aceratherium* (A1-A2). The remaining browsers (later, larger rhinos) together are nearly non-overlapping with the grazers, but two of the browsers, the Javan rhino (JV) and PERA2S (P2), are morphometrically associated with the upper grazer group. The dietary differences between the Javan and Indian rhinos apparently have no effects on their skull morphology as measured here. In summary, dietary groupings for skulls are not unique. Rather, browsers and grazers are confounded in the morphometric space within groups united by other important factors.

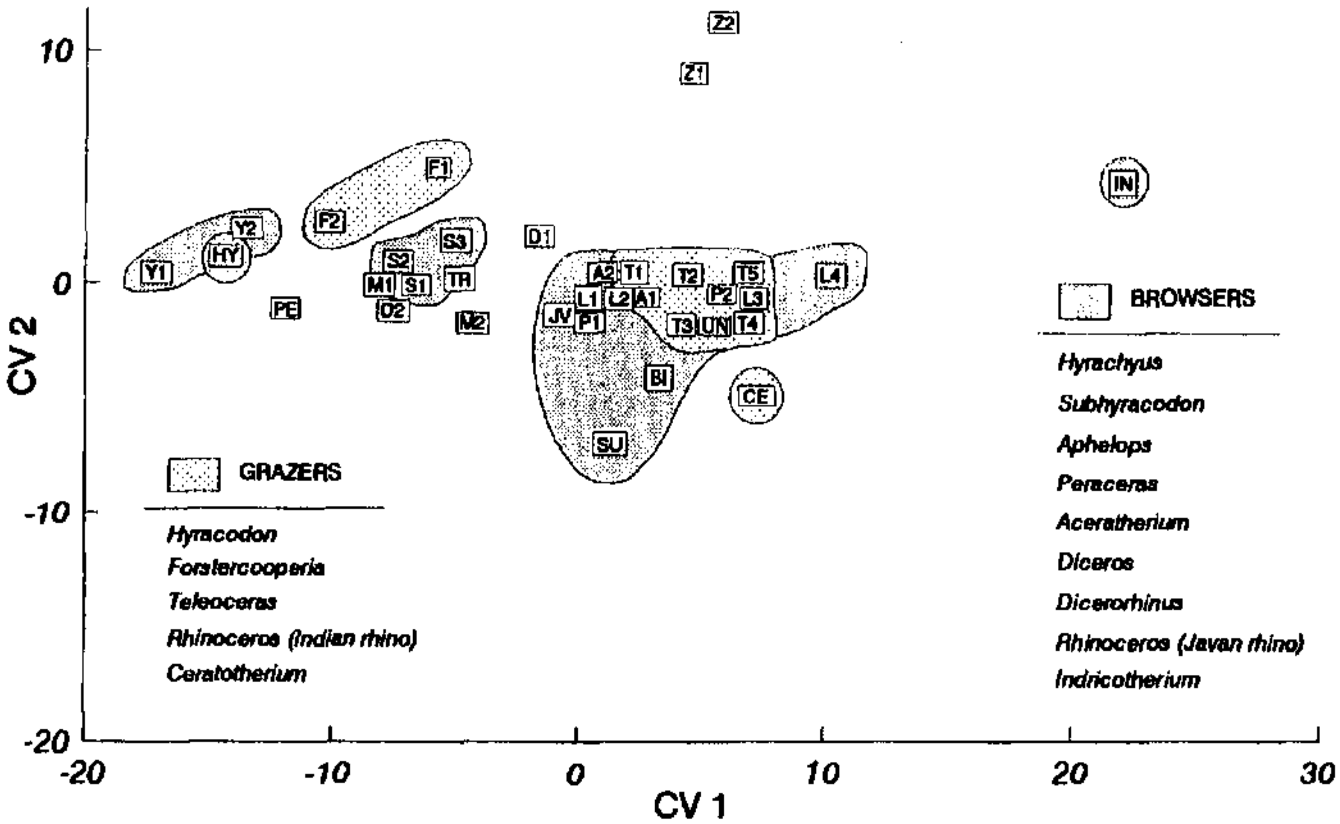
Mandible (Figure 69) -- Mandible results for *Hyrachyus* (Y1-Y2) and *Hyracodon* (HY) are similar to those for the skulls, with the two groups being essentially the same morphometrically. Increased tooth height in *Hyracodon* does not seem to have affected the mandible morphology quantified in this study. A different result from the skull is obtained for the *Subhyracodon* (S1-S3) - *Forstercooperia* (FO) contrast. For mandibles, the two genera are somewhat separated along the second axis. Within the context of this section, this can be hypothesized as due to the differences in diet. The remaining genera are less separated than the skulls, with major overlap of two of the groups. Close inspection of the plot reveals the same confounding arrangement as seen in the skull plot. That is, both grazers and browsers are separated along the second axis with representatives of each dietary type associated together. This result for mandibles shows that dietary type has not been important in determining the morphometric relationships of living and fossil rhinoceroses.

FIGURE 69. Canonical variates plot of living and fossil subgroup means for mandible data with subgroups shown by herbivory type. Means are grouped by hypothesized type of herbivory.

Key to symbols (listed alphabetically):

A1	ACER1M	*Aceratherium*
A2	ACER2M	*Aceratherium*
BI	BICOM	*Diceros* (black rhino)
CE	CERAM	*Ceratotherium* (white rhino)
D1	DICE1M	*Diceratherium*
D2	DICE2M	*Diceratherium*
F1	FORS1M	*Forstercooperia*
F2	FORS2M	*Forstercooperia*
HY	HYCOM	*Hyracodon*
IN	INDRM	*Indricotherium*
JV	JAVAM	*Rhinoceros* (Javan rhino)
L1	APHE1M	*Aphelops*
L2	APHE2M	*Aphelops*
L3	APHE3M	*Aphelops*
L4	APHE4M	*Aphelops*
M1	MENO1M	*Menoceras*
M2	MENO2M	*Menoceras*
PE	PENE1M	*Penetrigonias*
P1	PERA1M	*Peraceras*
P2	PERA2M	*Peraceras*
S1	SUBH1M	*Subhyracodon*
S2	SUBH2M	*Subhyracodon*
S3	SUBH3M	*Subhyracodon*
SU	SUMAM	*Dicerorhinus* (Sumatran rhino)
T1	TELE1M	*Teleoceras*
T2	TELE2M	*Teleoceras*
T3	TELE3M	*Teleoceras*
T4	TELE4M	*Teleoceras*
T5	TELE5M	*Teleoceras*
TR	TRIGM	*Teleoceras*
UN	UNICM	*Rhinoceros* (Indian rhino)
Y1	HYRA1M	*Hyrachyus*
Y2	HYRA2M	*Hyrachyus*
Z1	ZAIS1M	*Zaisanamynodon*
Z2	ZAIS2M	*Zaisanamynodon*

CANONICAL VARIATE MEANS - MANDIBLE SUBGROUPS - HERBIVORY TYPES



Temporal Patterns - Intergeneric Phylogenies

The last two sections of this chapter discuss the skull and mandible morphometric patterns in a temporal-phylogenetic context. This provides an overall impression and comparison of morphological evolution between and within genera. Straight arrows are used to indicate a resultant morphological vector from earlier to later groups in the CV morphospace. Where a genus has multiple subgroups, the arrowheads end at a point approximating the average of those groups (for example, halfway between two subgroups). The arrows are not meant to imply that the actual evolutionary trajectory was necessarily linear. Arrow length has no necessary meaning in terms of length of time or rate of change (CV 1 is a size, not necessarily a time, axis). Length of the arrows does indicate relative amounts of size and shape change. In this section, the vectors correspond to phylogenetic arrows shown in Figure 3. In effect, Figure 3 is mapped, where possible, onto the canonical variate plane represented by CV1-CV2. Arrows from *Trigonias* (TR) to *Subhyracodon* (S1-S4) and from *Subhyracodon* to *Diceratherium* (D1-D3) are not shown because of the close morphometric affinity of those genera. Also, arrows to the living genera are not included because their phylogeny is poorly known.

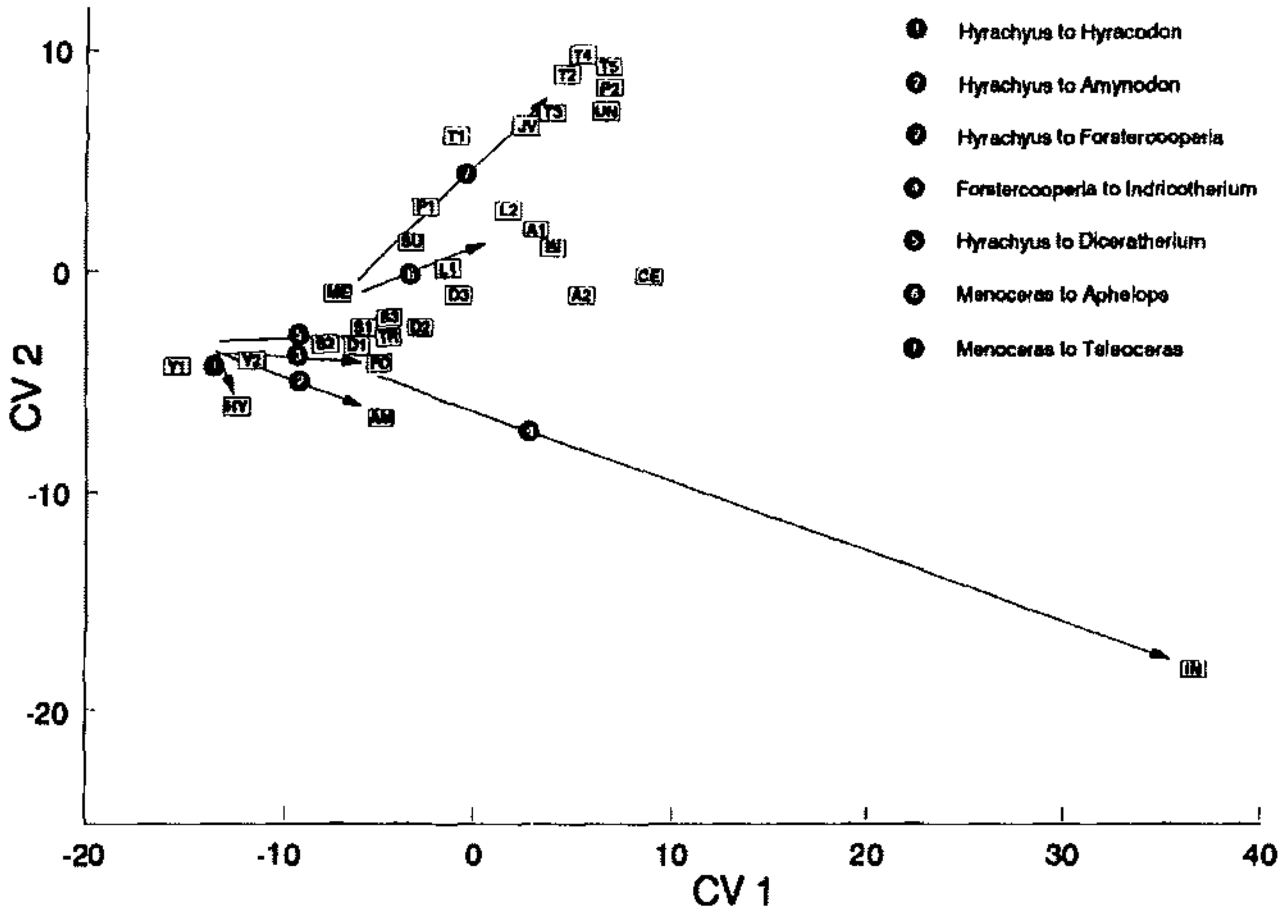
<u>Skull</u> (Figure 70) -- This plot is a basic synthesis of morphology, phylogeny, and time at the generic level. The general impression observed is that rhinoceroses diverge in both size and

FIGURE 70. Canonical variates plot of living and fossil subgroup means for skull data with showing intergeneric phylogenies. Hypothesized phylogenetic trends among genera are indicated by arrows.

Key to symbols (listed alphabetically):

A1 - ACER1S *Aceratherium*
A2 - ACER2S *Aceratherium*
AM - AMYNS *Amynodon*
BI - BICOS *Diceros* (black rhino)
CE - CERAS *Ceratotherium* (white rhino)
D1 - DICE1S *Diceratherium*
D2 - DICE2S *Diceratherium*
D3 - DICE3S *Diceratherium*
FO - FORSS *Forstercooperia*
HY - HYCOS *Hyracodon*
IN - INDRS *Indricotherium*
JV - JAVAS *Rhinoceros* (Javan rhino)
L1 - APHE1S *Aphelops*
L1 - APHE2S *Aphelops*
ME - MENOS *Menoceras*
P1 - PERA1S *Peraceras*
P2 - PERA2S *Peraceras*
S1 - SUBH1S *Subhyracodon*
S2 - SUBH2S *Subhyracodon*
S3 - SUBH3S *Subhyracodon*
SU - SUMAS *Dicerorhinus* (Sumatran rhino)
T1 - TELE1S *Teleoceras*
T2 - TELE2S *Teleoceras*
T3 - TELE3S *Teleoceras*
T4 - TELE4S *Teleoceras*
T5 - TELE5S *Teleoceras*
TR - TRIGS *Teleoceras*
UN - UNICS *Rhinoceros* (Indian rhino)
Y1 - HYRA1S *Hyrachyus*
Y2 - HYRA2S *Hyrachyus*

CANONICAL VARIATE MEANS - SKULL SUBGROUPS - INTERGENERIC PHYLOGENIES



shape with time and that shape diverges with increasing size. It also shows (especially by comparison with the intrageneric analysis below) that most of rhinocerotoid trends in size and shape evolution occur at the generic level. The trends toward size increase from ancestral to descendant genera illustrate well Cope's rule of evolutionary size increase which is observed in the fossil record for many groups.

Mandible (Figure 71) -- Inspection of the time-phylogeny vectors for mandibles shows lesser degrees of divergence than skulls. Size increase is clearly the dominant change between ancestral and descendant genera. This result supports earlier conclusions about the conservativeness of rhinocerotoid mandible evolution.

Temporal Patterns - Intrageneric Time Vectors

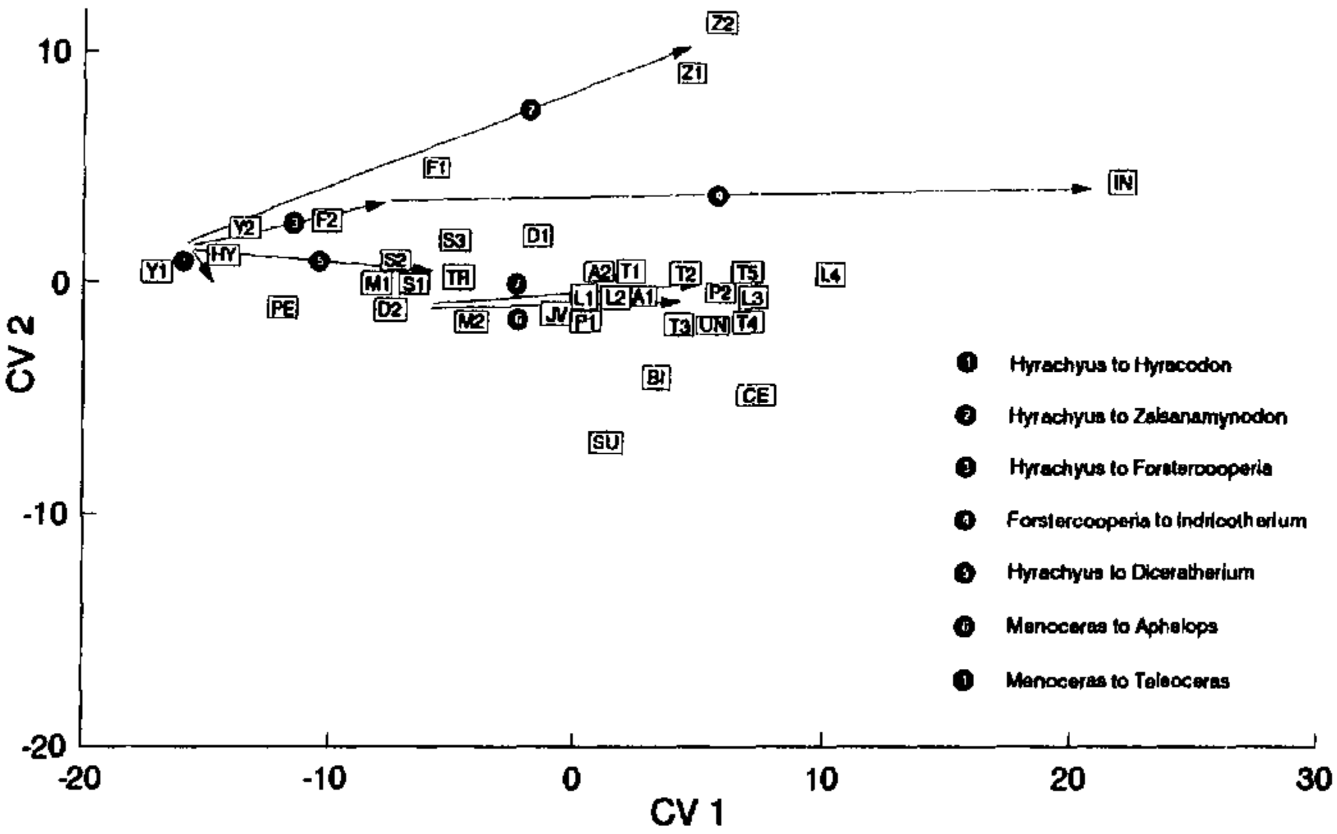
Many of the subgeneric groups determined in Chapter 3 were based in part on temporal-stratigraphic data (NALMA's). It is thus possible to track those subgroups through time in the canonical variates space. In this section, pairs of subgroups within genera are connected by arrows indicating direction from the earlier to the later subgroup. As in the intergeneric analysis, the arrows do not indicate duration or rate, and CV1 is not a time axis. Many of the arrows probably reflect some degree of phylogeny. Only those subgroups for which time vectors could be determined are shown.

FIGURE 71. Canonical variates plot of living and fossil subgroup means for mandible data showing intergeneric phylogenies. Hypothesized phylogenetic trends among genera are indicated by arrows.

Key to symbols (listed alphabetically):

A1 - ACER1M *Aceratherium*
A2 - ACER2M *Aceratherium*
BI - BICOM *Diceros* (black rhino)
CE - CERAM *Ceratotherium* (white rhino)
D1 - DICE1M *Diceratherium*
D2 - DICE2M *Diceratherium*
F1 - FORS1M *Forstercooperia*
F2 - FORS2M *Forstercooperia*
HY - HYCOM *Hyracodon*
IN - INDRM *Indricotherium*
JV - JAVAM *Rhinoceros* (Javan rhino)
L1 - APHE1M *Aphelops*
L2 - APHE2M *Aphelops*
L3 - APHE3M *Aphelops*
L4 - APHE4M *Aphelops*
M1 - MENO1M *Menoceras*
M2 - MENO2M *Menoceras*
PE - PENE1M *Penetrigonias*
P1 - PERA1M *Peraceras*
P2 - PERA2M *Peraceras*
S1 - SUBH1M *Subhyracodon*
S2 - SUBH2M *Subhyracodon*
S3 - SUBH3M *Subhyracodon*
SU - SUMAM *Dicerorhinus* (Sumatran rhino)
T1 - TELE1M *Teleoceras*
T2 - TELE2M *Teleoceras*
T3 - TELE3M *Teleoceras*
T4 - TELE4M *Teleoceras*
T5 - TELE5M *Teleoceras*
TR - TRIGM *Teleoceras*
UN - UNICM *Rhinoceros* (Indian rhino)
Y1 - HYRA1M *Hyrachyus*
Y2 - HYRA2M *Hyrachyus*
Z1 - ZAIS1M *Zaisanamynodon*
Z2 - ZAIS2M *Zaisanamynodon*

CANONICAL VARIATE MEANS - MANDIBLE SUBGROUPS - INTERGENERIC PHYLOGENIES



The purpose of observing the time vectors is to compare the overall generic and subgeneric patterns of morphological change, and to detect any generalizations or trends they may reveal about rhinocerotoid evolution.

Skull (Figure 72) -- The important features in this plot are the directions and lengths of the time vectors where direction indicates the relative amounts of size versus shape change, and length indicates amount of change between two subgroups. Of the ten vectors shown, six indicate size increases. Included in these are all of the longer vectors of which one (Y1-Y2) shows a size increase without much associated shape change. Among the shorter vectors, two indicate size decreases (T4-T5, S1-S2) and two appear to indicate mostly shape change (T2-T3, D2-D3). At face value, these patterns show that changes in both size and shape have been predominant while changes mostly in size or mostly in shape have been less common at the subgeneric (species?) level. At least three of the types of evolutionary change occur within the most diverse genus *Teleoceras* (T1-T5). These changes correspond to the changes discussed in the PCA for *Teleoceras* (Figure 47). The diversity of vectors in this plot distinctly contrasts with the pattern in the intergeneric plot. Within rhino genera, evolution appears to be less directed morphologically.

Mandible (Figure 73) -- The characterizations of Figure 72 for skulls also apply to Figure 73. The diversity of vectors is a mixture of size increases, size decreases, and shape

FIGURE 72. Canonical variates plot of living and fossil subgroup means for skull data showing only those subgroups defined wholly or partly by time. Arrows indicate direction of time (earlier to later) and connect age-adjacent (time-sequential) subgroups within each genus.

Key to symbols (listed alphabetically):

A1 - ACER1S *Aceratherium*
A2 - ACER2S *Aceratherium*
D2 - DICE2S *Diceratherium*
D3 - DICE3S *Diceratherium*
L1 - APHE1S *Aphelops*
L1 - APHE2S *Aphelops*
S1 - SUBH1S *Subhyracodon*
S2 - SUBH2S *Subhyracodon*
S3 - SUBH3S *Subhyracodon*
T1 - TELE1S *Teleoceras*
T2 - TELE2S *Teleoceras*
T3 - TELE3S *Teleoceras*
T4 - TELE4S *Teleoceras*
T5 - TELE5S *Teleoceras*
Y1 - HYRA1S *Hyrachyus*
Y2 - HYRA2S *Hyrachyus*

CANONICAL VARIATE MEANS - SKULL SUBGROUPS - INTERSUBGROUP TIME VECTORS

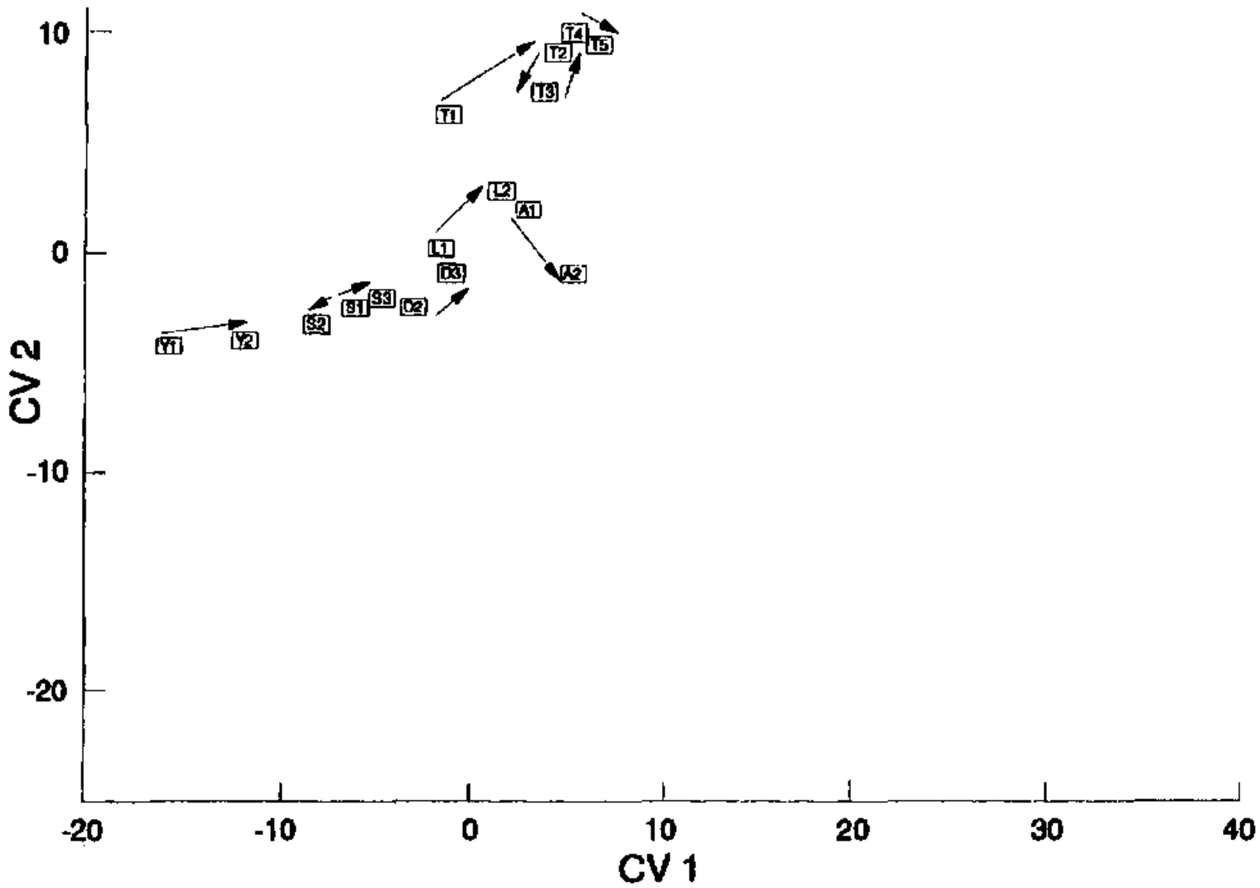
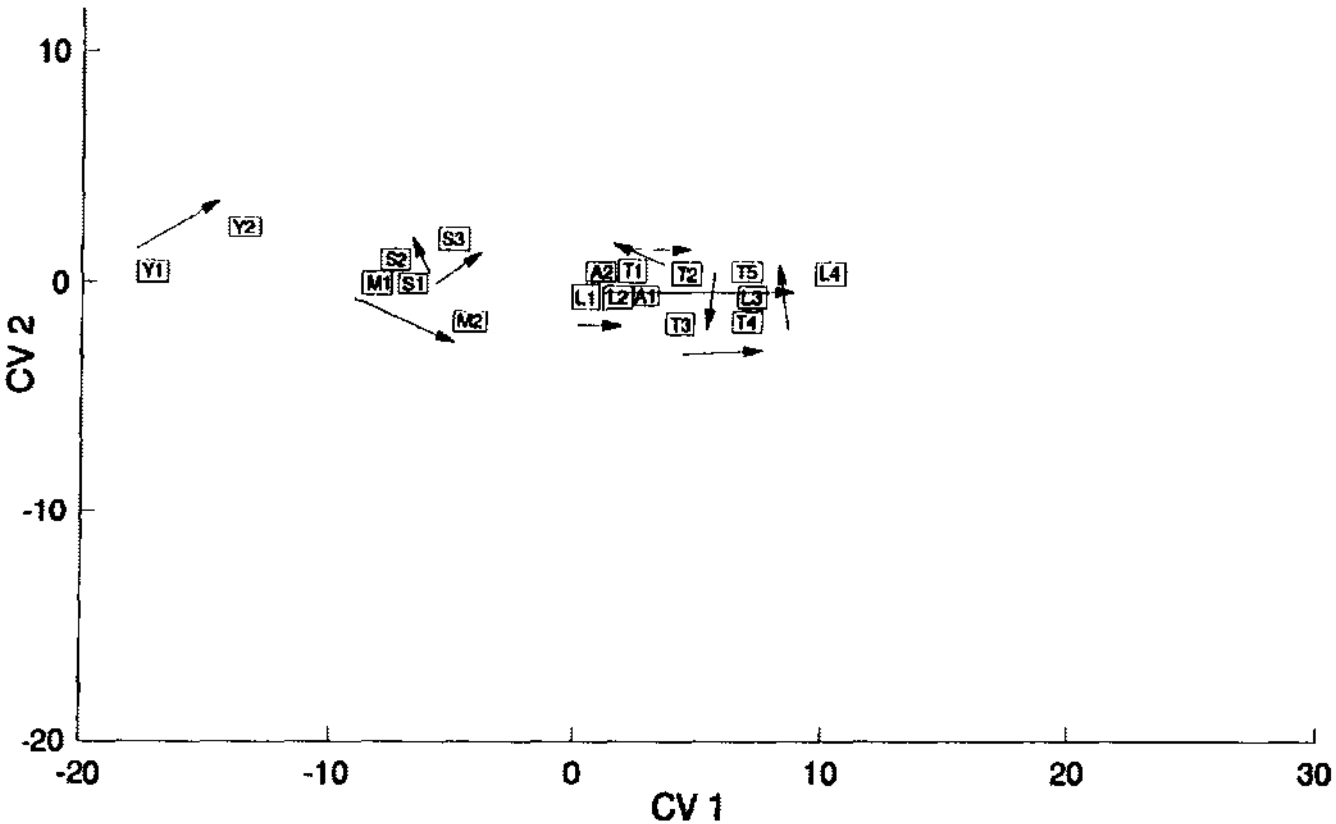


FIGURE 73. Canonical variates plot of living and fossil subgroup means for mandible data. Only intrageneric subgroups defined wholly or partly by time are shown. Arrows indicate direction of time (earlier to later) and connect age-adjacent (time-sequential) subgroups within each genus.

Key to symbols (listed alphabetically):

A1 - ACER1M *Aceratherium*
A2 - ACER2M *Aceratherium*
L1 - APHE1M *Aphelops*
L2 - APHE2M *Aphelops*
L3 - APHE3M *Aphelops*
L4 - APHE4M *Aphelops*
M1 - MENO1M *Menoceras*
M2 - MENO2M *Menoceras*
S1 - SUBH1M *Subhyracodon*
S2 - SUBH2M *Subhyracodon*
S3 - SUBH3M *Subhyracodon*
SU - SUMAM *Dicerorhinus* (Sumatran rhino)
T1 - TELE1M *Teleoceras*
T2 - TELE2M *Teleoceras*
T3 - TELE3M *Teleoceras*
T4 - TELE4M *Teleoceras*
T5 - TELE5M *Teleoceras*
Y1 - HYRA1M *Hyrachyus*
Y2 - HYRA2M *Hyrachyus*

CANONICAL VARIATE MEANS - MANDIBLE SUBGROUPS - INTERSUBGROUP TIME VECTORS



changes but there are no clear trends. *Teleoceras* (T1-T5) exhibits several types of change. Overall, the mandible vectors have smaller angles with respect to CV1 than in Figure 72. This indicates less shape change which is consistent with earlier conclusions about the conservativeness of rhinocertoid mandibles. Comparison of the time vector results with the intergeneric vectors suggest that general morphological trends in the Rhinocerotoidea occur at the generic level, while at the subgeneric and specific level, evolutionary changes are more varied. Much of these evolutionary changes at lower levels may be considered noise relative to higher level trends.

CHAPTER 5.

DISCUSSION

This discussion is an overview of issues related to materials, methods, results, and interpretations, including assumptions, problems, and caveats. Much of the detailed discussion of the principal component and canonical variate results was given in Chapters 2 and 3, respectively. Discussed topics related to sampling and data included specimen distortion and the limitation of the measurement subset. The role and usefulness of the living analogues is briefly discussed in terms of implications for future studies of fossils. A brief section on the nature of morphological evolution in rhinoceroses is followed by a discussion of particular aspects of skull shape change. The latter is illustrated by the results of a landmark morphometric method applied to the Rhinocerotidae. Lastly, some general systematic implications are discussed.

Methodologically, this study affirms the power of multivariate methods for discriminating among morphologies correlated with significant biological and nonbiological variables. The fidelity of the principal components method in discriminating similar specimens of like geologic age, sex, or geography from disimilar ones is a satisfying result given several anticipated, but unrealized, problems. One problem is that of (plastic) deformation of fossil specimens during the time they are embedded in sedimentary rock. Differential movements of the rock may alter (distort) the morphology of specimens in both regular and random ways. Morphological variation is, thus, also affected. It is probably axiomatic that every fossil specimen is distorted to some degree. However, only a single instance was recognized where an outlying specimen appeared to be so because of distortion (see *Trigonias*, Chapter 3). In general, the effects of distortion were insufficient to obscure real morphological relationships. This lack of any significant effect of distortion across many taxa from many ages, and many sedimentary conditions is an important result. It shows that rhino skulls that have survived the geological cycle have retained most of their biologically determined morphology.

A second important result deriving from the PC fidelity relates to the suite of measurements upon which the morphological discriminations were based. The majority of the original measurements were excluded from analysis because of the number of missing values. For example, since premaxillae and the anterior dentition were often absent, measurements related to those areas were excluded by necessity from further consideration. The remaining measurements are therefore a non-random selection representing those parts of the skull or mandible which most often survive the rigors of fossilization. It was a concern that this subset of measurements might not contain enough morphological information to provide meaningful results. The PC analyses show that the "surviving" measurements do characterize much of the biologically relevant morphology. Differences between the skull and mandible results, however, might be partially attributable to differences in the degree to which the respective sets of measurements adequately characterize the morphology. The minimal effect of these potential problems shows that the "signal-to-noise ratio" in fossil rhino skulls is relatively high.

This study benefited greatly from the availability of living rhino taxa to serve as true biological analogues, providing an important link between biology and paleontology. The amount and kind of variation in the monotypic genera (black and white rhinos) turned out to be fairly representative of recognizable monotypic groups or presumed populational samples among the fossils. Thus, the analogues played more of a corroborative role since there were no cases were fossils were arbitrarily made to "fit" them. Ironically, the demonstration of similarity of analogue and fossil variation suggests that studies of variation in similar fossil groups without analogues (for example, titanotheres) may be reasonable with as few as one good geographically and temporally circumscribed quarry sample to serve as a standard of variation. Of course, when living analogues are available, they should be used.

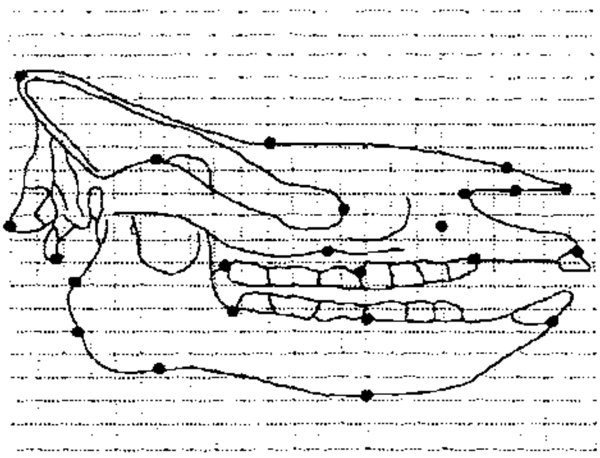
The dissection of variation within the rhinoceros genera, the nature of the pooled within-group dispersion, and the variational overlap within and among genera show that evolutionary change in rhinoceros skull form is more or less continuous. That is, the "average" morphology (from species to species, or genus to genus) shifts across a continuum of morphospace and is characterized by variational overlap among temporally adjacent, phylogenetically related groups. It is significant that this pattern emerges when what is considered a relatively good fossil record is observed. Although, there is much current interest in the presence or absence (appearance or disappearance) of qualitative taxonomic characters in regards to deciphering phylogenies, the morphological "base" to which characters are added or subtracted appears to evolve conservatively in rhinocerotoids. The complimentarity of overall morphology to character studies provides a richer, more complete picture of skull evolution. It may also provide insight into the relationships of development and evolution. There does not appear to have been any major reorganizations of skull morphology as might be expected if early changes in development were the causation of morphological differences. Rather, the kinds and amounts of overall morphological change among rhino species and genera appear to be consistent with those expected from natural selection acting on populations of individuals who vary in their terminal developmental morphologies. Although *Indricotherium* might be an exception, achieving large size and shape differences relatively quickly, it is more likely that the gap between *Indricotherium* and its ancestors represents unfound (or unfossilized) morphologies whose variational patterns would be continuous across the morphometric gap. Even if *Indricotherium* was the product of some saltatory type process, it is the exception rather than the rule among rhinocerotoids.

Investigation of more specific aspects of morphological change in rhino skulls was beyond the scope of this study. There are difficulties associated with identifying these from multivariate results, and some details were certainly lost in the unused measurements. One limitation is the number and distribution of measurements across the morphology; generally smaller, more local measurements are more difficult to obtain. Another limitation results from correlations and redundancies of information in multiple measurements making interpretation of PC loadings difficult.

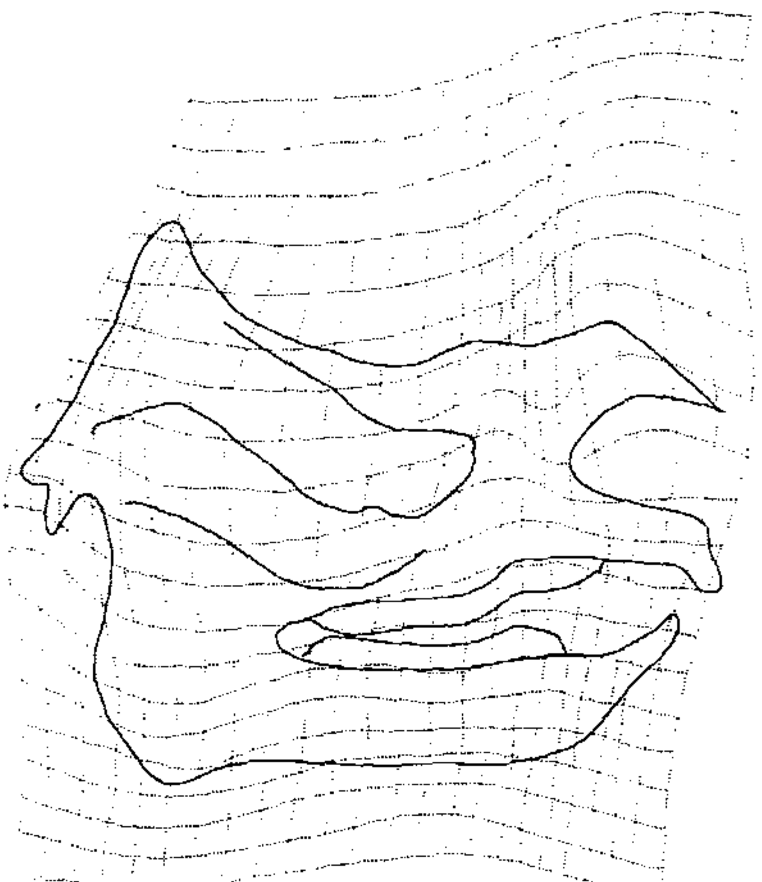
Because of the difficulty in interpreting morphology from multivariate results, there has been much interest in the use of landmark methods for the characterization of shape changes. Although the number and distribution of landmarks result in similar limitations for characterizing details of morphological change, the graphical nature of the methods makes them potentially easier to interpret. Currently, such methods are more developed for two-dimensional rather than three-dimensional problems. Together, measurement and landmark methods provide a complimentary and more complete view of morphology. A preliminary study of evolutionary shape change in rhinoceros skulls was undertaken using the method of Thin Plate Splines (TPS). This is a recent computer implementation of Thompsonian transformation grids based on landmarks (Bookstein, 1991). TPS was applied to the shape transformation from *Subhyracodon* to *Rhinoceros* (Indian rhino), as seen in lateral view. This problem was originally studied by Colbert (1935) who prepared the deformation grids manually (Bales, 1992). The results of TPS analysis (Figure 74) illustrate some specific changes in this particular phylogenetic path (within Rhinocerotidae). These changes include shortening of the distance between the orbit and nasal incision, elevation and rounding of the nasal region, conversion of the dorsal skull profile from relatively flat to concave (saddle-shaped), forward rotation of the occiput and expansion of the occipital region. Little deformation in the region of the mandibular body supports the notion stated earlier that the mandible is more evolutionarily conservative. The concave dorsal profile appears to be the result two separate effects: the elevation of nasals and the forward rotation of the occiput. The former is probably related to the presence of horns. Functionally, the occipital change may have two effects. The forward position of the occiput relative to the occipital condyles may allow a greater range of head extension. More significantly, occiput position effects the direction of pull of the temporalis muscle, a major muscle of mastication which lies in the temporal fossa. In *Subhyracodon*, many temporalis fibers would have a strong posterior component (retraction) to their pull. In *Rhinoceros*, much of the temporal fossa lies above the coronoid process

FIGURE 74. Thin-plate spline (TPS) analysis of shape transformation from *Subhyracodon* to *Rhinoceros* (Indian rhino). (a) Untransformed *Subhyracodon* with landmarks and reference grid. (b) Transformed grid showing the deformation required to map *Subhyracodon* landmarks on to a homologous set of landmarks on *Rhinoceros* (not shown; outline represents deformed *Subhyracodon*).

a.



b.



resulting in a primarily vertical pull (elevation). Thus, one of the major changes in skull shape in the Rhinocerotidae may have been related to aspects of mastication, bite force, and diet.

Because only a subsample of the known rhinocerotoid genera was analyzed, the question arises about how idiosyncratic the results of this study might be. There remains the possibility that some of the unanalyzed fossil genera and lineages might have unique aspects to their biological variation and evolution. This is probably more true at the family level because the two main outliers (*Zaisanamynodon* and *Indricotherium*) are each members of different families and are outlying from Rhinocerotidae. It is clear that one commonality among families is the evolution of larger sizes. This phenomenon, generalized among all animals as Cope's Rule, is exemplified by the Rhinocerotoidea.

Taxonomic revision was not a goal of this study. Indeed, some stability and accuracy of classification was desired *a priori*. However, because many specimens are unallocated, especially at the species level, and because multivariate data has not played a significant role in current taxonomies, the morphometric results may be helpful in clarifying, supporting, or questioning the taxonomic affinities of specimens to each other and to existing taxa. For example, in subgeneric groups where unidentified specimens were grouped with specimens given species names, the provisional assumption is that they are the same species, in the absence of contrary information. In terms of sorting out potential systematic relationships, the most interesting results are the morphometric affinities of the living rhinos with the fossils. The close similarity of morphology of *Rhinoceros* or *Dicerorhinus* to extinct forms may help to clarify the phylogenies of extant rhinos. The affinities also confirm the notion that these living rhinos are indeed "living fossils".

The many fossils which record the long history of the Rhinocerotoidea, provide a rare observation into the nature of morphological evolution in a well-defined mammalian clade. This natural sampling of the evolutionary process in rhinoceroses should continue to be a rich source for analyses of morphological, systematic, and evolutionary problems. Here, several specific quantitative methods were used to characterize the nature of variation in the skull and mandible using a limited sample of taxa and measurements. The application of many methods, both old and new, to cranial and postcranial elements, should continue to improve our understanding of rhinoceros evolution.

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APPENDIX 1.

SPECIMEN IDENTIFICATION

Specimens used in this study are listed by number in ascending order with skulls listed first. Codes represent the first four letters of the subgroup codes listed in Tables 2 and 3. Identical specimen numbers in both skull and mandible lists indicate a matched skull-mandible pair.

MUSEUM ABBREVIATIONS

AMNH - American Museum of Natural History
DMNH - Denver Museum of Natural History
FAM - Fricke Collection of the American Museum of Natural History
FMNH - Field Museum of Natural History
KUVP - University of Kansas Museum of Natural History
MCZ - Museum of Comparative Zoology, Harvard University
USNM - National Museum of Natural History

SKULL SPECIMENS

Code	Spec. #	Museum #
HYRA	4	AMNH 11651
HYRA	5	AMNH 13756
HYRA	6	AMNH 12364
HYRA	10	AMNH 12371
HYRA	12	AMNH 107978
JAVA	17	AMNH 43
JAVA	18	AMNH 146718
SUMA	21	AMNH 81892
CERA	22	AMNH 51854
TRIG	23	ANNH 12389
SUBH	27	AMNH 522
SUBH	28	AMNH 529
SUBH	29	AMNH 1489
SUBH	31	AMNH 1131
SUBH	32	FAM 112162

Genus	Spec. #	Museum #
SUBH	35	AMNH 38995
SUBH	38	AMNH SD-211-3667
SUMA	46	AMNH 54763
UNIC	48	AMNH 54454
UNIC	53	AMNH 54455
UNIC	55	AMNH 35759
CERA	59	AMNH 51856
SUBH	63	AMNH 1144
SUBH	64	AMNH 12295
CERA	99	AMNH [cabinet 940]
CERA	101	AMNH 51860
CERA	102	AMNH 51861
CERA	103	AMNH 51859
CERA	104	AMNH 51857
AMYN	111	AMNH 13189

Genus	Spec. #	Museum #
HYCO	116	FAM 112168
HYCO	117	AMNH 12296
HYCO	120	AMNH 38996
OACE	124	AMNH 1000
FORS	127	AMNH 26037
FORS	130	AMNH 21608
CERA	141	AMNH 51858
CERA	142	AMNH 51855
MENO	143	FAM 112228
BICO	147	AMNH 90055
BICO	149	AMNH 118602
BICO	150	AMNH 85175
BICO	151	AMNH 85181
BICO	152	AMNH 85176
BICO	155	AMNH 27755
BICO	157	AMNH 54311
MENO	158	AMNH 112255
BICO	161	AMNH 27758
BICO	166	AMNH 85174
BICO	167	AMNH 85179
BICO	168	AMNH 85178
BICO	169	AMNH 85180
BICO	170	AMNH 85181
MENO	171	AMNH 14236
MENO	172	FAM 112244
BICO	174	AMNH 85182
BICO	176	AMNH 90204
BICO	177	AMNH 54383
BICO	178	AMNH 34739
BICO	181	AMNH 34742
MENO	186	FAM 112245
MENO	187	FAM 112250
MENO	188	FAM 112254
MENO	195	AMNH [shelf 3.133]
MENO	196	AMNH [shelf 3.133]
MENO	197	AMNH 27866
MENO	198	AMNH [shelf 3.131]
MENO	200	AMNH 86220
MENO	201	AMNH 14213
BICE	203	FAM 112194
DICE	204	FAM 112187
APHE	205	AMNH 95544
SUBH	228	AMNH 1124
SUBH	229	AMNH 541
SUBH	231	AMNH 1137
SUBH	233	AMNH 1121

Genus	Spec. #	Museum #
SUBH	236	AMNH 11865
DICE	239	AMNH 7324
DICE	240	FAM 112176
OACE	245	AMNH 26215
TELE	255	AMNH 115297
INDR	258	AMNH 18650
DICE	266	AMNH 82591
DICE	267	AMNH Lusk 119-707
APHE	268	FAM 114313
APHE	269	AMNH Ains. 108
APHE	270	FAM 114314
APHE	271	AMNH 104624
APHE	272	AMNH 114315
PERA	276	AMNH 108338
SUBH	278	AMNH 1122
TELE	281	FAM 114588
TELE	284	FAM 114590
TELE	287	FAM 114547
TELE	291	FAM 114577
BICO	295	MCZ 27135
CERA	298	MCZ 24917
JAVA	299	MCZ 27324
UNIC	303	MCZ 26269
BICO	305	MCZ 15695
TELE	311	FAM 114524
TELE	312	FAM 114526
TELE	313	FAM 114523
TELE	314	FAM 104209
TELE	315	FAM 114540
TELE	316	FAM 114538
TELE	317	FAM 42979
TELE	318	FAM 42978
PERA	324	FAM 109360
PERA	326	FAM 114409
PERA	327	AMNH 8380
PERA	329	FAM 114396
APHE	330	FAM 114317
APHE	334	FAM 114321
APHE	335	FAM 114327
TELE	341	FAM 114414
TELE	342	FAM 114416
TELE	344	FAM 144422
UNIC	348	USNM 54587
JAVA	351	USNM 156507
CERA	360	USNM 199709
CERA	366	USNM 164592

Genus	Spec. #	Museum #
CERA	367	USNM 164593
CERA	368	USNM 164594
CERA	369	USNM 164595
CERA	370	USNM 164596
CERA	371	USNM 164597
CERA	372	USNM 164598
BICO	379	USNM 161924
BICO	382	USNM 162931
BICO	384	USNM 162933
BICO	386	USNM 162935
BICO	387	USNM 162937
BICO	388	USNM 162936
BICO	389	USNM 162939
BICO	390	USNM 162938
BICO	393	USNM 162943
BICO	394	USNM 162942
BICO	395	USNM 162945
BICO	396	USNM 162944
BICO	397	USNM 162946
BICO	398	USNM 162948
BICO	402	USNM 182018
BICO	404	USNM 182029
BICO	405	USNM 182046
BICO	407	USNM 182194
BICO	408	USNM 199068
BICO	409	USNM 182195
BICO	410	USNM 199067
BICO	411	USNM 199069
BICO	412	USNM 199070
BICO	414	USNM 199522
BICO	418	USNM 540004
TRIG	422	USNM 15666
TELE	424	KUVP (mounted)
UNIC	426	FMNH 25707
UNIC	427	FMNH 25708
UNIC	430	FMNH 57822
CERA	431	FMNH 29174
BICO	436	FMNH 34278
BICO	437	FMNH 85429
BICO	441	FMNH 127849
MENO	452	FMNH P15150
MENO	453	FMNH P12850
MENO	454	FMNH UC1355
MENO	456	FMNH UC1352
MENO	457	FMNH P15146
DICE	458	FMNH P12018

Genus	Spec. #	Museum #
HYCO	460	FMNH P12011
AMYN	461	FMNH P12184
TRIG	462	DMNH 1746
TRIG	463	DMNH 1850
TRIG	468	DMNH 1029
TRIG	469	DMNH 421
TRIG	470	DMNH 1056
TRIG	471	DMNH 880 Q
TRIG	472	DMNH 420 M
TRIG	475	DMNH 1053
TRIG	476	DMNH 414
TRIG	490	DMNH 886
TRIG	492	DMNH 878 G
TELE	496	DMNH 309
TELE	497	DMNH 715

MANDIBLE SPECIMENS

Genus	Spec. #	Mus. #
HYRA	4	AMNH 11651
HYRA	6	AMNH 12364
HYRA	8	AMNH 12355
PENE	15	AMNH 1110
JAVA	17	AMNH 43
JAVA	18	AMNH 146718
SUMA	21	AMNH 81892
CERA	22	AMNH 51854
SUBH	28	AMNH 529
SUBH	29	AMNH 1489
SUBH	32	FAM 112162
SUBH	33	FAM LUSK 0-117-2113
SUBH	35	AMNH 38995
SUBH	38	AMNH SD-211-3667
SUBH	40	AMNH SD-18-444
SUBH	43	AMNH 1134
SUBH	44	AMNH 1128
SUMA	46	AMNH 54763
UNIC	48	AMNH 54454
UNIC	53	AMNH 54455
UNIC	55	AMNH 35759
CERA	59	AMNH 51856
SUBH	65	AMNH 454-22186
CERA	99	AMNH [cabinet 940]
CERA	101	AMNH 51860
CERA	102	AMNH 51861
CERA	103	AMNH 51859
CERA	104	AMNH 51857
ZAIS	107	AMNH 26102
ZAIS	114	AMNH 99381
HYCO	117	AMNH 12296
HYCO	120	AMNH 38996
ACER	124	AMNH 1000
FORS	126	AMNH 20286
FORS	128	AMNH 26660
FORS	129	AMNH 26666
MENO	132	FAM 116063
CERA	141	AMNH 51858
CERA	142	AMNH 51855
BICO	147	AMNH 90055
BICO	149	AMNH 118602
BICO	150	AMNH 85175
BICO	151	AMNH 85181

Genus	Spec. #	Museum #
BICO	155	AMNH 27755
BICO	157	AMNH 54311
MENO	158	AMNH 112255
BICO	161	AMNH 27758
BICO	166	AMNH 85174
BICO	167	AMNH 85179
BICO	168	AMNH 85178
BICO	169	AMNH 85180
BICO	170	AMNH 85181
MENO	172	FAM 112244
BICO	174	AMNH 85182
BICO	176	AMNH 90204
BICO	177	AMNH 54383
BICO	178	AMNH 34739
BICO	181	AMNH 34742
MENO	186	FAM 112245
MENO	189	AMNH Agate E
MENO	190	AMNH Agate L
MENO	191	AMNH Agate M
MENO	192	AMNH Agate AA
MENO	194	AMNH 86218
ACER	206	AMNH 26218
APHE	207	FAM 114647
APHE	208	AMNH 114650
APHE	209	FAM 114651
APHE	211	FAM 114672
ACER	212	AMNH 98036
APHE	213	FAM 114780
APHE	214	FAM 114826
APHE	215	FAM 114840
APHE	216	AMNH FLA186-2725
TELE	217	FAM 115266
TELE	218	FAM 115267
TELE	219	FAM 115275
TELE	221A	FAM 115618
TELE	221B	AMNH 13874
TELE	223	FAM 115782
TELE	224	FAM 115951
TELE	225	FAM 115958
TELE	226	FAM 115880
TELE	227	FAM 115967
SUBH	231	AMNH 1137
SUBH	232	AMNH 543

Genus	Spec. #	Museum #
SUBH	234	AMNH 1121
DICE	241	AMNH (box 117 - #710)
ACER	245	AMNH 26215
TELE	249	AMNH 18924
TELE	250	AMNH 21496
TELE	253	AMNH 115026
TELE	254	AMNH 115079
TELE	255	AMNH 115297
INOR	258	AMNH 18650(see footnote)
TELE	259	FAM 115370
TELE	260	FAM 115371
TELE	261	AMNH 10878
TELE	262	FAM 11509
TELE	263	FAM 115582
TELE	264	FAM 115252
APHE	273	AMNH Ains.74-2
APHE	274	FAM 104623
APHE	275	AMNH FLA 166-2565
PERA	276	AMNH 108338
SUBH	279	AMNH 1109
HYCO	280	AMNH 14433
TELE	281	FAM 114588
TELE	282	FAM 114585
TELE	283	FAM 114597
TELE	286	AMNH 2623
TELE	290	AMNH 8391
TELE	292	FAM 114570
BICO	294	MCZ 41993
BICO	295	MCZ 27135
CERA	297	MCZ 34850
CERA	298	MCZ 24917
JAVA	299	MCZ 27324
UNIC	303	MCZ 26269
BICO	305	MCZ 15695
TELE	312	FAM 114526
TELE	313	FAM 114523
TELE	314	FAM 104209
PERA	319	FAM 114310
APHE	322	FAM 114358
HYRA	323	FAM 12664
PERA	324	FAM 109360
PERA	325	FAM 114412
APHE	330	FAM 114317
APHE	331	FAM 114319
APHE	333	FAM 114322
APHE	338	FAM 114352

Genus	Spec. #	Museum #
APHE	339	FAM 114357
PERA	340	FAM 114407
TELE	346	FAM 114436
TELE	347	FAM 114437
UNIC	348	USNM 545847
UNIC	349	USNM 545848
CERA	360	USNM 199709
CERA	366	USNM 164592
CERA	367	USNM 164593
CERA	368	USNM 164594
CERA	369	USNM 164595
CERA	370	USNM 164596
CERA	371	USNM 164597
BICO	379	USNM 161924
BICO	382	USNM 162931
BICO	384	USNM 162933
BICO	386	USNM 162935
BICO	387	USNM 162937
BICO	388	USNM 162936
BICO	389	USNM 162939
BICO	390	USNM 162938
BICO	392	USNM 162941
BICO	393	USNM 162943
BICO	394	USNM 162942
BICO	396	USNM 162944
BICO	397	USNM 162946
BICO	398	USNM 162948
BICO	402	USNM 182018
BICO	405	USNM 182046
BICO	407	USNM 182194
BICO	408	USNM 199068
BICO	410	USNM 199067
BICO	411	USNM 199069
BICO	412	USNM 199070
BICO	414	USNM 199522
BICO	418	USNM 540004
TRIG	421	USNM 4815
TRIG	423	USNM 5667
TELE	424	KUVP (mounted)
SUBH	425	KUVP 2787
UNIC	426	FMNH 25707
UNIC	427	FMNH 25708
UNIC	429	FMNH 57639
CERA	431	FMNH 29174
BICO	436	FMNH 34278
BICO	437	FMNH 85429

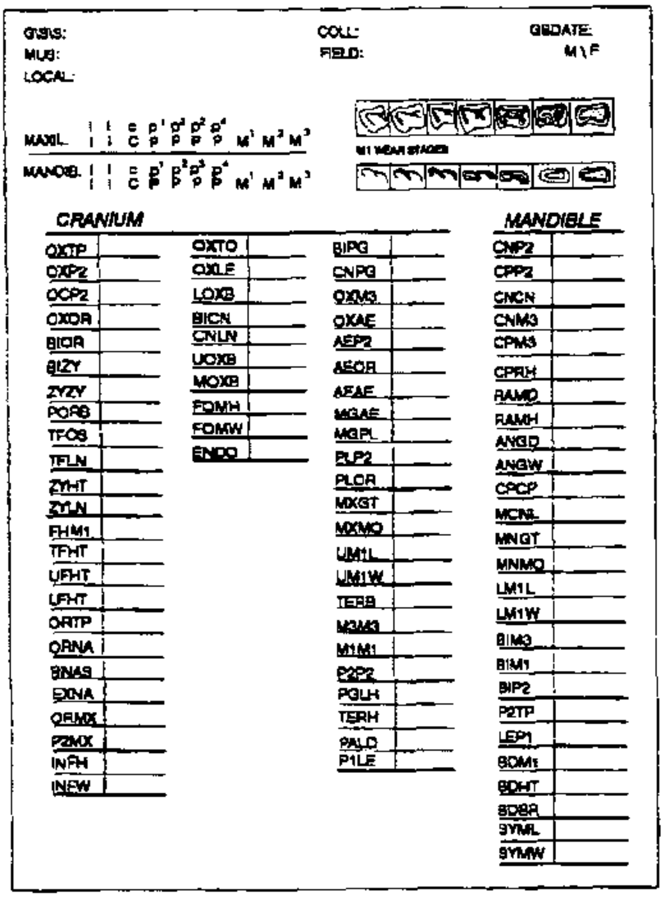
Genus	Spec. #	Museum #
BICO	441	FMNH 127849
BICO	443	FMNH 127851
DICE	451	FMNH UC385
MEND	454	FMNH UC1355
MEND	457	FMNH P15146
SUBH	458	FMNH P12018
NYCO	460	FMNH P12011
TRIG	470	DMNH 1510
TRIG	474	DMNH F-126
TRIG	477	DMNH 2712
TRIG	479	DMNH 2670
TRIG	480	DMNH 412
TRIG	481	DMNH 2695
TRIG	483	DMNH 891
TRIG	484	DMNH 2674
TRIG	485	DMNH 1037
TRIG	486	DMNH 2724
TRIG	491	DMNH 1029
PERA	494	DMNH 732

Note: AMNH 18650 is a cast.

APPENDIX 2.

DATA SHEET

Data form used for each specimen (shown reduced in size). Measurements were taken from top-to-bottom, left-to-right. Ancillary data included genus/species/subspecies designations (G\S\S), collection information (COLL.), museum identification (MUS.), field notes (FIELD), male/female (M\F), and locality-stratigraphy (LOCAL). Teeth present and first molar wear stage were also recorded (p^1 = first deciduous premolar; P = first permanent premolar).


G\S\S: COLL: GSDATE:
MUS: FIELD: M\F
LOCAL:

MAXIL. I I c C p¹ P p² P p³ P p⁴ P M¹ M² M³
MANDIB. I I c C p¹ P p² P p³ P p⁴ P M₁ M₂ M₃

M1 WEAR STAGES

CRANIUM

OXTP, OXP2, OCP2, OXOR, BIOR, BIZY, ZYZY, PORB, TFOS, TFLN, ZYHT, ZYLN, FHM1, TFHT, UFHT, LFHT, ORTP, ORNA, BNAS, EXNA, ORMX, P2MX, INFH, INFW

OXTO, OXLF, LOXB, BICN, CNLN, UOXB, MOXB, FOMH, FOMW, ENDO

BIPG, CNPG, OXM3, OXAE, AEP2, AEOR, AEAE, MGAE, MGPL, PLP2, PLOR, MXGT, MXMO, UM1L, UM1W, TERB, M3M3, M1M1, P2P2, PGLH, TERH, PALD, P1LE

MANDIBLE

CNP2, CPP2, CNCN, CNM3, CPM3, CPRH, RAMD, RAMH, ANGD, ANGW, CPCP, MCNL, MNGT, MNMO, LM1L, LM1W, BIM3, BIM1, BIP2, P2TP, LEP1, BDM1, BDHT, BDBR, SYML, SYMW

APPENDIX 3.

MEASUREMENT DEFINITIONS

APPARATUS

Roman numerals indicate instrument (caliper) type or measurement aid (plexiglas); lowercase letters refer to caliper subparts or to different aids. The numerals and letters are referred to in the descriptions of measurements.

I. *Fowler 12" Digital Caliper.*(Swiss). This allows outside measurements only using longer squared-tip jaws (I.a) or shorter pointed-tip jaws (I.b). The metric range is 0 - 369 mm, accurate to 0.01 mm.

II. *Fowler (Sylvac) Ultracal II 6" Digital Caliper.*(Swiss). Includes longer, pointed jaws for outside measurement (II.a), shorter, pointed jaws for inside diameters (II.b), and a depth gauge (II.c). The metric range is 0 - 153 mm, accurate to 0.01 mm.

III. *GPM Anthropometer.*(Swiss). A specialized caliper designed for taking human somatic measurements. Jaws are long (22cm) and the tip-to-tip measurement range is 0 - 210 cm, accurate to 0.5 mm.

IV. *Helios 12" Dial Caliper.*(West German). Similar to I, but non-digital. Includes depth gage (IV.a) with maximim depth of 33 cm, accurate to 0.05 mm.

V. *Plexiglas Plates.* Rectangles, 10" by 1", 2", or 3" (V.a). Oddcut, 21" X 3" with 2" X 8" corner removed (V.b). 12" by 4" rectangle with ruler attached to surface (V.c). Plate thickness is 6 mm (nearest mm).

LANDMARK DEFINITIONS

Uppercase letters identify specific landmarks and are referred to in the description of measurements.

A. *Most posterior point in the median plane along the nuchal margin*

Given the diversity and irregularity of the occipital region, some judgement is required to locate this point. When there is a distinct nuchal ridge, it is simply followed to the median plane, and if the ridge is thick, the superior margin is used. Where the ridge is less distinct, it must be decided where the dorsal surface of the skull "ends" and the occipital surface "begins". Because the ridge may turn inferiorly as it approaches the midline, this landmark does not necessarily correspond to the most superior point of the occiput, nor to the most posterior point of the occiput, depending on the inclination of the occipital "plane" and the presence of tuberous and rugose areas.

Measurements to this point: OXTP, OXP2, OXPO, OXTO, OXLE, OXAE, OXOR, OXM3

B. *Posterior margin on the basiocciput*

Between the occipital condyles inferiorly, the basiocciput presents a rounded posterior margin which is somewhat external and inferior to the true foramen magnum aperture. The most posterior point of the margin in the median plane is marked while observing the skull posteriorly at the level of the occipital condyles.

Measurements to this point: OXTO, MGPL

C. *Most lateral point on the articular eminence*

The articular surface is usually smoother than surrounding bone and may have a different hue. These two factors help in following the margin to its most lateral extent. This point does not necessarily correspond to the most lateral point of bone in the region, or of the zygomatic arch.

Measurements to this point: OXAE, AEAE, AEP2, AEOR

D. *Most anterior point on the margin of the orbit*

This point is difficult to determine for several reasons: the orbital margin is not well-defined, being rather rounded and smoothly continuous with adjacent bone, and the lacrimal process and foraminae may appear to occupy the position. In such cases, the point is considered as just inferior to the lacrimal process.

Measurements to this point: OXOR, AEOR, BIOR, ORP2, ORNA, ORTP, ORMX

E. *Most anterolateral point on the alveolar margin of the second upper premolar*

The anterior and lateral margins of the alveolus are continuous at the anterolateral "corner". The center of this curved part is determined by eye.

Measurements to this point: OXP2, OCP2, AEP2, P2MX

F. *Most posterior point on the palate in the median plane*

This is straightforward when the suture between the palatine bones is tight or fused. If there is a cleft between the two bones, the point must be imagined as lying on the plane tangent to the posteromost medial points of both sides.

Measurements to this point: MGPL, PALL,

G. *Most lateral point on the mandibular condylar articular surface*

As with the articular eminence, texture and hue usually distinguish it from the surrounding bone. It is usually at or just medial to the most lateral point of bone.

Measurements to this point: CNCN, MCNL, CNP2, CNM3

H. *Anterior margin of the mandibular ramus in the occlusal plane of the tooth row*

This point is constructed by placing the broad part of V.c on the mandibular teeth such that the narrower section passes along the lateral surface of the mandibular ramus and the indented edge abuts the anterior margin of the ramus. The inferior surface of the plastic is used to mark the point.

Measurements to this point: RAMD

I. (Note: "I" is omitted as a landmark identifier to avoid confusion with the Roman numeral I above, indicating an instrument type).

J. *Posterior margin of the mandibular ramus in the plane of the tooth row*

Position V.c as for H. With the projecting flange against the ramus, mark the posterior margin of the ramus in the plane of the inferior surface of the flange.

Measurements to this point: RAMD

K. *Most posterolateral point on the grinding surface of the lower third molar*

When the posterior loph is worn, its most posterior point is easily identified. In the unworn tooth, the grinding surface is considered to be the ridge of the loph.

Measurements to this point: OXM3

L. *Most superior point on the coronoid process*

From the side, mark the top of the arc of the superior surface of the coronoid process. If the coronoid process is flattened superiorly, the point is considered to lie midway along the superiormost extent.

Measurements to this point: CPCP, CPP2 , CPM3 , CPRH

M. *Anterior limit of the temporal line*

The temporal line may be distinguished as a ridge or line separating the relatively smooth bone of the temporal fossa from the rougher bone of the dorsal skull surface. Anteriorly, the line ends above and behind the orbit. Posteriorly, the line turns laterally and may grade into the rugosity of the nuchal ridge. Some judgement is therefore required to determine the exact points. Measure using I.b. In *Diceros bicornis*, the temporal line intersects a second ridge coursing anterosuperiorly from the optic and mandibular foraminae. The intersection is the marked point in this case.

Measurements to this point: TFLN

N. *Posterior limit of the temporal fossa*

As the temporal line courses posteriorly (see M), it eventually arches laterally along the occipital margin. Judging the most posterior point of this arch requires care, and it may be more lateral or more medial depending on the species.

Measurements to this point: TFLN

O. *Intersection of the alveolar margin with the plane passing through the anterior margin of the orbit and perpendicular to the tooth row*

Use V.a to approximate the plane and its orientation.

Measurements to this point: TFHT, LFHT

P. *Most anterior point on the maxillary bones*

Where functional incisors are absent, this point is on a projection of bone. Care must be taken to assess any breakage. In species with incisors, the point is located sagittally between first incisors.

Measurements to this point: P2MX, ORMX

Q. *Most posterior point on the alveolar margin of the third upper molar*

Measurements to this point: OXM3, M3M3, MXGT, MXMO

R. *Most posterior point on the occlusal surface of the most posterior molar*

Measurements to this point: CNM3, CPM3, BIM3, MNGT, MNMO

S. *Most anterior extent of the attachment of the masseter to the zygomatic arch*

The inferior margin of the zygomatic arch is marked by ridges and/or rugosities. The point is marked where these appear to end at or near the maxillary root of the arch.

Measurements to this point: ZYLN

T. *Point on the inferior margin of the mandible in the plane passing through the mandibular notch and perpendicular to the plane of the tooth row*

Measurements to this point: RAMH

MEASUREMENT DESCRIPTIONS

The following descriptions are grouped by skull and mandible. Within each group, measurements are listed alphabetically.

Skull

AEAE - *Biarticular eminence breadth.* Distance between the most lateral points of the articular eminences (C to C).

AEOR - *Articular eminence to orbit.* C to D using I.

AEP2 - *Articular eminence to second upper premolar* Most lateral point of the TMJ articular surface to most posterior margin of P2.

BICN - *Bicondylar breadth.* Horizontal distance between the most lateral points on the occipital condyles using I.a.

BIOR - *Biorbital breadth.* D to D using III. The orientation of the caliper is not important as long as the tips are in the sagittal planes through the points. If lacrimal processes prevent placement of the tips directly on the points, position the tips by eye so that a line along the caliper jaw projects through the point.

BIPG - *Bipostglenoid breadth.* Inside distance between the postglenoid processes measured at their bases.

BIZY - *Outer bizygomatic breadth.* Distance between the most lateral points of the zygomatic arches. Place jaw of III vertically against the arch and close against the corresponding point on the opposite side.

BNAS - *Binasal breadth.* Nasal breadth measured at an estimated point 50% of the distance between the most posterior point of the nasal incision and the midline in the plane of the nasal tips.

CNLN - *Occipital condyle length.* Place I.a against the most medial margin of the condyle and close down against the most lateral margin of the condyle. This measurement should be approximately parallel to the long axis of the condyle.

CNPG - *Condyle to postglenoid process.* Distance between the occipital condyles and the postglenoid processes. Place III against the posterior surfaces of the occipital condyles and close down against the processes anteriorly.

ENDO - *Endocranial length.* Endocranial length measured from the superior margin of the foramen magnum (as defined for FOMH) in the median plane to either side of the cribriform plate using IV.a.

EXNA - *External nasal aperture breadth.* Outside diameter of the anterior nasal aperture measured at its most lateral points when viewed anteriorly. Pace I.a against the lateral side of the nasal wall and close the opposite jaw against the analogous point on the opposite side of the skull.

FHM1 - *Face height including upper first molar.* Distance from the lateral occlusal margin of te first upper molar to the dorsal midline of the cranium in a plane passing through **D**.

FOMH - *Foramen magnum height.* Foramen magnum height from the superior to inferior margins using II.b. Place a jaw against the table of bone forming the floor of the foramen and spread the other jaw to the superior margin. The superior margin often includes irregular bony outgrowths or a vertical slit in the midline. In either case, the "upper margin" is obtained by estimating a smoothly extrapolated curvature based on the remaining margin of the foramen. Smaller specimens may require the use of II.b.
FOMW - *Foramen magnum width.* Distance between the most lateral margins of the foramen magnum. Use the jaws of III (either end) as inside calipers. True distance is the reading plus 20.0 mm to correct for the width of the caliper jaws (as in ZYZY). Smaller specimens may require the use of II.b.

INFH - *Infraorbital foramen height.* Vertical height of the infraorbital foramen. Using I.a, make a judgement as to the boundary of the foramen and measure in the most convenient orientation of the caliper.

INFW - *Infraorbital foramen width.* Horizontal width of the infraorbital foramen. Measured as for INFH but in the horizontal plane.

LFHT - *Lower face height.* **D** to **O** using I.b.
LOXB - *Lower occipital breadth.* Breadth of the occiput in the horizontal plane passing through the superior margin of the occipital condyles.

MGAE - *Foramen magnum to articular eminence.* Posterior margin of the basiocciput to the lateral articular eminence.

MGPL - *Foramen magnum to palate.* Distance from **B** to the posterior margin of the hard palate in the median plane. Place a jaw of I.a at **B** and the other jaw tip at the posterior median point of the palate.

MOXB - *Middle occipital breadth.* Distance between lateral occipital margins at a level between LOXB and UOXB and measured in two ways depending on the nature of the occipital region: (a) where the occiput is concave, the minimum distance is measured, (b) where it is straight or convex, the distance is measured in an estimated plane 50% of the distance between **A** and LOXB.

MXGT - *Maxillary grinding tooth row length.* Distance from the most anterior point of P2 to the most posterior point of M3 along the grinding surface.

MXMO - *Maxillary molar tooth row length.* Distance from the most anterior point of M1 to the most posterior point of M3 along the grinding surface.

M1M1 - *Breadth across upper first molars.* Distance across across the first upper molars measured between the buccal crown surfaces at their most lateral points inferior to the alveolar margin. Place tip or edge of I.a against one tooth and close against opposite tooth such that comparable parts of the jaws are in contact with the tooth. If the teeth are loose, they must be stabilised (with the free hand) in the position which is judged most natural.

M3M3 - *Breadth across upper third molars.* Outside diameter across the third upper molars measured at the distal root. Place I.a with tip in the plane of the alveolar margin and side vertical against most lateral surface of tooth. With calipers horizontal, close jaw against opposite tooth. If the teeth are loose, they must be stabilised (with the free hand) in the position which seems most natural.

OCP2 - *Occipital condyle to second upper premolar.* Occipital condyle to **D**. Hold jaw of III against the posterior surface of the occipital condyle. Spread second jaw point to **D** of same side.

ORMX - *Orbit to maxillary tip.* **D** to the midline in the plane of the most anterior projection of the maxillary/premaxillary bones.

ORNA - *Orbit to nasal incision.* Most posterior point on the margin of nasal incision to **D**. Place jaw of I.a against the margin of the incision and the other jaw tip at the indicated point.

ORTP - *Orbit to nasal tips.* **D** to the midline in the vertical plane of the nasal tips using V.a.

OXAE - *Occiput to articular eminence.* **A** to **C** using I.a.

OXLE - *Occipital length.* Distance from **A** to **B** using I.b.

OXM3 - *Occiput to third upper molar.* **A** to **Q** using I.b.

OXOR - *Occiput to anterior orbital margin* **A** to **D** using III.

OXP2 - *Occiput to second upper premolar.* **A** to **D**. From the side of the skull, place the tips of III at the indicated points. In cases where both points cannot be seen at the same time, it must be decided which point is most easily held in place while out of view.

OXTO - *Total occipital height.* Total vertical length of the occipital region measured from the external surface of the inferior margin of the foramen magnum to **A**.

OXTP - *Occiput to nasal tips.* Plane of the most anterior points of the nasal bones to **A**. Place V.b across nasal tips to define plane. Place a jaw of III. against the plate in the midline and close opposite jaw point to **A**. This method does not account for distances between the nasal tips or presence or absence of bone in the midline posterior to the tips.

PALD - *Palate depth.* Depth of the palate measured across the first molar. Place V.a across the first molars. Measure anteriorly from the plate to the midline of the palate with II.c.

PGLH - *Postglenoid process height.* Place V.a (1") horizontally across the tip of the postglenoid process. Use II.c to measure vertically from the plate to the bone at the base of the process. Correct for thickness of the plastic.

PLOR - *Palate to orbit.* Posterior margin of the palate in the median plane (F) to the most anterior point on the margin of the orbit (D).

PLP2 - *Palate to second upper premolar.* Posterior margin of the palate in the median plane to the anterolateral margin of the alveolus of the second upper premolar.

PORB - *Postorbital constriction width.* Distance across the narrowest constriction of the cranium posterior to the orbits and medial to the zygomatic archs. Judging from directly above, place one jaw of III vertically against one side at the narrowest point and close opposite jaw against corresponding surface on the opposite side.

P1LE - *First upper premolar length.* Length of the upper first premolar measured with I.b. from the anterior to posterior margins along the midtoothrow axis.

P2MX - *Second upper premolar to maxillary tip.* Anterolateral margin of the second upper premolar to the midline in the plane passing through the tips of the (pre)maxillary bones.

P2P2 - *Breadth across second upper premolars.* Outside diameter across the second upper premolars measured beween the most lateral partat the distal root. Place I.a with tip in the plane of the alveolar margin and side vertical against most lateral surface of tooth. With calipers horizontal, close jaw against opposite tooth. If the teeth are loose, they must be stabilised (with the free hand) in the position which seems most natural.

TERB - *Biterygoid process breadth.* Breadth of the pterygoid processes measured between their most lateral points. Place a jaw of I.a against the most lateral point of one process and close down the other jaw on the corresponding opposite point.

TERH - *Pterygoid process height.* Vertical height of the pterygoid processes. Place V.a (1") across the inferior limits of the pterygoid processes and balance perpendicular to the processes. At the posterior edge of the plate in the midline, use II.c to measure the distance to the bone.

TFHT - *Total face height.* Distance from **O** to the midline dorsally in the plane passing through the anterior margin of the orbit and perpendicular to the tooth row.

TFLN - *Temporal fossa length.* **M** to **N** using I.a or III.

TFOS - *Temporal fossa opening.* Distance across the temporal fossa, approximately anteroposteriorly, where the fossa opens inferiorly. Place the jaws of III through the fossa and spread to the widest points, making sure that comparable parts of the jaws are touching bone.

UFHT - *Upper face height.* Distance from **D** to the dorsal median surface in the plane passing through **D** and **O**.

UM1L - *Maxillary first molar length.* Length of the first upper molar measured across the greatest extent of the buccal surface.

UM1W - *Maxillary first molar breadth.* Width of the first upper molar measured between roots as close as possible to both alveolar margins.

UOXB - *Upper occipital breadth.* Breadth of the occiput superiorly either: (a) where the nuchal ridge ends and the margin turns anteriorly or inferiorly, or (b) where the margin has a maximum distinguished from the minimum in MOXB

ZYHT - *Zygomatic height.* Measure vertically in the plane passing through **AE** and approximately parallel to the external surface of the arch.

ZYLN - *Zygomatic process length.* Masseter attachment along the length of the zygomatic arch measured from **C** to **S**.

ZYZY - *Inner bizygomatic breadth.* Distance between the medial sides of the zygomatic arches in the coronal plane that passes through the most lateral points on the medial sides of the arches. Using III as an inside caliper, place one jaw against the internal surface of the zygomatic arch where the internal surface is farthest from the sagittal plane. The true distance equals the reading plus 20.0 mm to correct for the width of the jaws.

Mandible

ANGD - *Mandibular angle depth.* Distance across the lateral surface of the mandibular angle measured from H to a point approximately 50% of the distance along the arc between J and T.

ANGW - *Mandibular angle width.* Mediolateral width of the mandibular ramus measured at a point 50% of the distance along the arc between J and T. With I.a, grip the mandible at and gently rock until minimum distance is attained.

BDM1 - *Mandibular body plus first molar height.* Distance from the lateral upper edge of the first molar crown to the inferior margin of the body in the plane between the roots of M1 and perpendicular to the tooth row (as for BDHT).

BDHT - *Mandibular body height.* Vertical depth of the mandibular body measured from the margin of the alveolus between the roots of M1 perpendicular to the tooth row and body along the external surface. Place VI against mandible inferior to the first molar. Place I.a tip at alveolar margin and close opposite jaw against plastic.

BDBR - *Mandibular body breadth.* Mediolateral width of the mandibular body in the plane through the roots of M1. Place I.a vertically against the body then close down jaw against opposite surface.

BIM3 - *Breadth across third lower molars.* R to R using II.

BIM1 - *Breadth across first lower molars.* Distance across the first lower molars measured between the buccal crown surfaces at their most lateral points above the alveolar margins.

BIP2 - *Breadth across seond lower premolar.* Distance across both tooth rows at the level of the second lower premolar mesaured from D to D using I.a.

CNP2 - *Condyle to second lower premolar.* Most lateral point of the occipital condyle to the most anterior point of P2 at the grinding surface.

CPCP - *Bicoronoid process breadth.* Distance between the the most superior points of the coronoid processes (L to L) using I.b.

CPP2 - *Coronoid process to second lower premolar.* Superiormost point of the coronoid process to the most anterior point of the second lower premolar at the grinding surface.

CNCN - *Mandibular bicondyle breadth.* Distance between the most lateral points of the articular surfaces of the mandibular condyles (G to G). Position opposite jaw points of I.a at the marked points indicated.

CNM3 - *Condyle to third lower molar.* G to K using I.b.

CPM3 - *Coronoid process to third lower molar.* Most superior point on the coronoid process (L) to the most posterior point of M3 (K) at the grinding surface. If the top of the coronoid process appears flattened then take the midpoint.

CPRH - *Coronoid process height.* From a tangent plane passing through the inferiormost part of the mandibular notch and parallel to the tooth row to L. Place a jaw of I.a adjacent to the lateral side of the ramus in the appropriate plane of the notch, then close down the opposite jaw to the top of the process. This measurement is usually slightly off vertical.

LEP1 - *First lower premolar length.* Length of the first lower premolar measured at the grinding surface along the axis of the tooth row using I.b.

MCNL - *Mandibular condyle length.* Length of the mandibular condylar articular surface measured from the most medial point to G. The discussion of G above also applies to the most medial point.

MNGT - *Mandibular grinding tooth row length.* Distance from the most anterior point of P2 at the grinding surface to the most posterior point of M3 along the grinding surface perpendicular to the tooth row.

MNMO - *Mandibular molar tooth row length.* Distance from the most anterior point of M1 to the most posterior point of M3 along the grinding surface perpendicular to the tooth row.

LM1L - *Lower first molar length.* Length of the first lower molar at the grinding surface. Place the tip of II.b across the most anterior point of the tooth surface with the jaw perpendicular to the tooth row. Close down the opposite jaw to the tooth or an analogous plane.

LM1W - *Lower first molar width.* Mediolateral width of M1 perpendicular to the tooth row measured across the middle of the distal root. Place the tip of I.a at the alveolar margin midway between the posterior margin and the tooth constriction. With the first jaw vertical, close the second jaw against the lateral surface of the tooth.

P2TP - *Second lower premolar to nasal tip.* Distance from the anterior margin of the occlusal surface of the second lower premolar to the anterior limit of the mandibular symphysis in the midsaggital plane. Use I.a.

RAMD - *Mandibular ramus depth.* Distance from **G** to **T** using I.a.

RAMH - *Mandibular ramus height.* Distance from the inferiormost point of the mandibular notch to the inferior margin of the mandible, perpendicular to the plane of the tooth row.

SYML - *Mandibular symphysis length.* Greatest length of the mandibular symphysis in the median plane. Place tip I.a against the most anterior limit then close opposite jaw against posterior limit such that corresponding parts of the caliper jaws are touching bone. May measured from above or below.

SYMW - *Mandibular symphysis depth.* Maximum thickness of the mandibular symphysis in the median plane measured from the posterior aspect. From below and between the bodies, place I.a against internal (superior) surface of symphysis and close opposite jaw against external (inferior surface) surface. Some rugosity of the lower surface may be included but any distinct ridge or other boney exensions not directly contributing to the connection of the mandibular bodies should be excluded.

APPENDIX 4.

RAW DATA

Raw data for specimens used in analyses. Skulls (N=184) are listed first, followed by mandibles (N=187). Genera and specimens are listed in the same order as in Tables 2 (skull) and 3 (mandible). Skull data is presented in two parts: AEAE - MXGT and MXMO - ZYLN. Estimated measurements are indicated by brackets (). All measurements are in millimeters.

SKULL (AEAE - MXGT)

ID	GENUS	SUBGEN	AEAE	AEOR	AEP2	BICN	BIZY	LFHT	LOXB	M1M1	M3M3	MGAE	MXGT
CERA 22	CERA	CERAS	332	250	455	151	332	125	226	211	138	229	280
CERA 59	CERA	CERAS	331	235	449	151	334	123	239	218	134	229	279
CERA 99	CERA	CERAS	361	234	453	152	363	139	216	210	146	257	279
CERA 101	CERA	CERAS	344	247	451	154	357	130	267	224	144	239	287
CERA 102	CERA	CERAS	309	211	431	136	317	125	228	201	136	215	260
CERA 103	CERA	CERAS	337	251	454	145	360	126	242	210	134	236	263
CERA 104	CERA	CERAS	340	242	448	150	358	151	241	201	132	244	263
CERA 141	CERA	CERAS	349	242	451	147	342	132	245	220	144	234	265
CERA 142	CERA	CERAS	342	244	460	154	345	163	257	205	124	240	275
CERA 298	CERA	CERAS	330	258	451	154	334	146	255	207	135	233	251

ID	GENUS	SUBGEN	AEAE	AEOR	AEP2	BICN	BIZY	LFHT	LOXB	M1M1	M3M3	MGAE	MXGT
CERA 360	CERA	CERAS	326	242	439	152	325	130	238	203	130	221	269
CERA 366	CERA	CERAS	318	250	457	139	318	138	239	214	134	226	256
CERA 367	CERA	CERAS	323	245	445	142	322	129	258	203	140	236	262
CERA 368	CERA	CERAS	338	262	455	142	338	139	246	205	136	226	270
CERA 369	CERA	CERAS	320	241	435	136	318	128	242	197	129	221	262
CERA 370	CERA	CERAS	343	265	453	147	341	125	259	219	139	241	275
CERA 371	CERA	CERAS	335	239	433	134	335	126	235	214	130	228	257
CERA 372	CERA	CERAS	372	264	444	143	375	145	255	201	145	255	251
CERA 431	CERA	CERAS	336	255	443	145	340	138	248	207	140	242	272
SUMA 21	SUMA	SUMAS	284	185	304	97	310	96	198	178	111	169	187
SUMA 46	SUMA	SUMAS	142	186	300	123	300	86	194	171	115	171	204
BICO 147	BICO	BICOS	335	222	384	138	340	100	227	206	138	228	255
BICO 149	BICO	BICOS	316	244	377	135	332	91	229	193	122	209	249
BICO 150	BICO	BICOS	310	223	374	128	326	97	225	192	121	197	231
BICO 151	BICO	BICOS	317	232	374	149	322	91	255	196	119	210	272
BICO 152	BICO	BICOS	328	238	382	132	336	80	238	198	133	216	249
BICO 155	BICO	BICOS	289	212	356	131	310	73	215	186	115	182	245
BICO 157	BICO	BICOS	347	248	408	152	358	95	249	199	126	221	251
BICO 161	BICO	BICOS	331	230	380	125	340	92	232	203	121	222	246
BICO 166	BICO	BICOS	313	237	386	132	324	95	243	192	135	202	236
BICO 167	BICO	BICOS	327	233	382	126	338	95	242	202	123	215	265
BICO 168	BICO	BICOS	325	245	399	137	345	97	237	188	135	223	243
BICO 169	BICO	BICOS	311	232	368	133	328	184	215	179	129	195	241
BICO 170	BICO	BICOS	314	223	376	134	334	89	236	200	129	217	250
BICO 174	BICO	BICOS	330	233	379	137	343	100	252	208	132	208	259
BICO 176	BICO	BICOS	317	248	375	126	327	97	237	203	117	205	259

ID	GENUS	SUBGEN	AEAE	AEOR	AEP2	BICN	BIZY	LFHT	LOXB	M1M1	M3M3	MGAE	MKGT
BICO 177	BICO	BICOS	321	245	382	128	332	89	237	203	125	215	263
BICO 178	BICO	BICOS	310	215	357	111	323	92	212	178	125	201	234
BICO 181	BICO	BICOS	318	226	363	124	330	87	233	187	124	208	239
BICO 295	BICO	BICOS	305	216	353	123	312	77	217	184	116	195	238
BICO 305	BICO	BICOS	338	241	387	125	348	83	231	198	127	213	263
BICO 379	BICO	BICOS	310	226	354	128	323	80	224	197	120	213	241
BICO 382	BICO	BICOS	320	247	382	130	346	99	246	210	132	212	244
BICO 384	BICO	BICOS	324	231	389	141	346	96	239	211	138	217	260
BICO 386	BICO	BICOS	314	242	369	151	340	89	238	197	135	209	235
BICO 387	BICO	BICOS	313	252	383	138	329	94	264	203	121	212	273
BICO 388	BICO	BICOS	332	224	384	149	342	100	242	191	137	214	239
BICO 389	BICO	BICOS	297	237	398	132	317	104	228	192	144	211	246
BICO 390	BICO	BICOS	318	219	383	131	334	96	241	197	123	220	253
BICO 393	BICO	BICOS	341	249	391	152	356	100	254	200	133	223	250
BICO 394	BICO	BICOS	324	235	383	133	337	87	251	209	121	214	259
BICO 395	BICO	BICOS	318	231	383	139	339	102	233	214	128	213	263
BICO 396	BICO	BICOS	324	237	405	144	357	90	240	208	123	216	270
BICO 397	BICO	BICOS	317	239	387	142	334	90	229	210	118	212	272
BICO 398	BICO	BICOS	310	223	362	133	325	78	220	193	114	209	258
BICO 402	BICO	BICOS	316	229	356	132	331	90	220	195	135	206	241
BICO 404	BICO	BICOS	324	244	377	133	331	85	222	199	130	215	252
BICO 405	BICO	BICOS	299	243	370	138	313	91	222	200	111	198	258
BICO 407	BICO	BICOS	308	210	330	124	325	98	215	183	120	202	222
BICO 408	BICO	BICOS	317	227	377	131	327	87	230	194	116	205	245
BICO 409	BICO	BICOS	306	218	360	135	317	86	217	179	113	202	236
BICO 410	BICO	BICOS	312	224	356	134	321	85	221	195	120	197	256
BICO 411	BICO	BICOS	299	217	351	134	310	90	218	177	137	198	226
BICO 412	BICO	BICOS	308	217	361	139	324	78	213	192	132	202	241

ID	GENUS	SUBGEN	AEAE	AEOR	AEP2	BICN	B12Y	LFHT	LOXB	M1M1	M3M3	MGAE	MXGT
BICO 414	BICO	BICOS	316	237	376	131	321	96	221	184	124	209	237
BICO 418	BICO	BICOS	313	237	370	128	345	85	232	193	126	205	242
BICO 436	BICO	BICOS	298	225	359	129	305	87	226	182	114	198	239
BICO 437	BICO	BICOS	315	226	366	128	331	87	229	199	120	207	259
BICO 441	BICO	BICOS	317	234	372	126	341	91	234	197	121	206	247
UNIC 48	UNJA	UNICS	342	265	380	136	356	98	273	215	142	217	260
UNIC 53	UNJA	UNICS	328	239	365	141	347	109	270	204	127	226	257
UNIC 55	UNJA	UNICS	347	247	380	135	372	91	286	222	146	221	262
UNIC 303	UNJA	UNICS	370	251	376	147	377	117	287	220	115	240	264
UNIC 348	UNJA	UNICS	365	268	409	137	372	126	296	224	146	231	255
UNIC 426	UNJA	UNICS	343	256	379	138	359	102	286	215	152	216	234
UNIC 427	UNJA	UNICS	351	267	381	138	360	110	272	227	143	217	253
UNIC 430	UNJA	UNICS	352	249	386	142	370	114	227	224	127	228	261
JAVA 17	UNJA	JAVAS	332	236	327	136	344	69	298	193	112	204	231
JAVA 18	UNJA	JAVAS	319	234	317	125	331	77	285	190	110	188	221
JAVA 299	UNJA	JAVAS	332	242	319	151	346	65	278	197	110	215	223
JAVA 351	UNJA	JAVAS	328	248	323	143	338	61	282	(191)	114	206	220
ACER 245	ACER	ACER1S	290	232	352	114	293	73	226	(186)	102	210	239
ACER 124	ACER	ACER2S	365	196	342	130	357	121	258	206	129	268	245
AMYN 111	AMYN	AMYNS	194	123	228	85	130	48	102	123	96	148	154
AMYN 461	AMYN	AMYNS	195	130	221	84	205	53	100	107	82	138	140

ID	GENUS	SUBGEN	AEAE	AEOR	AEP2	BICN	BIZY	LFHT	LOXB	M1M1	M3M3	MGAE	MKGT
APHE 205	APHE	APHE1S	262	169	286	96	236	86	140	119	91	165	192
APHE 268	APHE	APHE2S	315	194	345	135	325	85	235	180	128	196	226
APHE 269	APHE	APHE2S	292	210	350	123	295	95	216	179	113	178	273
APHE 270	APHE	APHE2S	294	209	356	126	299	80	202	180	124	185	226
APHE 271	APHE	APHE2S	327	217	365	137	336	76	227	184	147	196	240
APHE 272	APHE	APHE2S	310	194	337	122	306	71	208	164	107	171	217
APHE 330	APHE	APHE2S	325	216	377	134	327	107	241	172	124	192	219
APHE 334	APHE	APHE2S	297	213	379	127	300	92	212	186	118	180	245
APHE 335	APHE	APHE2S	283	188	330	124	288	75	194	186	115	183	243
DICE 239	DICE	DICE1S	213	162	243	80	236	45	122	142	87	154	169
DICE 203	DICE	DICE1S	194	167	241	84	(226)	42	122	128	83	132	166
DICE 204	DICE	DICE1S	207	168	259	93	229	55	127	141	74	138	195
DICE 266	DICE	DICE2S	214	181	268	95	226	65	125	130	87	154	182
DICE 240	DICE	DICE3S	243	208	317	118	247	54	149	130	89	174	217
DICE 267	DICE	DICE3S	271	195	320	112	285	61	158	159	117	164	204
FORS 127	FORS	FORSS	230	160	275	84	249	47	133	138	102	156	165
FORS 130	FORS	FORSS	236	135	255	76	(236)	65	104	127	81	132	157
HYRA 4	HYRA	HYRA1S	111	88	139	48	122	31	67	78	59	75	83
HYRA 5	HYRA	HYRA1S	73	76	123	38	86	27	55	54	35	46	72
HYRA 10	HYRA	HYRA2S	126	103	168	51	133	35	71	98	62	90	106
HYRA 6	HYRA	HYRA2S	162	112	184	58	179	32	90	110	76	106	116
HYRA 12	HYRA	HYRA2S	112	116	167	46	82	39	67	75	49	74	92

ID	GENUS	SUBGEN	AEAE	AEOR	AEP2	BICH	BIZY	LFHT	LOXB	M1M1	M3M3	MGAE	MKGT
HYCO 116	HYCO	HYCOS	130	95	151	52	135	33	82	82	55	101	104
HYCO 117	HYCO	HYCOS	107	88	151	49	128	38	66	90	42	83	109
HYCO 120	HYCO	HYCOS	108	98	160	48	115	45	71	86	52	93	113
HYCO 460	HYCO	HYCOS	115	88	141	46	125	38	71	89	51	88	101
INDR 258	INDR	INDRS	570	374	632	309	588	145	358	279	214	498	376
MENO 171	MENO	MENOS	208	164	257	79	240	44	143	130	89	129	175
MENO 195	MENO	MENOS	171	147	228	71	175	41	109	111	58	116	159
MENO 196	MENO	MENOS	156	139	221	70	161	42	113	117	59	104	156
MENO 197	MENO	MENOS	181	135	228	70	186	42	131	111	69	115	147
MENO 198	MENO	MENOS	165	129	214	71	206	50	131	110	60	121	156
MENO 200	MENO	MENOS	160	129	212	65	162	47	103	104	61	113	154
MENO 201	MENO	MENOS	178	147	236	74	182	55	116	102	61	114	163
MENO 453	MENO	MENOS	177	129	254	78	213	51	126	129	87	128	160
MENO 454	MENO	MENOS	201	142	236	84	238	46	138	122	77	119	156
MENO 456	MENO	MENOS	180	144	232	73	184	43	116	123	79	121	156
MENO 457	MENO	MENOS	192	133	241	81	198	41	(127)	128	81	120	167
MENO 452	MENO	MENOS	180	135	217	74	189	(39)	113	121	62	111	168
MENO 143	MENO	MENOS	188	145	231	78	231	47	129	117	74	121	152
MENO 158	MENO	MENOS	198	152	243	80	200	56	129	128	70	119	163
MENO 172	MENO	MENOS	168	153	236	65	170	49	109	105	50	113	164
MENO 186	MENO	MENOS	191	146	230	76	203	48	122	102	66	134	160
MENO 187	MENO	MENOS	198	160	251	84	227	49	130	118	72	124	171
MENO 188	MENO	MENOS	(181)	157	236	70	194	51	114	106	52	117	166

ID	GENUS	SUBGEN	AEAE	AEOR	AEP2	BICN	BIZY	LFNT	LONB	M1M1	M3M3	MGAE	MXGT
PERA 324	PERA	PERA1S	226	178	[289]	85	237	63	142	[148]	94	140	182
PERA 276	PERA	PERA1S	280	186	305	90	253	79	176	156	98	165	208
PERA 326	PERA	PERA2S	345	210	352	140	359	85	239	209	152	225	263
PERA 327	PERA	PERA2S	405	258	399	151	429	96	268	260	153	234	272
PERA 329	PERA	PERA2S	387	250	417	162	412	91	279	236	140	238	287
SUBH 28	SUBH	SUBH1S	191	152	242	72	196	50	115	[117]	[75]	130	163
SUBH 29	SUBH	SUBH1S	170	145	238	72	176	57	101	105	75	126	146
SUBH 31	SUBH	SUBH1S	196	160	242	77	219	56	125	129	81	135	178
SUBH 27	SUBH	SUBH1S	188	136	217	73	197	39	116	112	76	137	143
SUBH 32	SUBH	SUBH1S	189	152	256	76	200	70	112	131	89	137	170
SUBH 38	SUBH	SUBH2S	195	146	247	80	200	64	116	116	85	[140]	163
SUBH 64	SUBH	SUBH2S	221	154	252	94	235	75	141	130	93	164	169
SUOH 35	SUBH	SUBH2S	208	158	257	95	220	69	130	146	92	138	176
SUBH 63	SUBH	SUBH2S	190	162	264	86	197	56	122	106	61	140	186
SUBH 228	SUBH	SUBH3S	239	189	271	105	280	37	161	140	102	166	177
SUBH 229	SUBH	SUBH3S	235	176	295	96	264	56	152	124	83	141	182
SUBH 231	SUBH	SUBH3S	232	173	271	110	269	55	145	151	107	160	192
SUBH 233	SUBH	SUBH3S	225	167	265	96	263	44	147	140	102	133	156
SUBH 236	SUBH	SUBH3S	246	165	281	99	257	60	155	144	107	156	180
SUBH 278	SUBH	SUBH3S	227	175	270	102	237	52	139	146	95	154	188
SUBH 458	SUBH	SUBH3S	244	170	278	95	260	[62]	143	131	99	162	192

ID	GENUS	SUBGEN	AEAE	AEOR	AEP2	BICN	BIZY	LFNT	LDNB	M1M1	M3M3	MGAE	MXGT
TELE 341	TELE	TELE1S	281	232	328	124	320	70	198	181	102	163	225
TELE 342	TELE	TELE1S	288	221	325	99	306	59	211	178	(98)	161	230
TELE 317	TELE	TELE2S	333	241	351	132	360	93	231	185	123	207	245
TELE 318	TELE	TELE2S	318	276	365	108	355	78	227	186	107	192	254
TELE 344	TELE	TELE2S	347	259	374	134	386	94	289	181	118	207	237
TELE 255	TELE	TELE2S	308	263	372	127	319	68	237	163	115	180	250
TELE 311	TELE	TELE3S	296	248	361	111	305	111	206	173	122	192	233
TELE 312	TELE	TELE3S	318	251	(369)	123	331	99	216	183	127	190	200
TELE 313	TELE	TELE3S	307	230	355	124	310	98	216	94	(112)	196	160
TELE 314	TELE	TELE3S	312	244	351	131	323	80	237	173	101	187	227
TELE 315	TELE	TELE3S	300	268	394	130	323	87	228	194	130	170	253
TELE 316	TELE	TELE3S	273	251	376	113	265	101	198	149	91	161	231
TELE 281	TELE	TELE4S	294	268	397	132	305	126	224	170	84	168	258
TELE 496	TELE	TELE4S	319	256	412	141	340	108	236	213	125	190	270
TELE 497	TELE	TELE4S	332	270	420	128	352	113	234	208	128	190	256
TELE 284	TELE	TELE5S	335	294	428	142	374	115	[257]	195	128	205	260
TELE 287	TELE	TELE5S	343	265	416	136	347	90	227	198	117	196	[267]
TELE 291	TELE	TELE5S	370	281	420	145	372	105	283	205	133	224	280
TELE 424	TELE	TELE5S	298	246	356	113	314	93	(221)	192	(119)	175	269

ID	GENUS	SUBGEN	AEAE	AEOR	AEPZ	BICN	BIZY	LFHT	LOXB	M1M1	M3M3	MGAE	MXGT
TRIG 462	TRIG	TRIGS	210	164	254	87	227	54	128	132	86	148	187
TRIG 422	TRIG	TRIGS	208	162	265	78	228	53	121	149	82	168	194
TRIG 463	TRIG	TRIGS	172	140	232	72	177	64	147	105	74	130	159
TRIG 468	TRIG	TRIGS	212	135	230	89	234	66	136	131	84	158	170
TRIG 469	TRIG	TRIGS	206	175	286	77	217	66	111	126	96	150	184
TRIG 470	TRIG	TRIGS	209	170	261	74	219	65	121	131	73	154	176
TRIG 471	TRIG	TRIGS	201	173	261	73	208	69	105	124	80	137	170
TRIG 472	TRIG	TRIGS	193	175	290	66	205	67	82	118	72	131	177
TRIG 476	TRIG	TRIGS	226	156	262	87	249	41	126	152	93	149	168
TRIG 475	TRIG	TRIGS	231	170	260	86	246	42	120	148	84	160	186
TRIG 492	TRIG	TRIGS	221	162	273	(84)	244	51	129	150	106	148	189
TRIG 490	TRIG	TRIGS	230	167	262	85	260	60	116	141	95	157	168
TRIG 23	TRIG	TRIGS	244	183	281	88	292	59	128	146	108	159	174

SKULL (MXMO - ZYLN)

ID	GENUS	SUBGEN	MXMO	OCP2	OXAE	OXOR	PORB	TFLN	ZYHT	ZYLN
CERA 22	CERA	CERAS	167	628	315	480	109	357	66	286
CERA 59	CERA	CERAS	161	626	330	486	105	343	69	270
CERA 99	CERA	CERAS	172	643	335	492	108	370	69	278
CERA 101	CERA	CERAS	161	632	335	492	112	360	77	278
CERA 102	CERA	CERAS	158	590	301	435	110	315	71	244
CERA 103	CERA	CERAS	162	628	310	470	112	336	73	295
CERA 104	CERA	CERAS	166	643	343	504	110	363	78	288
CERA 141	CERA	CERAS	151	606	343	514	114	363	78	283
CERA 142	CERA	CERAS	180	646	354	520	119	372	62	282
CERA 298	CERA	CERAS	151	638	338	498	116	370	77	301
CERA 360	CERA	CERAS	169	603	303	445	103	329	76	254
CERA 366	CERA	CERAS	157	627	317	479	112	355	58	277
CERA 367	CERA	CERAS	142	634	329	503	115	369	68	295
CERA 368	CERA	CERAS	149	624	310	472	112	347	65	270
CERA 369	CERA	CERAS	147	599	299	439	109	349	65	237
CERA 370	CERA	CERAS	155	644	325	488	121	376	76	292
CERA 371	CERA	CERAS	151	610	321	473	112	359	75	263
CERA 372	CERA	CERAS	158	636	356	516	119	372	79	298
CERA 431	CERA	CERAS	163	632	321	464	112	348	69	257
SUMA 21	SUMA	SUMA	119	400	222	313	115	211	44	179
SUMA 46	SUMA	SUMA	120	414	212	289	116	189	43	169

ID	GENUS	SUBGEN	MKMO	OCP2	OKAE	OKOR	PORB	TFLW	ZYHT	ZYLW
BICO 147	BICO	BICOS	155	550	295	411	122	295	53	220
BICO 149	BICO	BICOS	146	526	264	385	117	282	48	227
BICO 150	BICO	BICOS	145	509	267	384	119	280	51	210
BICO 151	BICO	BICOS	162	514	274	387	118	290	52	211
BICO 152	BICO	BICOS	151	529	274	403	118	280	42	215
BICO 155	BICO	BICOS	143	490	256	347	103	240	48	204
BICO 157	BICO	BICOS	148	555	301	435	124	306	57	226
BICO 161	BICO	BICOS	151	536	299	339	140	289	60	218
BICO 166	BICO	BICOS	144	528	270	417	122	280	49	225
BICO 167	BICO	BICOS	160	520	279	397	122	272	54	242
BICO 168	BICO	BICOS	145	547	299	429	131	312	55	222
BICO 169	BICO	BICOS	147	493	265	391	116	295	49	215
BICO 170	BICO	BICOS	149	522	279	406	120	275	53	212
BICO 174	BICO	BICOS	152	521	279	396	134	273	49	218
BICO 176	BICO	BICOS	154	510	272	395	131	286	50	201
BICO 177	BICO	BICOS	157	528	284	426	122	290	46	231
BICO 178	BICO	BICOS	135	488	259	364	116	272	47	198
BICO 181	BICO	BICOS	142	508	275	383	108	269	48	238
BICO 295	BICO	BICOS	141	482	250	345	110	244	52	207
BICO 305	BICO	BICOS	154	514	279	410	125	296	50	240
BICO 379	BICO	BICOS	148	505	255	367	110	277	51	225
BICO 382	BICO	BICOS	103	532	268	409	127	309	51	234
BICO 384	BICO	BICOS	156	542	286	412	128	299	49	227
BICO 386	BICO	BICOS	141	520	276	415	116	323	45	235
BICO 387	BICO	BICOS	146	530	279	414	120	298	47	226
BICO 388	BICO	BICOS	141	535	286	403	119	277	57	278
BICO 389	BICO	BICOS	149	552	261	395	118	293	46	228
BICO 390	BICO	BICOS	156	542	276	393	112	295	54	262

ID	GENUS	SUBGEN	MKMO	OCP2	BXAE	OXOR	PORB	TFLN	ZYRT	ZYLN
BICO 393	BICO	BICOS	150	545	298	445	123	311	57	239
BICO 394	BICO	BICOS	153	525	275	414	119	270	48	243
BICO 395	BICO	BICOS	165	537	270	447	118	278	48	224
BICB 396	BICO	BICOS	162	560	285	420	125	298	45	229
BICB 397	BICO	BICOS	153	540	282	398	118	281	51	238
BICB 398	BICO	BICOS	154	516	273	338	111	291	42	235
BICO 402	BICO	BICOS	141	501	265	379	115	281	52	211
BICB 404	BICB	BICOS	144	532	268	387	124	270	50	227
BICB 405	BICB	BICBS	152	511	269	403	115	287	45	218
BICO 407	BICO	BICBS	136	474	249	355	110	250	45	192
BICO 408	BICO	BICBS	145	516	271	373	116	269	53	222
BICO 409	BICO	BICOS	146	490	249	369	115	263	50	209
BICO 41B	BICO	BICOS	148	488	255	358	103	273	53	203
BICO 411	BICO	BICOS	136	493	250	365	111	245	45	244
BICO 412	BICB	BICOS	149	505	270	376	123	261	49	227
BICO 414	BICO	BICOS	145	525	275	399	114	277	54	207
BICO 41B	BICB	BICOS	148	510	270	390	111	272	49	211
BICO 436	BICO	BICOS	144	495	257	367	107	265	46	207
BICO 437	BICB	BICOS	151	513	275	396	125	276	45	215
BICO 441	BICO	BICOS	148	513	266	408	117	290	46	206
UNIC 48	UNJA	UNICS	145	512	263	361	111	268	73	232
UNIC 53	UNJA	UNICS	145	508	259	356	100	253	70	225
UNIC 55	UNJA	UNICS	147	517	271	358	110	251	88	226
UNIC 303	UNJA	UNICS	150	519	284	365	116	250	80	236
UNIC 348	UNJA	UNICS	155	556	281	391	120	284	77	257
UNIC 426	UNJA	UNICS	145	518	256	367	112	289	72	237
UNIC 427	UNJA	UNICS	155	517	269	378	126	292	72	242

ID	GENUS	SUBGEN	MXMO	OCP2	OXAE	OXOR	PORB	TFLN	ZYHT	ZYLN
UNIC 430	UNJA	UNICS	147	535	262	358	108	277	67	240
JAVA 17	UNJA	JAVAS	126	456	233	314	121	236	52	193
JAVA 18	UNJA	JAVAS	130	432	229	299	110	205	56	182
JAVA 299	UNJA	JAVAS	131	463	252	319	118	218	54	204
JAVA 351	UNJA	JAVAS	129	461	229	334	114	234	54	207
ACER 245	ACER	ACER1S	145	484	270	394	91	267	67	219
ACER 124	ACER	ACER2S	144	517	294	377	138	277	63	192
AMYN 111	AMYN	AMYNS	112	323	170	281	61	201	34	120
AMYN 461	AMYN	AMYNS	95	328	160	268	63	208	35	121
APHE 205	APHE	APHE1S	115	399	192	291	72	230	52	179
APHE 268	APHE	APHE2S	134	455	250	382	106	263	69	213
APHE 269	APHE	APHE2S	132	469	241	359	110	234	76	215
APHE 270	APHE	APHE2S	135	480	230	341	113	239	71	216
APHE 271	APHE	APHE2S	145	470	235	366	112	259	71	219
APHE 272	APHE	APHE2S	126	438	260	374	107	263	56	204
APHE 330	APHE	APHE2S	125	493	263	383	121	256	67	229
APHE 334	APHE	APHE2S	144	508	241	361	102	251	67	216
APHE 335	APHE	APHE2S	141	445	229	296	94	218	68	184
DICE 239	DICE	BICE1S	99	350	178	294	81	215	36	164
DICE 203	BICE	DICE1S	182	336	164	251	93	181	37	148
DICE 204	DICE	DICE1S	117	358	155	260	91	200	43	147
DICE 266	DICE	DICE2S	187	379	184	297	84	232	49	159

ID	GENUS	SUBGEN	MKMO	OCP2	OXAE	OXOR	PORB	TFLN	ZYHT	ZYLN
DICE 240	DICE	DICE3S	140	451	229	337	101	260	65	186
DICE 267	DICE	DICE3S	129	429	223	373	113	273	51	177
FORS 127	FORS	FORSS	104	388	175	294	116	220	36	149
FORS 138	FORS	FORSS	105	366	187	285	61	217	(39)	142
HYCO 116	HYCO	HYCOS	59	236	140	205	57	156	29	93
HYCO 117	HYCO	HYCOS	63	219	116	186	42	146	34	86
HYCO 120	HYCO	HYCOS	62	240	125	205	40	152	33	94
HYCO 460	HYCO	HYCOS	58	215	110	179	44	145	32	86
HYRA 4	HYRA	HYRA1S	52	190	100	168	48	120	22	91
HYRA 5	HYRA	HYRA1S	44	167	71	131	37	92	(21)	73
HYRA 10	HYRA	HYRA2S	68	232	105	176	49	132	25	108
HYRA 6	HYRA	HYRA2S	73	261	134	205	61	163	25	100
HYRA 12	HYRA	HYRA2S	58	216	86	183	43	140	28	105
INDR 258	INDR	INDRS	232	1025	525	802	194	662	101	371
MENO 171	MENO	MENOS	106	338	149	231	79	175	45	149
MENO 195	MENO	MENOS	90	311	142	219	81	161	44	149
MENO 196	MENO	MENOS	97	306	136	226	65	168	40	139
MENO 197	MENO	MENOS	88	279	138	221	68	160	40	137
MENO 198	MENO	MENOS	97	303	153	197	62	160	51	135
MENO 200	MENO	MENOS	91	294	125	212	69	145	39	129
MENO 201	MENO	MENOS	103	312	116	233	83	146	52	143
MENO 453	MENO	MENOS	97	327	137	230	80	168	54	131
MENO 454	MENO	MENOS	98	313	161	240	82	172	46	132

ID	GENUS	SUBGEN	MXMO	OCP2	OXAE	OXOR	PORB	TFLN	ZYHT	ZYLN
MENO 456	MENO	MENOS	95	319	136	219	77	160	37	141
MENO 457	MENO	MENOS	98	315	145	219	82	159	42	141
MENO 143	MENO	MENOS	92	312	152	225	90	151	42	127
MENO 158	MENO	MENOS	97	323	164	234	80	160	52	126
MENO 172	MENO	MENOS	93	320	(137)	237	63	162	44	141
MENO 186	MENO	MENOS	98	329	146	236	71	144	61	138
MENO 187	MENO	MENOS	101	324	157	214	79	160	55	150
MENO 188	MENO	MENOS	99	324	164	234	68	167	53	138
MENO 452	MENO	MENOS	103	295	131	189	76	148	42	132
PERA 324	PERA	PERA1S	107	355	175	255	70	192	51	168
PERA 276	PERA	PERA1S	132	415	202	280	82	229	61	185
PERA 326	PERA	PERA2S	155	495	250	320	102	216	78	214
PERA 327	PERA	PERA2S	177	531	294	352	125	245	82	250
PERA 329	PERA	PERA2S	164	552	261	361	124	248	76	254
SUOH 28	SUBH	SUBH1S	101	341	160	265	55	201	42	128
SUBH 29	SUBH	SUBH1S	88	336	146	256	56	177	43	135
SUBH 31	SUBH	SUBH1S	103	350	153	258	77	174	46	134
SUBH 27	SUBH	SUBH1S	87	314	151	247	77	172	40	142
SUBH 32	SUBH	SUBH1S	100	357	174	277	65	166	48	139
SUBH 38	SUBH	SUBH2S	95	340	176	280	72	192	44	129
SUBH 64	SUBH	SUBH2S	101	369	184	290	68	215	41	149
SUBH 35	SUBH	SUBH2S	114	354	177	285	72	209	44	136
SUBH 63	SUBH	SUBH2S	110	366	175	287	63	205	53	148
SUBH 228	SUBH	SUBH3S	105	395	281	326	101	227	44	153

ID	GENUS	SUBGEN	MXMO	OCP2	OXAE	OXOR	PORB	TFLN	ZYHT	ZYLN
SUBH 229	SUBH	SUBH3S	116	387	216	336	77	245	61	184
SUBH 231	SUBH	SUBH3S	119	410	208	322	86	226	47	168
SUBH 233	SUBH	SUBH3S	109	344	208	311	88	206	53	158
SUBH 236	SUBH	SUBH3S	118	383	222	348	79	250	59	179
SUBH 278	SUBH	SUBH3S	114	381	185	317	80	229	44	162
SUBH 458	SUBH	SUBH3S	115	395	188	294	86	210	48	165
TELE 341	TELE	TELE1S	138	428	210	306	116	213	76	204
TELE 342	TELE	TELE1S	146	408	205	304	93	217	59	186
TELE 317	TELE	TELE2S	161	459	228	325	89	236	79	178
TELE 318	TELE	TELE2S	170	471	219	342	84	259	79	205
TELE 344	TELE	TELE2S	152	490	247	358	101	247	96	220
TELE 255	TELE	TELE2S	162	505	214	350	89	241	86	229
TELE 311	TELE	TELE3S	147	499	252	344	92	222	76	205
TELE 312	TELE	TELE3S	148	(487)	238	360	86	228	80	219
TELE 313	TELE	TELE3S	(131)	480	227	337	79	236	79	200
TELE 314	TELE	TELE3S	149	483	243	355	87	266	83	206
TELE 315	TELE	TELE3S	168	493	215	338	89	246	73	229
TELE 316	TELE	TELE3S	153	471	209	313	59	254	87	203
TELE 281	TELE	TELE4S	161	519	239	345	69	243	83	235
TELE 496	TELE	TELE4S	177	519	228	382	85	242	74	221
TELE 497	TELE	TELE4S	169	540	241	367	97	256	80	239
TELE 284	TELE	TELE5S	173	558	242	388	102	268	87	268
TELE 287	TELE	TELE5S	179	(546)	242	371	85	267	92	252
TELE 291	TELE	TELE5S	185	562	260	382	106	282	79	254
TELE 424	TELE	TELE5S	184	491	207	331	72	273	73	211

ID	GENUS	SUBGEN	MXMO	OCP2	OMAE	OXOR	PORB	TFLN	ZYHT	ZYLN
TRIG 422	TRIG	TRIGS	125	370	181	298	73	232	56	159
TRIG 462	TRIG	TRIGS	119	371	280	317	69	247	50	140
TRIG 463	TRIG	TRIGS	99	346	160	254	56	195	33	127
TRIG 468	TRIG	TRIGS	114	331	192	262	67	204	65	125
TRIG 469	TRIG	TRIGS	116	413	190	320	77	242	61	169
TRIG 470	TRIG	TRIGS	118	386	192	383	65	221	62	156
TRIG 471	TRIG	TRIGS	118	364	180	305	67	245	65	159
TRIG 472	TRIG	TRIGS	113	338	190	324	64	267	52	164
TRIG 476	TRIG	TRIGS	112	359	175	295	75	211	36	144
TRIG 475	TRIG	TRIGS	121	367	177	296	72	220	37	165
TRIG 492	TRIG	TRIGS	122	376	183	311	81	242	44	143
TRIG 490	TRIG	TRIGS	109	363	253	307	91	226	47	155
TRIG 23	TRIG	TRIGS	109	388	183	386	93	236	44	163

MANDIBLE

ID	GENUS	SUBGEN	ANGD	ANGW	BDBR	BDHT	BDM1	CNM3	LM1L	LM1W	MNMO	RAMD	RAMH
CERA 22	CERA	CERAM	152	54	59	116	149	260	43	30	150	158	224
CERA 59	CERA	CEAAM	147	53	59	121	148	243	47	35	153	159	223
CERA 99	CERA	CERAM	153	64	70	117	152	264	39	30	151	171	251
CERA 101	CERA	CERAM	164	61	64	122	157	281	46	30	148	173	225
CERA 102	CERA	CERAM	141	59	58	109	133	262	29	33	124	164	208
CERA 103	CERA	CERAM	163	52	65	121	157	268	43	29	144	174	240
CERA 104	CERA	CERAM	152	62	68	132	161	256	51	33	139	166	232
CERA 141	CERA	CERAM	165	51	60	119	152	264	46	28	141	169	215
CERA 142	CERA	CERAM	166	60	63	117	154	280	32	33	147	186	211
CERA 297	CERA	CERAM	177	55	60	127	149	298	31	28	138	177	248
CERA 298	CERA	CERAM	168	62	61	120	156	272	35	34	138	178	234
CERA 360	CERA	CERAM	146	55	59	112	144	251	37	29	147	157	218
CERA 366	CERA	CERAM	160	48	62	110	138	265	32	36	140	175	231
CERA 367	CERA	CERAM	162	55	62	112	146	273	44	28	146	182	239
CERA 368	CERA	CERAM	175	42	58	112	141	254	49	28	152	187	222
CERA 369	CERA	CERAM	154	48	55	114	142	249	43	27	138	170	212
CERA 370	CERA	CERAM	164	50	65	119	149	271	47	27	144	184	234
CERA 371	CERA	CERAM	169	54	57	117	146	273	39	30	140	185	230
CERA 431	CERA	CERAM	173	49	61	121	150	258	49	27	152	188	249

ID	GENUS	SUBGEN	ANGD	ANGW	BOBR	BOHT	BOM1	CNM3	LM1L	LM1W	MNMO	RAND	RAMH
SUMA 21	SUMA	SUMAN	113	38	34	63	83	189	40	22	166	166	152
SUMA 46	SUMA	SUMAN	112	37	36	61	134	165	36	21	120	117	166
BICO 147	BICO	BICOM	123	48	52	89	124	185	52	32	155	124	178
BICO 149	BICO	BICOM	140	40	52	87	124	194	50	30	152	142	181
BICO 150	BICO	BICOM	127	43	48	89	116	217	41	26	133	135	177
BICO 151	BICO	BICOM	145	49	51	88	123	207	46	29	143	155	188
BICO 155	BICO	BICOM	111	47	44	79	109	174	48	30	146	116	160
BICO 157	BICO	BICOM	140	47	51	85	120	227	48	28	141	155	202
BICO 161	BICO	BICOM	137	54	59	101	132	204	46	27	147	140	182
BICO 166	BICO	BICOM	130	45	51	83	110	219	41	29	131	143	176
BICO 167	BICO	BICOM	132	48	54	80	116	196	48	31	155	140	180
BICO 168	BICO	BICOM	135	50	54	98	121	225	41	30	135	143	191
BICO 169	BICO	BICOM	130	47	50	84	112	203	43	30	133	127	166
BICO 170	BICO	BICOM	118	47	47	84	119	205	44	26	138	133	182
BICO 174	BICO	BICOM	130	51	52	88	123	195	49	29	148	136	186
BICO 176	BICO	BICOM	135	51	57	89	126	197	46	30	151	139	197
BICO 177	BICO	BICOM	125	48	53	88	121	201	49	29	154	132	183
BICO 178	BICO	BICOM	114	34	57	73	96	197	42	29	135	123	168
BICO 181	BICO	BICOM	126	47	49	75	108	197	45	27	145	134	177
BICO 294	BICO	BICOM	123	48	48	76	110	167	43	21	148	125	180
BICO 295	BICO	BICOM	115	48	51	79	109	187	43	29	137	115	181
BICO 305	BICO	BICOM	135	54	53	85	123	209	50	30	151	132	180
BICO 379	BICO	BICOM	140	50	53	77	111	182	48	29	150	147	155
BICO 382	BICO	BICOM	140	48	55	92	126	214	47	27	147	148	194

ID	GENUS	SUBGEN	ANGD	ANGW	BDBR	BDHT	BBM1	CNM3	LM1L	LM1W	MNMO	RAND	RAMH
BICO 384	BICO	BICOM	133	50	56	87	119	213	45	28	144	140	189
BICO 386	BICO	BICOM	124	50	50	81	108	209	42	29	133	139	189
BICO 387	BICO	BICOM	139	41	56	96	123	201	43	28	141	130	164
BICO 388	BICO	BICOM	129	55	49	101	123	233	40	27	133	140	189
BICO 389	BICO	BICOM	141	40	48	93	119	218	43	27	142	150	181
BICO 390	BICO	BICOM	141	45	53	89	124	220	49	30	147	145	201
BICO 392	BICO	BICOM	133	41	56	85	113	198	48	28	148	135	188
BICO 393	BICO	BICOM	149	49	53	92	122	224	44	31	143	156	186
BICO 394	BICO	BICOM	134	41	58	100	132	207	48	27	146	137	180
BICO 396	BICO	BICOM	133	48	54	82	109	178	52	26	154	133	179
BICO 397	BICO	BICOM	142	33	50	84	122	192	49	25	149	147	192
BICO 398	BICO	BICOM	131	44	48	84	118	188	47	27	149	137	182
BICO 402	BICO	BICOM	122	45	50	81	105	194	44	28	141	130	172
BICO 405	BICO	BICOM	125	40	57	97	130	193	47	28	151	128	167
BICO 407	BICO	BICOM	106	43	48	88	106	204	41	28	133	121	163
BICO 408	BICO	BICOM	124	39	49	74	106	199	46	28	147	130	163
BICO 410	BICO	BICOM	128	35	51	85	114	192	45	27	140	126	181
BICO 411	BICO	BICOM	121	36	46	81	98	199	39	22	128	127	177
BICO 412	BICO	BICOM	131	42	54	85	113	210	43	27	140	140	195
BICO 414	BICO	BICOM	129	50	50	90	115	206	40	27	131	134	183
BICO 418	BICO	BICOM	127	43	52	83	114	207	46	29	138	124	191
BICO 436	BICO	BICOM	120	41	48	84	118	181	47	28	144	130	171
BICO 437	BICO	BICOM	128	52	57	89	125	189	47	26	150	130	189
BICO 441	BICO	BICOM	139	48	57	93	122	204	44	27	138	148	177
BICO 443	BICO	BICOM	140	45	57	88	116	227	43	30	138	150	179

ID	GENUS	SUBGEN	ANGD	ANGW	BOBR	BDHT	BDH1	CNM3	LM1L	LM1W	MNMO	RAMO	RAMH
UNIC 48	UNJA	UNICM	151	39	51	83	112	228	42	26	143	158	238
UNIC 53	UNJA	UNICM	140	47	49	89	120	212	41	31	141	154	213
UNIC 55	UNJA	UNICM	150	47	54	83	116	233	43	29	147	151	251
UNIC 303	UNJA	UNICM	160	45	55	92	125	234	48	27	155	163	250
UNIC 348	UNJA	UNICM	165	47	55	95	113	263	42	31	145	173	249
UNIC 349	UNJA	UNICM	159	45	51	99	118	256	37	27	136	170	247
UNIC 426	UNJA	UNICM	145	49	53	93	116	254	37	31	133	155	239
UNIC 427	UNJA	UNICM	142	52	50	83	108	247	41	30	140	153	223
UNIC 429	UNJA	UNICM	161	46	56	102	118	243	43	31	135	167	247
JAVA 17	UNJA	JAVAM	129	37	41	74	101	186	40	23	124	133	179
JAVA 18	UNJA	JAVAM	143	36	42	66	96	175	39	22	129	144	181
JAVA 299	UNJA	JAVAM	141	39	42	68	95	185	41	24	128	144	186
ACER 206	ACER	ACER1M	150	28	47	87	112	198	42	28	135	131	212
ACER 245	ACER	ACER1M	151	32	42	85	107	206	41	27	134	152	197
ACER 124	ACER	ACER2M	156	36	44	78	109	201	43	29	125	150	221
ACER 212	ACER	ACER2M	152	37	41	87	106	218	34	24	112	152	220
APHE 209	APHE	APHE1M	137	27	51	89	111	194	36	26	123	137	205
APHE 211	APHE	APHE1M	138	23	49	79	97	209	34	24	115	140	192
APHE 207	APHE	APHE1M	133	21	(45)	66	87	179	37	25	124	135	195
APHE 208	APHE	APHE1M	141	20	38	91	109	193	36	28	121	133	202
APHE 213	APHE	APHE2M	150	26	45	78	107	186	44	25	135	140	200
APHE 273	APHE	APHE2M	150	35	42	91	112	199	37	26	121	142	204
APHE 274	APHE	APHE2M	151	30	51	91	108	205	41	30	130	152	220
APHE 330	APHE	APHE2M	(156)	34	45	105	121	234	38	24	121	150	229
APHE 331	APHE	APHE2M	153	32	41	97	117	210	41	28	125	135	210

ID	GENUS	SUBGEN	ANGO	ANGW	BDBR	BDHT	BDM1	CNM3	LM1L	LM1W	MNMO	RAMO	RAMH
APHE 333	APHE	APHE2M	143	32	39	82	108	213	32	19	126	152	227
APHE 214	APHE	APHE3M	150	28	55	86	111	224	46	32	146	154	224
APHE 215	APHE	APHE3M	163	36	58	105	128	225	49	38	158	169	228
APHE 216	APHE	APHE3M	175	29	55	86	121	233	54	31	162	178	235
APHE 275	APHE	APHE3M	201	32	57	116	153	252	54	31	163	181	278
APHE 322	APHE	APHE4M	182	34	61	121	151	229	56	(38)	180	175	272
APHE 338	APHE	APHE4M	190	32	60	138	169	253	58	39	181	166	264
APHE 339	APHE	APHE4M	188	28	65	115	149	270	51	36	162	191	280
APHE 494	APHE	APHE4M	168	29	58	120	151	224	49	33	172	160	238
DICE 241	DICE	DICE1M	134	14	29	73	94	152	43	23	136	112	171
DICE 451	DICE	DICE2M	104	40	25	57	71	144	23	18	85	88	138
FORS 126	FORS	FORS1M	141	18	25	66	78	145	32	22	106	101	153
FORS 128	FORS	FORS2M	127	11	23	56	66	130	24	17	84	102	137
FORS 129	FORS	FORS2M	97	7	26	50	62	97	27	15	80	78	124
HYRA 4	HYRA	HYRA1M	80	11	17	35	45	69	15	9	48	63	82
HYRA 323	HYRA	HYRA1M	63	7	15	28	34	62	14	10	44	52	73
HYRA 6	HYRA	HYRA2M	103	9	20	49	60	97	21	14	66	89	118
HYRA 8	HYRA	HYRA2M	92	(8)	18	44	52	79	19	15	61	66	101
HYCD 117	HYCD	HYCDM	90	6	23	42	54	71	18	12	59	78	107
HYCD 120	HYCD	HYCDM	89	7	23	41	53	87	19	13	60	74	121
HYCD 280	HYCD	HYCDM	85	6	20	42	49	82	17	12	60	77	98
HYCD 460	HYCD	HYCDM	81	6	22	40	51	74	18	12	57	68	100
INDR 258	INDR	INDRM	255	67	79	129	166	353	75	53	223	226	330

ID	GENUS	SUBGEN	ANGD	ANGW	BDBR	BDHT	BDM1	CNM3	LM1L	LM1W	MNMO	RAMD	RAMH
MENO 189	MENO	MENO1M	96	36	26	53	67	111	30	19	98	78	137
MENO 190	MENO	MENO1M	92	30	25	51	69	110	26	18	86	78	129
MENO 191	MENO	MENO1M	108	39	25	55	68	129	25	17	90	85	141
MENO 192	MENO	MENO1M	96	27	22	52	63	116	25	19	90	79	138
MENO 194	MENO	MENO1M	96	29	26	51	64	120	25	18	90	92	132
MENO 454	MENO	MENO1M	113	43	29	51	65	(147)	24	19	89	77	144
MENO 457	MENO	MENO1M	103	42	24	56	70	(141)	27	18	90	75	136
MENO 158	MENO	MENO1M	108	34	28	59	78	129	29	20	92	89	138
MENO 172	MENO	MENO1M	100	24	27	48	74	116	31	20	100	100	147
MENO 186	MENO	MENO1M	99	46	31	57	72	134	24	21	91	96	148
MENO 132	MENO	MENO2M	100	31	35	64	85	141	31	22	114	92	158
PENE 15	PENE	PENE1M	81	10	22	47	57	105	20	13	70	82	115
PERA 276	PERA	PERA1M	133	19	43	79	101	180	41	29	136	135	189
PERA 340	PERA	PERA1M	121	22	40	67	97	162	42	27	135	111	168
PERA 324	PERA	PERA1M	113	13	38	82	94	173	35	26	116	117	164
PERA 319	PERA	PERA2M	155	25	52	90	115	219	43	31	148	147	210
PERA 325	PERA	PERA2M	162	26	(53)	87	119	216	50	33	167	163	209
SUBH 35	SUBH	SUBH1M	103	19	28	52	68	117	38	22	110	101	133
SUBH 43	SUBH	SUBH1M	126	19	30	55	75	135	34	18	105	111	146
SUBH 44	SUBH	SUBH1M	126	21	33	73	84	150	27	25	97	102	159
SUBH 28	SUBH	SUBH1M	102	15	27	52	70	120	28	18	97	88	127
SUBH 29	SUBH	SUBH1M	103	13	28	57	70	141	25	18	85	102	138
SUBH 38	SUBH	SUBH1M	108	15	27	55	65	138	27	19	89	107	129
SUBH 40	SUBH	SUBH1M	121	14	22	73	86	127	30	20	104	112	158
SUBH 65	SUBH	SUBH1M	104	14	27	58	72	125	28	19	69	98	133

ID	GENUS	SUBGEN	ANGD	ANGW	BDBR	BDHT	BDM1	CNM3	LM1L	LM1W	MHMO	RAMD	RAMH
SUBH 32	SUBH	SUBH2M	120	13	30	63	75	128	27	21	96	115	146
SUBH 33	SUBH	SUBH2M	114	15	31	60	76	120	28	20	95	105	141
SUBH 231	SUBH	SUBH3M	133	18	35	60	79	(140)	33	21	112	108	148
SUBH 232	SUBH	SUBH3M	117	17	36	56	71	146	37	24	113	94	148
SUBH 234	SUDH	SUBH3M	129	24	(38)	77	90	148	27	22	98	125	154
SUBH 279	SUBH	SUBH3M	129	13	37	57	74	137	32	21	108	112	149
SUBH 458	SUBH	SUBH3M	122	25	36	64	82	155	33	25	112	95	148
SUBH 425	SUBH	SUBH3M	121	12	26	61	(75)	139	32	21	104	108	146
TELE 249	TELE	TELE1M	144	22	45	77	108	175	48	30	157	123	189
TELE 250	TELE	TELE1M	154	21	42	72	102	184	44	30	140	148	183
TELE 253	TELE	TELE1M	149	28	39	88	106	207	37	20	131	142	183
TELE 346	TELE	TELE2M	152	30	49	86	114	201	46	36	150	146	218
TELE 347	TELE	TELE2M	149	26	49	83	109	185	48	34	159	132	183
TELE 259	TELE	TELE2M	141	31	53	103	121	215	41	29	153	124	227
TELE 260	TELE	TELE2M	144	30	49	96	117	214	50	31	160	128	228
TELE 254	TELE	TELE2M	167	(32)	46	101	121	221	38	32	143	172	222
TELE 255	TELE	TELE2M	154	33	45	94	114	229	41	31	138	153	236
TELE 217	TELE	TELE3M	152	20	44	90	124	186	48	29	155	131	202
TELE 218	TELE	TELE3M	164	23	47	102	125	217	44	27	144	148	240
TELE 219	TELE	TELE3M	136	33	46	118	136	218	48	23	155	144	210
TELE 221A	TELE	TELE3M	127	29	48	84	112	196	48	27	154	128	200
TELE 221B	TELE	TELE3M	138	15	44	69	100	181	49	25	155	115	175
TELE 262	TELE	TELE3M	133	24	48	76	112	191	48	27	157	142	186
TELE 263	TELE	TELE3M	139	(30)	47	83	101	216	41	33	143	140	201
TELE 264	TELE	TELE3M	135	41	49	87	113	188	44	31	158	135	208
TELE 312	TELE	TELE3M	162	37	50	106	125	221	42	27	142	153	235
TELE 313	TELE	TELE3M	148	24	48	95	119	201	45	29	144	134	205

ID	GENUS	SUBGEN	ANGD	ANGW	BOBR	BOHT	BOM1	CNM3	LM1L	LM1W	MHMO	RAMO	RAMH
TELE 314	TELE	TELE3M	150	39	54	81	102	226	47	29	145	162	203
TELE 261	TELE	TELE3M	152	34	55	109	123	247	40	24	(160)	147	232
TELE 226	TELE	TELE4M	150	33	51	90	105	246	43	28	142	165	213
TELE 281	TELE	TELE4M	158	35	45	112	132	239	47	32	159	160	249
TELE 282	TELE	TELE4M	141	52	60	113	135	241	52	32	126	141	212
TELE 283	TELE	TELE4M	167	39	70	120	133	250	54	35	173	178	255
TELE 286	TELE	TELE5M	138	24	50	98	121	202	45	33	160	129	216
TELE 424	TELE	TELE5M	154	27	45	98	(124)	191	49	31	170	123	207
TELE 223	TELE	TELE5M	167	46	60	112	138	264	46	32	163	(162)	230
TELE 224	TELE	TELE5M	141	22	48	102	136	214	59	30	181	131	221
TELE 225	TELE	TELE5M	161	27	48	98	131	215	53	32	178	144	228
TELE 227	TELE	TELE5M	146	34	57	93	122	213	46	31	162	146	230
TELE 290	TELE	TELE5M	138	26	55	109	123	(227)	49	30	163	136	225
TELE 292	TELE	TELE5M	152	34	65	99	136	210	56	30	171	152	228
TRIG 421	TRIG	TRIGM	126	12	32	65	80	156	33	23	115	(120)	168
TRIG 491	TRIG	TRIGM	125	15	31	67	81	148	27	22	102	126	154
TRIG 423	TRIG	TRIGM	134	18	34	62	76	132	32	22	110	120	147
TRIG 470	TRIG	TRIGM	128	15	31	65	81	167	31	22	106	129	162
TRIG 474	TRIG	TRIGM	115	17	31	66	79	145	28	20	98	112	156
TRIG 477	TRIG	TRIGM	129	17	32	70	85	159	28	20	99	122	154
TRIG 479	TRIG	TRIGM	117	20	40	71	85	138	32	22	111	106	170
TRIG 480	TRIG	TRIGM	120	18	32	66	83	137	30	23	112	116	152
TRIG 481	TRIG	TRIGM	123	18	30	69	83	152	33	20	111	114	168
TRIG 483	TRIG	TRIGM	110	11	37	63	73	158	30	24	109	106	146
TRIG 484	TRIG	TRIGM	126	13	35	75	89	119	31	21	111	118	155
TRIG 485	TRIG	TRIGM	123	11	32	60	74	136	31	21	113	117	146
TRIG 486	TRIG	TRIGM	122	19	29	64	80	164	28	20	106	107	159

ID	GENUS	SUBGEN	ANGD	ANGW	BDBR	BDHT	BDM1	CNM3	LM1L	LM1W	MNMD	RAMD	RAMH
ZAIS 107	ZAIS	ZAIS1M	232	26	57	87	120	200	46	31	166	196	257
ZAIS 114	ZAIS	ZAIS2M	225	16	33	98	119	202	52	32	182	170	271

APPENDIX 5.

UNIVARIATE STATISTICS

Summary univariate statistics for skull and mandible subgeneric groups respectively. Within each section, living groups are followed by fossil groups. Subgroups are listed by code in the same order as in Table 2 (skull) and Table 3 (mandible).

SKULL

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
CERAS	19	AEAE	19	309	372	335.6	14.80	4.4
		AEOR	19	211	265	246.1	12.56	5.1
		AEP2	19	431	460	447.7	8.33	1.8
		BICN	19	134	154	146.0	6.53	4.4
		BIZY	19	317	375	339.2	16.82	4.9
		LFHT	19	123	163	134.2	10.71	7.9
		LOXB	19	216	267	244.0	12.75	5.2
		M1M1	19	197	224	208.9	7.56	3.6
		M3M3	19	124	146	136.3	5.99	4.3
		MGAE	19	215	257	234.3	10.96	4.6
		MXGT	19	251	287	267.1	10.24	3.8
		MXMO	19	142	180	158.9	9.43	5.9
		OCP2	19	590	646	625.7	16.50	2.6
		OXAE	19	299	356	325.5	17.05	5.2
		OXOR	19	435	520	482.6	24.87	5.1
		PORB	19	103	121	112.1	4.59	4.0
		TFLN	19	315	376	355.4	16.26	4.5
		ZTHT	19	58	79	71.1	6.10	8.5
		ZYLN	19	237	301	276.2	18.34	6.6

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
SUMAS	2	AEAE	2	142	284	213.0	100.40	47.1
		AEOR	2	185	186	185.5	0.70	0.3
		AEPZ	2	300	304	302.0	2.82	0.9
		BICN	2	97	123	110.0	18.38	16.7
		BIZY	2	300	310	305.0	7.07	2.3
		LFHT	2	86	96	91.0	7.07	7.7
		LOXB	2	194	198	196.0	2.82	1.4
		M1M1	2	171	178	174.5	4.94	2.8
		M3M3	2	111	115	113.0	2.82	2.5
		MGAE	2	169	171	170.0	1.41	0.8
		MXGT	2	187	204	195.5	12.02	6.1
		MXMO	2	119	120	119.5	0.70	0.5
		OCPZ	2	400	414	407.0	9.89	2.4
		OXAE	2	212	222	217.0	7.07	3.2
		OXOR	2	289	313	301.0	16.97	5.6
		PORB	2	115	116	115.5	0.70	0.6
		TFLN	2	189	211	200.0	15.55	7.7
		ZYHT	2	43	44	43.5	0.70	1.6
		ZYLN	2	169	179	174.0	7.07	4.0
BICOS	48	AEAE	48	289	347	316.9	11.56	3.6
		AEOR	48	210	252	231.7	10.80	4.6
		AEPZ	48	330	408	374.5	15.13	4.0
		BICN	48	111	152	133.5	8.23	6.1
		BIZY	48	305	358	331.5	12.41	3.7
		LFHT	48	73	104	90.9	7.33	8.0
		LOXB	48	210	264	231.7	12.61	5.4
		M1M1	48	177	214	195.7	9.33	4.7
		M3M3	48	111	144	125.3	7.88	6.2
		MGAE	48	182	228	208.8	8.93	4.2
		MXGT	48	222	273	249.0	12.24	4.9
		MXMO	48	103	165	147.7	9.38	6.3
		OCPZ	48	474	560	519.1	20.59	3.9
		OXAE	48	249	301	272.4	13.26	4.8
		OXOR	48	338	447	392.4	26.12	6.6
		PORB	48	103	140	118.5	7.57	6.3
		TFLN	48	240	323	281.3	17.66	6.2
		ZYHT	48	42	60	49.7	4.00	8.0
		ZYLN	48	192	278	222.7	16.26	7.3

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
UNICS	8	AEAE	8	328	370	349.7	13.28	3.7
		AEOR	8	239	268	255.2	10.59	4.1
		AEP2	8	365	409	382.0	12.46	3.2
		BICN	8	135	147	139.2	3.91	2.8
		BIZY	8	347	377	364.1	10.19	2.7
		LFHT	8	91	126	108.3	11.14	10.2
		LOXB	8	227	296	274.6	21.27	7.7
		M1M1	8	204	227	218.8	7.37	3.3
		M3M3	8	115	152	137.2	12.71	9.2
		MGAE	8	216	240	224.5	8.40	3.7
		MXGT	8	234	264	255.7	9.52	3.7
		NDNO	8	145	155	148.6	4.27	2.8
		OCP2	8	508	556	522.7	15.54	2.9
		OKAE	8	256	284	268.1	10.14	3.7
		OXOR	8	356	391	366.7	12.06	3.2
		PORB	8	100	126	112.8	7.88	6.9
		TFLN	8	250	292	270.5	17.49	6.4
		ZYHT	8	67	88	74.8	6.64	8.8
		ZYLN	8	225	257	236.8	10.17	4.2
JAVAS	4	AEAE	4	319	332	327.7	6.13	1.8
		AEOR	4	234	248	240.0	6.32	2.6
		AEP2	4	317	327	321.5	4.43	1.3
		BICN	4	125	151	138.7	11.02	7.9
		BIZY	4	331	346	339.7	6.75	1.9
		LFHT	4	61	77	68.0	6.83	10.0
		LOXB	4	278	298	285.7	8.65	3.0
		M1M1	4	190	197	192.7	3.09	1.6
		M3M3	4	110	114	111.5	1.91	1.7
		MGAE	4	188	215	203.2	11.23	5.5
		MXGT	4	220	231	223.7	4.99	2.2
		NDNO	4	126	131	129.0	2.16	1.6
		OCP2	4	432	463	453.0	14.30	3.1
		OKAE	4	229	252	235.7	10.99	4.6
		OXOR	4	299	334	316.5	14.43	4.5
		PORB	4	110	121	115.7	4.78	4.1
		TFLN	4	205	236	223.2	14.59	6.5
		ZYHT	4	52	56	54.0	1.63	3.0
		ZYLN	4	182	207	196.5	11.38	5.7

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
ACER1S	1	AEAE	1	290	290	290.0		
		AEOR	1	232	232	232.0		
		AEP2	1	352	352	352.0		
		BICN	1	114	114	114.0		
		BIZY	1	293	293	293.0		
		LFHT	1	73	73	73.0		
		LOXB	1	226	226	226.0		
		M1M1	1	186	186	186.0		
		M3M3	1	102	102	102.0		
		MGAE	1	210	210	210.0		
		MXGT	1	239	239	239.0		
		MXMO	1	145	145	145.0		
		OCP2	1	484	484	484.0		
		OXAE	1	270	270	270.0		
		OXOR	1	394	394	394.0		
		PORB	1	91	91	91.0		
		TFLN	1	267	267	267.0		
		ZYHT	1	67	67	67.0		
		ZYLN	1	219	219	219.0		
ACER2S	1	AEAE	1	365	365	365.0		
		AEOR	1	196	196	196.0		
		AEP2	1	342	342	342.0		
		BICN	1	130	130	130.0		
		BIZY	1	357	357	357.0		
		LFHT	1	121	121	121.0		
		LOXB	1	258	258	258.0		
		M1M1	1	206	206	206.0		
		M3M3	1	129	129	129.0		
		MGAE	1	268	268	268.0		
		MXGT	1	245	245	245.0		
		MXMO	1	144	144	144.0		
		OCP2	1	517	517	517.0		
		OXAE	1	294	294	294.0		
		OXOR	1	377	377	377.0		
		PORB	1	138	138	138.0		
		TFLN	1	277	277	277.0		
		ZYHT	1	63	63	63.0		
		ZYLN	1	192	192	192.0		

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
AMYNS	2	AEAE	2	194	195	194.5	0.70	0.3
		AEOR	2	123	130	126.5	4.94	3.9
		AEP2	2	221	228	224.5	4.94	2.2
		BICN	2	84	85	84.5	0.70	0.8
		BIZY	2	130	205	167.5	53.03	31.6
		LFHT	2	48	53	50.5	3.53	7.0
		LOXB	2	100	102	101.0	1.41	1.4
		M1M1	2	107	123	115.0	11.31	9.8
		M3M3	2	82	96	89.0	9.89	11.1
		MGAE	2	138	148	143.0	7.07	4.9
		MXGT	2	140	154	147.0	9.89	6.7
		MOMO	2	95	112	103.5	12.02	11.6
		OCP2	2	323	328	325.5	3.53	1.0
		OXAE	2	160	170	165.0	7.07	4.2
		OXOR	2	268	281	274.5	9.19	3.3
		PORB	2	61	63	62.0	1.41	2.2
		TFLN	2	201	208	204.5	4.94	2.4
		ZYHT	2	34	35	34.5	0.70	2.0
		ZYLN	2	120	121	120.5	0.70	0.5
APHEIS	1	AEAE	1	262	262	262.0		
		AEOR	1	169	169	169.0		
		AEP2	1	286	286	286.0		
		BICN	1	96	96	96.0		
		BIZY	1	236	236	236.0		
		LFHT	1	86	86	86.0		
		LOXB	1	140	140	140.0		
		M1M1	1	119	119	119.0		
		M3M3	1	91	91	91.0		
		MGAE	1	165	165	165.0		
		MXGT	1	192	192	192.0		
		MOMO	1	115	115	115.0		
		OCP2	1	399	399	399.0		
		OXAE	1	192	192	192.0		
		OXOR	1	291	291	291.0		
		PORB	1	72	72	72.0		
		TFLN	1	230	230	230.0		
		ZYHT	1	52	52	52.0		
		ZYLN	1	179	179	179.0		

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
APHE2S	8	AEAE	8	283	327	305.3	16.23	5.3
		AEOR	8	188	217	205.1	11.34	5.5
		AEP2	8	330	379	354.8	17.86	5.0
		BICN	8	122	137	128.5	5.92	4.6
		BIZY	8	288	336	309.5	17.46	5.6
		LFMT	8	71	107	85.1	12.15	14.2
		LOMB	8	194	241	216.8	16.30	7.5
		M1M1	8	164	186	178.8	7.54	4.2
		M3M3	8	107	147	122.0	12.18	9.9
		MGAE	8	171	196	185.1	8.98	4.8
		MXGT	8	217	273	236.1	18.38	7.7
		MXMO	8	125	145	135.2	7.62	5.6
		OCP2	8	438	500	468.7	22.01	4.6
		OXAE	8	229	263	243.6	12.93	5.3
		OXOR	8	296	383	357.7	28.44	7.9
		PORB	8	94	121	108.1	8.02	7.4
		TFLN	8	218	263	247.8	16.12	6.5
		ZYHT	8	56	76	68.1	5.71	8.3
		ZYLN	8	184	229	212.0	13.24	6.2
DICE1S	3	AEAE	3	194	213	204.6	9.71	4.7
		AEOR	3	162	168	165.6	3.21	1.9
		AEP2	3	241	259	247.6	9.86	3.9
		BICN	3	80	93	85.6	6.65	7.7
		BIZY	3	226	236	230.3	5.13	2.2
		LFMT	3	42	55	47.3	6.80	14.3
		LOMB	3	122	127	123.6	2.88	2.3
		M1M1	3	128	142	137.0	7.81	5.7
		M3M3	3	74	87	81.3	6.65	8.1
		MGAE	3	132	154	141.3	11.37	8.0
		MXGT	3	166	195	176.6	15.94	9.0
		MXMO	3	99	117	106.0	9.64	9.0
		OCP2	3	336	358	348.0	11.13	3.1
		OXAE	3	155	178	165.6	11.59	6.9
		OXOR	3	251	294	268.3	22.67	8.4
		PORB	3	81	93	88.3	6.42	7.2
		TFLN	3	181	215	198.6	17.03	8.5
		ZYHT	3	36	43	38.6	3.78	9.7
		ZYLN	3	147	164	153.0	9.53	6.2

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
BICE2S	1	AEAE	1	244	244	244.0		
		AEOR	1	170	170	170.0		
		AEP2	1	278	278	278.0		
		BICN	1	95	95	95.0		
		BIZY	1	260	260	260.0		
		LFHT	1	62	62	62.0		
		LOXB	1	143	143	143.0		
		M1M1	1	131	131	131.0		
		M3M3	1	99	99	99.0		
		MGAE	1	162	162	162.0		
		MXGT	1	192	192	192.0		
		MXMO	1	115	115	115.0		
		OCP2	1	395	395	395.0		
		OXAE	1	188	188	188.0		
		OXOR	1	294	294	294.0		
		PORB	1	86	86	86.0		
		TFLN	1	210	210	210.0		
		ZYHT	1	48	48	48.0		
		ZYLN	1	165	165	165.0		
DICE3S	2	AEAE	2	243	271	257.0	19.79	7.7
		AEOR	2	195	208	201.5	9.19	4.5
		AEP2	2	317	320	318.5	2.12	0.6
		BICN	2	112	118	115.0	4.24	3.6
		BIZY	2	247	285	266.0	26.87	10.1
		LFHT	2	54	61	57.5	4.94	8.6
		LOXB	2	149	158	153.5	6.36	4.1
		M1M1	2	130	159	144.5	20.50	14.1
		M3M3	2	89	117	103.0	19.79	19.2
		MGAE	2	164	174	169.0	7.07	4.1
		MXGT	2	204	217	210.5	9.19	4.3
		MXMO	2	129	140	134.5	7.77	5.7
		OCP2	2	429	451	440.0	15.55	3.5
		OXAE	2	223	229	226.0	4.24	1.8
		OXOR	2	337	373	355.0	25.45	7.1
		PORB	2	101	113	107.0	8.48	7.9
		TFLN	2	260	273	266.5	9.19	3.4
		ZYHT	2	51	65	58.0	9.89	17.0
		ZYLN	2	177	186	181.5	6.36	3.5

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
FORSS	2	AEAE	2	230	236	233.8	4.24	1.8
		AEOR	2	135	160	147.5	17.67	11.9
		AEP2	2	255	275	265.8	14.14	5.3
		BICN	2	76	84	80.8	5.65	7.0
		BIZY	2	236	249	242.5	9.19	3.7
		LFHT	2	47	65	56.8	12.72	22.7
		LOXB	2	104	133	118.5	20.50	17.3
		M1M1	2	127	138	132.5	7.77	5.8
		M3M3	2	81	102	91.5	14.84	16.2
		MGAE	2	132	156	144.0	16.97	11.7
		MXGT	2	157	165	161.0	5.65	3.5
		MXMO	2	104	105	104.5	0.70	0.6
		OCP2	2	366	388	377.0	15.55	4.1
		OXAE	2	175	187	181.0	8.48	4.6
		OXOR	2	285	294	289.5	6.36	2.1
		PORB	2	61	116	88.5	38.89	43.9
		TFLN	2	217	220	218.5	2.12	0.9
		ZYHT	2	36	39	37.5	2.12	5.6
		ZYLN	2	142	149	145.5	4.94	3.4
HYRA1S	2	AEAE	2	73	111	92.0	26.87	29.2
		AEOR	2	76	88	82.0	8.48	18.3
		AEP2	2	123	139	131.0	11.31	8.6
		BICN	2	38	48	43.0	7.07	16.4
		BIZY	2	86	122	104.0	25.45	24.4
		LFHT	2	27	31	29.0	2.82	9.7
		LBXB	2	55	67	61.0	8.48	13.9
		M1M1	2	54	78	66.8	16.97	25.7
		M3M3	2	35	59	47.8	16.97	36.1
		MGAE	2	46	75	60.5	20.50	33.8
		MXGT	2	72	83	77.5	7.77	10.0
		MXMO	2	44	52	48.0	5.65	11.7
		OCP2	2	167	190	178.5	16.26	9.1
		OXAE	2	71	108	85.5	20.50	23.9
		OXOR	2	131	168	149.5	26.16	17.5
		PORB	2	37	48	42.5	7.77	18.3
		TFLN	2	92	120	106.0	19.79	18.6
		ZYHT	2	21	22	21.5	0.70	3.2
		ZYLN	2	73	91	82.8	12.72	15.5

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
HYRAZS	3	AEAE	3	112	162	133.3	25.79	19.3
		AEOR	3	103	116	110.3	6.65	6.0
		AEPZ	3	167	184	173.0	9.53	5.5
		BICN	3	46	58	51.6	6.02	11.6
		BIZY	3	82	179	131.3	48.52	36.9
		LFHT	3	32	39	35.3	3.51	9.9
		LOXB	3	67	90	76.0	12.28	16.1
		M1M1	3	75	110	94.3	17.78	18.8
		M3M3	3	49	76	62.3	13.50	21.6
		MGAE	3	74	106	90.0	16.00	17.7
		MXGT	3	92	116	104.6	12.05	11.5
		MXMO	3	58	73	66.3	7.63	11.5
		OCPZ	3	216	261	236.3	22.81	9.6
		OXAE	3	86	134	108.3	24.17	22.3
		OXOR	3	176	205	188.0	15.13	8.0
		PORB	3	43	61	51.0	9.16	17.9
		TFLN	3	132	163	145.0	16.09	11.0
		ZYHT	3	25	28	26.0	1.73	6.6
		ZYLN	3	100	108	104.3	4.04	3.8
HYCOS	4	AEAE	4	107	130	115.0	10.61	9.2
		AEOR	4	88	98	92.2	5.05	5.4
		AEPZ	4	141	160	150.7	7.76	5.1
		BICN	4	46	52	48.7	2.50	5.1
		BIZY	4	115	135	125.7	8.30	6.6
		LFHT	4	33	45	38.5	4.93	12.8
		LOXB	4	66	82	72.5	6.75	9.3
		M1M1	4	82	90	86.7	3.59	4.1
		M3M3	4	42	55	50.0	5.59	11.1
		MGAE	4	83	101	91.2	7.67	8.4
		MXGT	4	101	113	106.7	5.31	4.9
		MXMO	4	58	63	60.5	2.38	3.9
		OCPZ	4	215	240	227.5	12.34	5.4
		OXAE	4	110	140	122.7	13.04	10.6
		OXOR	4	179	205	193.7	13.30	6.8
		PORB	4	40	57	45.7	7.67	16.7
		TFLN	4	145	156	149.7	5.18	3.4
		ZYHT	4	29	34	32.0	2.16	6.7
		ZYLN	4	86	94	89.7	4.34	4.8

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
INDRS	1	AEAE	1	570	570	570.0		
		AEOR	1	374	374	374.0		
		AEPZ	1	632	632	632.0		
		BICN	1	309	309	309.0		
		BIZY	1	588	588	588.0		
		LFHT	1	145	145	145.0		
		LOXB	1	358	358	358.0		
		M1M1	1	279	279	279.0		
		M3M3	1	214	214	214.0		
		MGAE	1	498	498	498.0		
		MXGT	1	376	376	376.0		
		MXMO	1	232	232	232.0		
		OCPZ	1	1025	1025	1025.0		
		OXAE	1	525	525	525.0		
		OXOR	1	802	802	802.0		
		PORB	1	194	194	194.0		
		TFLN	1	662	662	662.0		
		ZYHT	1	101	101	101.0		
		ZYLN	1	371	371	371.0		
MENOS	18	AEAE	18	156	208	181.3	14.10	7.7
		AEOR	18	129	164	143.6	10.78	7.5
		AEPZ	18	212	257	233.0	13.17	5.6
		BICN	18	65	84	74.6	5.78	7.7
		BIZY	18	161	240	197.7	24.59	12.4
		LFHT	18	39	56	46.7	4.88	10.4
		LOXB	18	103	143	122.1	11.00	9.0
		M1M1	18	102	130	115.7	9.73	8.4
		M3M3	18	50	89	68.1	11.35	16.6
		MGAE	18	104	134	118.8	7.10	5.9
		MXGT	18	147	175	160.7	7.08	4.4
		MXMO	18	88	106	96.8	4.76	4.9
		OCPZ	18	279	338	313.5	14.34	4.5
		OXAE	18	116	164	143.8	13.31	9.2
		OXOR	18	189	240	223.1	13.73	6.1
		PORB	18	62	90	75.2	7.93	10.5
		TFLN	18	144	175	159.2	9.21	5.7
		ZYHT	18	37	61	46.6	6.72	14.4
		ZYLN	18	126	150	137.6	7.33	5.3

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
PERA1S	2	AEAE	2	226	280	253.0	38.18	15.0
		AEOR	2	178	186	182.0	5.65	3.1
		AEP2	2	289	305	297.0	11.31	3.8
		BICN	2	85	90	87.5	3.53	4.0
		BIZY	2	237	253	245.0	11.31	4.6
		LFHT	2	63	79	71.0	11.31	15.9
		LOXB	2	142	176	159.0	24.04	15.1
		M1M1	2	148	156	152.0	5.65	3.7
		M3M3	2	94	98	96.0	2.82	2.9
		MGAE	2	140	165	152.5	17.67	11.5
		MXGT	2	182	208	195.0	18.38	9.4
		MXMO	2	107	132	119.5	17.67	14.7
		OCP2	2	355	415	385.0	42.42	11.0
		OXAE	2	175	202	188.5	19.09	10.1
		OXOR	2	255	280	267.5	17.67	6.6
		PORB	2	70	82	76.0	8.48	11.1
		TFLN	2	192	229	210.5	26.16	12.4
		ZYHT	2	51	61	56.0	7.07	12.6
		ZYLN	2	168	185	176.5	12.02	6.8
PERA2S	3	AEAE	3	345	405	379.0	30.78	8.1
		AEOR	3	210	258	239.3	25.71	10.7
		AEP2	3	352	417	389.3	33.56	8.6
		BICN	3	140	162	151.0	11.00	7.2
		BIZY	3	359	429	400.0	36.51	9.1
		LFHT	3	85	96	90.6	5.50	6.0
		LOXB	3	239	279	262.0	20.66	7.8
		M1M1	3	209	260	235.0	25.51	10.8
		M3M3	3	140	153	148.3	7.23	4.8
		MGAE	3	225	238	232.3	6.65	2.8
		MXGT	3	263	287	274.0	12.12	4.4
		MXMO	3	155	177	165.3	11.06	6.6
		OCP2	3	495	552	526.0	28.82	5.4
		OXAE	3	250	294	268.3	22.89	8.5
		OXOR	3	320	361	344.3	21.54	6.2
		PORB	3	102	125	117.0	13.00	11.1
		TFLN	3	216	248	236.3	17.67	7.4
		ZYHT	3	76	82	78.6	3.05	3.8
		ZYLN	3	214	254	239.3	22.03	9.2

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
SUBH1S	5	AEAE	5	170	196	186.8	9.88	5.2
		AEOR	5	136	160	149.0	9.00	6.0
		AEP2	5	217	256	239.0	14.07	5.8
		BICN	5	72	77	74.0	2.34	3.1
		BIZY	5	176	219	197.6	15.27	7.7
		LFHT	5	39	70	54.4	11.28	20.7
		LOXB	5	101	125	113.8	8.64	7.5
		M1M1	5	105	131	118.8	11.09	9.3
		M3M3	5	75	89	79.2	6.01	7.5
		MGAE	5	126	137	133.0	4.84	3.6
		MXGT	5	143	178	160.0	15.14	9.4
		MXMO	5	87	103	95.8	7.66	7.9
		OCP2	5	314	357	339.6	16.44	4.8
		OXAE	5	146	174	156.8	10.84	6.9
		OXOR	5	247	277	260.6	11.19	4.2
		PORB	5	55	77	66.0	10.77	16.3
		TFLN	5	166	201	178.0	13.47	7.5
		ZYHT	5	40	48	43.8	3.19	7.2
		ZYLN	5	128	142	135.6	5.31	3.9
SUBH2S	4	AEAE	4	190	221	203.5	13.91	6.8
		AEOR	4	146	162	155.0	6.83	4.4
		AEP2	4	247	264	255.0	7.25	2.8
		BICN	4	80	95	88.75	7.0	7.9
		BIZY	4	197	235	213.0	17.86	8.3
		LFHT	4	56	75	66.0	8.04	12.1
		LOXB	4	116	141	127.25	10.8	8.4
		M1M1	4	106	146	124.5	17.38	13.9
		M3M3	4	61	93	82.75	14.9	18.0
		MGAE	4	138	164	145.5	12.36	8.5
		MXGT	4	163	186	173.5	9.88	5.6
		MXMO	4	95	114	105.0	8.60	8.1
		OCP2	4	340	369	357.25	13.2	3.6
		OXAE	4	175	184	178.0	4.08	2.2
		OXOR	4	280	290	285.5	4.20	1.4
		PORB	4	63	72	68.7	4.2	6.2
		TFLN	4	192	215	205.2	9.7	4.7
		ZYHT	4	41	53	45.5	5.19	11.4
		ZYLN	4	129	149	140.5	9.67	6.8

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
SUBH3S	7	AEAE	7	225	246	235.4	8.05	3.4
		AEOR	7	165	189	173.5	7.91	4.5
		AEP2	7	265	295	275.8	9.97	3.6
		BICN	7	95	110	100.4	5.56	5.5
		BIZY	7	237	280	261.4	13.10	5.0
		LFHT	7	37	62	52.2	8.92	17.0
		LOXB	7	139	161	148.8	7.58	5.0
		M1M1	7	124	151	139.4	9.19	6.5
		M3M3	7	83	107	99.2	8.34	8.4
		MGAE	7	133	166	153.1	11.92	7.7
		MXGT	7	156	192	181.0	12.47	6.8
		MXMO	7	105	119	113.7	5.02	4.4
		OCP2	7	344	410	385.0	20.53	5.3
		OXAE	7	185	222	202.8	13.64	6.7
		OXOR	7	294	348	322.0	17.40	5.4
		PORB	7	77	101	85.2	8.07	9.4
		TFLN	7	206	250	227.5	16.25	7.1
		ZYHT	7	44	61	50.8	6.96	13.6
		ZYLN	7	153	184	167.0	11.10	6.6
TELETS	2	AEAE	2	281	288	284.5	4.94	1.7
		AEOR	2	221	232	226.5	7.77	3.4
		AEP2	2	325	328	326.5	2.12	0.6
		BICN	2	99	124	111.5	17.67	15.8
		BIZY	2	306	320	313.0	9.89	3.1
		LFHT	2	59	70	64.5	7.77	12.0
		LOXB	2	198	211	204.5	9.19	4.4
		M1M1	2	178	181	179.5	2.12	1.1
		M3M3	2	98	102	100.0	2.82	2.8
		MGAE	2	161	163	162.0	1.41	0.8
		MXGT	2	225	230	227.5	3.53	1.5
		MXMO	2	138	146	142.0	5.65	3.9
		OCP2	2	408	428	418.0	14.14	3.3
		OXAE	2	205	210	207.5	3.53	1.7
		OXOR	2	304	306	305.0	1.41	0.4
		PORB	2	93	116	104.5	16.26	15.5
		TFLN	2	213	217	215.0	2.82	1.3
		ZYHT	2	59	76	67.5	12.02	17.8
		ZYLN	2	186	204	195.0	12.72	6.5

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
TELE2S	4	AEAE	4	308	347	326.5	17.09	5.2
		AEOR	4	241	276	259.7	14.45	5.5
		AEPZ	4	351	374	365.5	10.40	2.8
		BICN	4	108	134	125.2	11.87	9.4
		BIZY	4	319	386	355.0	27.58	7.7
		LFHT	4	68	94	83.2	12.52	15.0
		LOXB	4	227	289	246.0	28.95	11.7
		M1M1	4	163	186	178.7	10.71	5.9
		M3M3	4	107	123	115.7	6.70	5.7
		MGAE	4	180	207	196.5	13.07	6.6
		MXGT	4	237	254	246.5	7.32	2.9
		MXMO	4	152	170	161.2	7.36	4.5
		OCPZ	4	459	505	481.2	20.33	4.2
		OXAE	4	214	247	227.0	14.53	6.4
		OXOR	4	325	358	343.7	14.10	4.1
		PORB	4	84	101	90.7	7.22	7.9
		TFLN	4	236	259	245.7	9.91	4.0
		ZYHT	4	79	96	85.0	8.04	9.4
		ZYLN	4	178	229	208.0	22.31	10.7
TELE3S	6	AEAE	6	273	318	301.0	15.84	5.2
		AEOR	6	230	268	248.6	12.29	4.9
		AEPZ	6	351	394	367.6	15.79	4.2
		BICN	6	111	131	122.0	8.39	6.8
		BIZY	6	265	331	309.5	23.78	7.6
		LFHT	6	80	111	96.0	10.95	11.4
		LOXB	6	198	237	216.8	14.17	6.5
		M1M1	6	94	194	161.0	36.03	22.3
		M3M3	6	91	130	113.8	15.43	13.5
		MGAE	6	161	196	182.6	13.90	7.6
		MXGT	6	160	253	217.3	32.81	15.1
		MXMO	6	131	168	149.3	11.87	7.9
		OCPZ	6	471	499	485.5	9.87	2.0
		OXAE	6	209	252	230.6	16.66	7.2
		OXOR	6	313	360	341.1	16.58	4.8
		PORB	6	59	92	82.0	12.06	14.7
		TFLN	6	222	266	242.0	16.54	6.8
		ZYHT	6	73	87	79.6	4.96	6.2
		ZYLN	6	200	229	210.3	11.23	5.3

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
TELE4S	3	AEAE	3	294	332	315.0	19.31	6.1
		AEOR	3	256	270	264.6	7.57	2.8
		AEP2	3	397	420	409.6	11.67	2.8
		BICN	3	128	141	133.6	6.65	4.9
		BIZY	3	305	352	332.3	24.41	7.3
		LFHT	3	108	126	115.6	9.29	8.0
		LOXB	3	224	236	231.3	6.42	2.7
		M1M1	3	170	213	197.0	23.51	11.9
		M3M3	3	84	128	112.3	24.58	21.8
		MGAE	3	168	190	182.6	12.70	6.9
		MXGT	3	256	270	261.3	7.57	2.8
		MXMO	3	161	177	169.0	8.0	4.7
		OCP2	3	519	540	526.0	12.12	2.3
		OXAE	3	228	241	236.0	7.0	2.9
		OXOR	3	345	382	364.6	18.61	5.1
		PORB	3	69	97	83.6	14.04	16.7
		TFLN	3	242	256	247.0	7.81	3.1
		ZYHT	3	74	83	79.0	4.58	5.8
		ZYLN	3	221	239	231.6	9.45	4.0
TELE5S	4	AEAE	4	298	370	336.5	29.71	8.8
		AEOR	4	246	294	271.5	20.72	7.6
		AEP2	4	356	428	405.0	33.04	8.1
		BICN	4	113	145	134.0	14.49	10.8
		BIZY	4	314	374	351.7	28.00	7.9
		LFHT	4	90	115	100.7	11.5	11.41
		LOXB	4	221	283	247.0	28.70	11.6
		M1M1	4	192	205	197.5	5.56	2.8
		M3M3	4	117	133	124.2	7.54	6.0
		MGAE	4	175	224	200.0	20.34	10.1
		MXGT	4	260	280	269.0	8.28	3.0
		MXMO	4	173	185	180.2	5.5	3.051
		OCP2	4	491	562	539.2	32.87	6.0
		OXAE	4	207	260	237.7	22.18	9.3
		OXOR	4	331	388	368.0	25.65	6.9
		PORB	4	72	106	91.2	15.73	17.2
		TFLN	4	267	282	272.5	6.85	2.5
		ZYHT	4	73	92	82.7	8.42	10.1
		ZYLN	4	211	268	246.2	24.55	9.9

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
TRIGS	13	AEAE	12	172	244	212.5	18.55	8.7
		AEOR	12	135	183	164.0	13.70	8.3
		AEP2	12	230	290	262.8	17.87	6.8
		BICN	12	66	89	80.4	7.50	9.3
		BIZY	12	179	292	231.3	28.22	12.1
		LFHT	12	41	69	58.2	9.37	16.0
		LOXB	12	82	147	120.7	15.78	13.0
		M1M1	12	105	152	134.8	14.34	10.6
		M3M3	12	72	108	87.1	11.78	13.5
		MGAE	12	130	168	149.9	11.44	7.6
		MXGT	12	159	194	177.0	10.23	5.7
		MXMO	12	99	125	115.5	6.84	5.9
		OCP2	12	331	413	367.0	21.77	5.9
		OXAE	12	160	253	188.9	21.66	11.4
		OXOR	12	254	324	299.8	20.63	6.8
		PORB	12	56	93	73.0	10.53	14.4
		TFLN	12	195	267	229.8	19.72	8.5
		ZYHT	12	33	65	50.1	11.14	22.2
		ZYLN	12	125	169	151.4	14.39	9.5

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Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
CERAM	19	ANGD	19	141	177	160.5	10.18	6.3
		ANGW	19	42	64	54.4	5.81	10.6
		BDBR	19	55	70	61.3	3.78	6.1
		BDM1	19	133	161	148.6	7.05	4.7
		BDHT	19	109	132	117.7	5.77	4.9
		CNM3	19	243	298	265.3	12.93	4.8
		LM1L	19	29	51	41.1	6.81	16.5
		LM1W	19	27	36	30.2	2.86	9.4
		MNMO	19	124	153	143.7	7.09	4.9
		RAMD	19	157	188	173.8	10.01	5.7
		RAMH	19	208	251	228.7	12.96	5.6
SUMAN	2	ANGD	2	112	113	112.5	0.70	0.6
		ANGW	2	37	38	37.5	0.70	1.8
		BDBR	2	34	36	35.0	1.41	4.0
		BDM1	2	83	134	108.5	36.06	33.2
		BDHT	2	61	63	62.0	1.41	2.2
		CNM3	2	165	189	177.0	16.97	9.5
		LM1L	2	36	40	38.0	2.82	7.4
		LM1W	2	21	22	21.5	0.70	3.2
		MNMO	2	120	166	143.0	32.52	22.7
		RAMD	2	117	166	141.5	34.64	24.4
		RAMH	2	152	166	159.0	9.89	6.2
BICON	47	ANGD	47	106	149	130.2	9.17	7.0
		ANGW	47	33	55	45.5	5.23	11.5
		BDBR	47	44	59	52.0	3.56	6.8
		BDM1	47	96	132	116.8	8.15	6.9
		BDHT	47	73	101	86.4	6.81	7.8
		CNM3	47	167	233	201.8	14.57	7.2
		LM1L	47	39	52	45.3	3.24	7.1
		LM1W	47	21	32	28.0	2.06	7.3
		MNMO	47	128	155	143.0	7.28	5.0
		RAMD	47	115	156	135.9	9.96	7.3
		RAMH	47	155	202	180.2	10.90	6.0

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
UNICM	9	ANGD	9	140	165	152.5	9.07	5.9
		ANGW	9	39	52	46.3	3.50	7.5
		BDBR	9	49	56	52.6	2.50	4.7
		BDM1	9	108	125	116.2	4.91	4.2
		BDMT	9	83	102	91.0	7.08	7.7
		CNM3	9	212	263	241.1	15.97	6.6
		LM1L	9	37	48	41.5	3.32	7.9
		LM1W	9	26	31	29.2	2.04	7.0
		MNMO	9	133	155	141.6	6.83	4.8
		RAMD	9	151	173	160.4	8.06	5.0
		RAMH	9	213	251	239.6	13.33	5.5
JAVAM	3	ANGD	3	129	143	137.6	7.57	5.5
		ANGW	3	36	39	37.3	1.52	4.0
		BDBR	3	41	42	41.6	0.57	1.3
		BDM1	3	95	101	97.3	3.21	3.3
		BDMT	3	66	74	69.3	4.16	6.0
		CNM3	3	175	186	182.0	6.08	3.3
		LM1L	3	39	41	40.0	1.00	2.5
		LM1W	3	22	24	23.0	1.00	4.3
		MNMO	3	124	129	127.0	2.64	2.0
		RAMD	3	133	144	140.3	6.35	4.5
		RAMH	3	179	186	182.0	3.60	1.9
ACER1M	2	ANGD	2	150	151	150.5	0.70	0.4
		ANGW	2	28	32	30.0	2.82	9.4
		BDBR	2	42	47	44.5	3.53	7.9
		BDM1	2	107	112	109.5	3.53	3.2
		BDMT	2	85	87	86.0	1.41	1.6
		CNM3	2	198	206	202.0	5.65	2.8
		LM1L	2	41	42	41.5	0.70	1.7
		LM1W	2	27	28	27.5	0.70	2.5
		MNMO	2	134	135	134.5	0.70	0.5
		RAMD	2	131	152	141.5	14.84	10.4
		RAMH	2	197	212	204.5	10.60	5.1

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
ACER2M	2	ANGD	2	152	156	154.0	2.82	1.8
		ANGW	2	36	37	36.5	0.70	1.9
		BDBR	2	41	44	42.5	2.12	4.9
		BDM1	2	106	109	107.5	2.12	1.9
		BDHT	2	78	87	82.5	6.36	7.7
		CNM3	2	201	218	209.5	12.02	5.7
		LM1L	2	34	43	38.5	6.36	16.5
		LM1W	2	24	29	26.5	3.53	13.3
		MNMO	2	112	125	118.5	9.19	7.7
		RAMD	2	150	152	151.0	1.41	0.9
		RAMH	2	220	221	220.5	0.70	0.3
APHE1M	4	ANGD	4	133	141	137.2	3.30	2.4
		ANGW	4	20	27	22.7	3.09	13.6
		BDBR	4	38	51	45.7	5.73	12.5
		BDM1	4	87	111	101.0	11.19	11.0
		BDHT	4	66	91	81.2	11.44	14.0
		CNM3	4	179	209	193.7	12.25	6.3
		LM1L	4	34	37	35.7	1.25	3.5
		LM1W	4	24	28	25.7	1.70	6.6
		MNMO	4	115	124	120.7	4.03	3.3
		RAMD	4	133	140	136.2	2.98	2.1
		RAMH	4	192	205	198.5	6.02	3.0
APHE2M	6	ANGD	6	143	156	150.5	4.32	2.8
		ANGW	6	26	35	31.5	3.20	10.1
		BDBR	6	39	51	43.8	4.21	9.6
		BDM1	6	107	121	112.1	5.70	5.0
		BDHT	6	78	105	90.6	9.81	10.8
		CNM3	6	186	234	207.8	15.99	7.6
		LM1L	6	32	44	38.8	4.16	10.7
		LM1W	6	19	30	25.3	3.77	14.9
		MNMO	6	121	135	126.3	5.42	4.2
		RAMD	6	135	152	145.1	7.16	4.9
		RAMH	6	200	229	215.0	12.13	5.6

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
APHE3M	4	ANGD	4	150	201	172.2	21.71	12.6
		ANGW	4	28	36	31.2	3.59	11.5
		BDBR	4	55	58	56.2	1.5	2.6
		BDM1	4	111	153	128.2	17.91	13.9
		BDHT	4	86	116	98.2	14.84	15.1
		CNM3	4	224	252	233.5	12.97	5.5
		LM1L	4	46	54	50.7	3.94	7.7
		LM1W	4	31	38	33.0	3.36	10.2
		MNMO	4	146	163	157.2	7.80	4.9
		RAMD	4	154	181	170.5	12.12	7.1
		RAMH	4	224	278	241.2	24.91	10.3
APHE4M	4	ANGD	4	168	190	182.0	9.93	5.4
		ANGW	4	28	34	30.7	2.75	8.9
		BDBR	4	58	65	61.0	2.94	4.8
		BBM1	4	149	169	155.0	9.38	6.0
		BDHT	4	115	138	123.5	10.01	8.1
		CNM3	4	224	270	244.0	21.46	8.7
		LM1L	4	49	58	53.5	4.20	7.8
		LM1W	4	33	39	36.5	2.64	7.2
		MNMO	4	162	181	173.7	8.80	5.0
		RAMD	4	160	191	173.0	13.49	7.7
		RAMH	4	238	280	263.5	18.21	6.9
DICE1M	1	ANGD	1	134	134	134.0		
		ANGW	1	14	14	14.0		
		BDBR	1	29	29	29.0		
		BDM1	1	94	94	94.0		
		BDHT	1	73	73	73.0		
		CNM3	1	152	152	152.0		
		LM1L	1	43	43	43.0		
		LM1W	1	23	23	23.0		
		MNMO	1	136	136	136.0		
		RAMD	1	112	112	112.0		
		RAMH	1	171	171	171.0		

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
DICE2M	1	ANGD	1	104	104	104.0		
		ANGW	1	40	40	40.0		
		BDBR	1	25	25	25.0		
		BDMT	1	71	71	71.0		
		BDHT	1	57	57	57.0		
		CNM3	1	144	144	144.0		
		LM1L	1	23	23	23.0		
		LM1W	1	18	18	18.0		
		MNMO	1	85	85	85.0		
		RAMO	1	88	88	88.0		
		RAMH	1	138	138	138.0		
FORS1M	1	ANGD	1	141	141	141.0		
		ANGW	1	18	18	18.0		
		BDBR	1	25	25	25.0		
		BDMT	1	78	78	78.0		
		BDHT	1	66	66	66.0		
		CNM3	1	145	145	145.0		
		LM1L	1	32	32	32.0		
		LM1W	1	22	22	22.0		
		MNMO	1	106	106	106.0		
		RAMO	1	101	101	101.0		
		RAMH	1	153	153	153.0		
FORS2M	2	ANGD	2	97	127	112.0	21.21	18.9
		ANGW	2	7	11	9.0	2.82	31.4
		BDBR	2	23	26	24.5	2.12	8.6
		BDMT	2	62	66	64.0	2.82	4.4
		BDHT	2	50	56	53.0	4.24	8.0
		CNM3	2	97	130	113.5	23.33	20.5
		LM1L	2	24	27	25.5	2.12	8.3
		LM1W	2	15	17	16.0	1.41	8.8
		MNMO	2	80	84	82.0	2.82	3.4
		RAMO	2	78	102	90.0	16.97	18.8
		RAMH	2	124	137	130.5	9.19	7.0

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
HYRA1M	2	ANGD	2	63	80	71.5	12.02	16.8
		ANGW	2	7	11	9.0	2.82	31.4
		BDBR	2	15	17	16.0	1.41	8.8
		BDM1	2	34	45	39.5	7.77	19.6
		BDMT	2	28	35	31.5	4.94	15.7
		CNM3	2	62	69	65.5	4.94	7.5
		LM1L	2	14	15	14.5	0.70	4.8
		LM1W	2	9	10	9.5	0.70	7.4
		MNMO	2	44	48	46.0	2.82	6.1
		RAMD	2	52	63	57.5	7.77	13.5
		RAMH	2	73	82	77.5	6.36	8.2
HYRA2M	2	ANGD	2	92	103	97.5	7.77	7.9
		ANGW	2	8	9	8.5	0.70	8.3
		BDBR	2	18	20	19.0	1.41	7.4
		BDM1	2	52	60	56.0	5.65	10.1
		BDMT	2	44	49	46.5	3.53	7.6
		CNM3	2	79	97	88.0	12.72	14.4
		LM1L	2	19	21	20.0	1.41	7.0
		LM1W	2	14	15	14.5	0.70	4.8
		MNMO	2	61	66	63.5	3.53	5.5
		RAMD	2	66	89	77.5	16.26	20.9
		RAMH	2	101	118	109.5	12.02	10.9
HYCOM	4	ANGD	4	81	90	86.2	4.11	4.7
		ANGW	4	6	7	6.2	0.50	8.0
		BDBR	4	20	23	22.0	1.41	6.4
		BDM1	4	49	54	51.7	2.21	4.2
		BDMT	4	40	42	41.2	0.95	2.3
		CNM3	4	71	87	78.5	7.32	9.3
		LM1L	4	17	19	18.0	0.81	4.5
		LM1W	4	12	13	12.2	0.50	4.0
		MNMO	4	57	60	59.0	1.41	2.3
		RAMD	4	68	78	74.2	4.50	6.0
		RAMH	4	98	121	106.5	10.40	9.7

Subgroup	#	Variable	N	Min	Max	Mean	S.D.	C.V.
INDRM	1	ANGD	1	255	255	255.0		
		ANGW	1	67	67	67.0		
		BDBR	1	79	79	79.0		
		BDM1	1	166	166	166.0		
		BDHT	1	129	129	129.0		
		CNM3	1	353	353	353.0		
		LM1L	1	75	75	75.0		
		LM1W	1	53	53	53.0		
		MNMO	1	223	223	223.0		
		RAMD	1	226	226	226.0		
		RAMH	1	330	330	330.0		
MENO1M	10	ANGD	10	92	113	101.1	6.72	6.6
		ANGW	10	24	46	35.0	7.43	21.2
		BDBR	10	22	31	26.3	2.58	9.8
		BDM1	10	63	78	69.0	4.69	6.7
		BDHT	10	48	59	53.3	3.36	6.3
		CNM3	10	110	147	125.3	12.73	10.1
		LM1L	10	24	31	26.6	2.54	9.5
		LM1W	10	17	21	18.9	1.19	6.3
		MNMO	10	86	100	91.6	4.22	4.6
		RAMD	10	75	100	84.9	8.87	10.4
		RAMH	10	129	148	139.0	6.12	4.4
MENO2M	1	ANGD	1	100	100	100.0		
		ANGW	1	31	31	31.0		
		BDBR	1	35	35	35.0		
		BDM1	1	85	85	85.0		
		BDHT	1	64	64	64.0		
		CNM3	1	141	141	141.0		
		LM1L	1	31	31	31.0		
		LM1W	1	22	22	22.0		
		MNMO	1	114	114	114.0		
		RAMD	1	92	92	92.0		
		RAMH	1	158	158	158.0		

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
PENE1M	1	ANGD	1	81	81	81		
		ANGW	1	10	10	10		
		BDBR	1	22	22	22		
		BDM1	1	57	57	57		
		BDHT	1	47	47	47		
		CNM3	1	105	105	105		
		LM1L	1	20	20	20		
		LM1W	1	13	13	13		
		MNMO	1	70	70	70		
		RAMD	1	82	82	82		
		RAMH	1	115	115	115		
PERA1M	3	ANGD	3	113	133	122.3	10.06	8.2
		ANGW	3	13	22	18.0	4.58	25.4
		BDBR	3	38	43	40.3	2.51	6.2
		BDM1	3	94	101	97.3	3.51	3.6
		BDHT	3	67	82	76.0	7.93	10.4
		CNM3	3	162	180	171.6	9.07	5.2
		LM1L	3	35	42	39.3	3.78	9.6
		LM1W	3	26	29	27.3	1.52	5.5
		MNMO	3	116	136	129.0	11.26	8.7
		RAMD	3	111	135	121.0	12.48	10.3
		RAMH	3	164	189	173.6	13.42	7.7
PERA2M	2	ANGD	2	155	162	158.5	4.94	3.1
		ANGW	2	25	26	25.5	0.70	2.7
		BDBR	2	52	53	52.5	0.70	1.3
		BDM1	2	115	119	117.0	2.82	2.4
		BDHT	2	87	90	88.5	2.12	2.3
		CNM3	2	216	219	217.5	2.12	0.9
		LM1L	2	43	50	46.5	4.94	10.6
		LM1W	2	31	33	32.0	1.41	4.4
		MNMO	2	148	167	157.5	13.43	8.5
		RAMD	2	147	163	155.0	11.31	7.2
		RAMH	2	209	210	209.5	0.70	0.3

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
SUBN1M	8	ANGD	8	102	126	111.6	10.78	9.6
		ANGW	8	13	21	16.2	2.96	18.2
		BDBR	8	22	33	27.7	3.10	11.1
		BDM1	8	65	86	73.7	7.53	10.2
		BDHT	8	52	73	59.3	8.66	14.5
		CNM3	8	117	150	131.6	11.28	8.5
		LM1L	8	25	34	28.6	2.72	9.5
		LM1W	8	18	25	19.8	2.47	12.4
		MNMD	8	85	110	97.0	8.89	9.1
		RAMD	8	88	112	102.6	7.70	7.5
		RAMH	8	127	159	140.3	12.60	8.97
SUBN2M	2	ANGD	2	114	120	117.0	4.24	3.6
		ANGW	2	13	15	14.0	1.41	10.1
		BDBR	2	30	31	30.5	0.70	2.3
		BDM1	2	75	76	75.5	0.70	0.9
		BDHT	2	60	63	61.5	2.12	3.4
		CNM3	2	120	128	124.0	5.65	4.5
		LM1L	2	27	28	27.5	0.70	2.5
		LM1W	2	20	21	20.5	0.70	3.4
		MNMD	2	95	96	95.5	0.70	0.7
		RAMD	2	105	115	110.0	7.07	6.4
		RAMH	2	141	146	143.5	3.53	2.4
SUBN3M	6	ANGD	6	117	133	125.1	6.08	4.8
		ANGW	6	12	25	18.1	5.41	29.8
		BDBR	6	26	38	34.6	4.36	12.5
		BDM1	6	71	90	78.5	6.83	8.7
		BDHT	6	56	77	62.5	7.66	12.2
		CNM3	6	137	155	144.1	6.79	4.7
		LM1L	6	27	37	32.3	3.20	9.9
		LM1W	6	21	25	22.3	1.75	7.8
		MNMD	6	98	113	107.8	5.87	5.4
		RAMD	6	94	125	107.0	11.52	10.7
		RAMH	6	146	154	148.8	2.71	1.8

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
TELE1M	3	ANGD	3	144	154	149.0	5.00	3.3
		ANGW	3	21	28	23.6	3.78	15.9
		BDBR	3	39	45	42.0	3.00	7.1
		BDM1	3	102	108	105.3	3.05	2.9
		BDHT	3	72	88	79.0	8.18	10.3
		CNM3	3	175	207	188.6	16.50	8.7
		LM1L	3	37	48	43.0	5.56	12.9
		LM1W	3	20	30	26.6	5.77	21.6
		MNMO	3	131	157	142.6	13.20	9.2
		RAMD	3	123	148	137.6	13.05	9.4
		RAMH	3	183	189	185.0	3.46	1.8
TELE2M	6	ANGD	6	141	167	151.1	9.15	6.0
		ANGW	6	26	33	30.3	2.42	7.9
		BDBR	6	45	53	48.5	2.81	5.7
		BDM1	6	109	121	116.0	4.64	4.0
		BDHT	6	83	103	93.8	7.98	8.5
		CNM3	6	185	229	210.8	15.65	7.4
		LM1L	6	38	50	44.0	4.69	10.6
		LM1W	6	29	36	32.1	2.48	7.7
		MNMO	6	138	160	150.5	8.73	5.8
		RAMD	6	124	172	142.5	18.19	12.7
		RAMH	6	183	228	215.6	16.69	7.7
TELE3M	12	ANGD	12	127	164	144.6	11.73	8.1
		ANGW	12	15	41	29.0	8.05	27.6
		BDBR	12	44	55	48.3	3.39	7.0
		BDM1	12	100	136	116.0	11.28	9.7
		BDHT	12	69	118	91.6	14.61	15.9
		CNM3	12	181	247	207.3	19.88	9.5
		LM1L	12	40	49	45.3	3.11	6.8
		LM1W	12	23	33	27.5	2.84	10.3
		MNMO	12	142	160	151.0	6.75	4.4
		RAMD	12	115	162	139.9	12.42	8.8
		RAMH	12	175	240	208.0	19.28	9.2

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
TELE4M	4	ANGD	4	141	167	154.0	11.10	7.2
		ANGW	4	33	52	39.7	8.53	21.4
		BDBR	4	45	70	56.5	10.90	19.3
		BDM1	4	105	135	126.2	14.22	11.2
		BDHT	4	90	120	108.7	12.99	11.9
		CHM3	4	239	250	244.0	4.96	2.0
		LM1L	4	43	54	49.0	4.96	10.1
		LM1W	4	28	35	31.7	2.87	9.0
		MNMD	4	126	173	150.0	20.41	13.6
		RAMD	4	141	178	161.0	15.34	9.5
		RAMH	4	212	255	232.2	22.94	9.8
TELE5M	8	ANGD	8	138	167	149.6	10.78	7.2
		ANGW	8	22	46	30.0	7.76	25.8
		BDBR	8	45	65	53.5	6.90	12.9
		BDM1	8	121	138	128.8	7.14	5.5
		BDHT	8	93	112	101.1	6.33	6.2
		CHM3	8	191	264	217.0	21.67	9.9
		LM1L	8	45	59	50.3	5.12	10.1
		LM1W	8	30	33	31.1	1.12	3.6
		MNMD	8	160	181	168.5	7.83	4.6
		RAMD	8	123	162	140.3	13.01	9.2
		RAMH	8	207	230	223.1	8.11	3.6
TRIGM	13	ANGD	13	110	134	122.9	6.34	5.1
		ANGW	13	11	20	15.6	3.09	19.7
		BDBR	13	29	40	32.7	3.03	9.2
		BDM1	13	73	89	80.6	4.53	5.6
		BDHT	13	60	75	66.3	4.05	6.1
		CHM3	13	119	167	147.0	14.07	9.5
		LM1L	13	27	33	30.3	2.01	6.6
		LM1W	13	20	24	21.5	1.33	6.1
		MNMD	13	98	115	107.9	5.37	4.9
		RAMD	13	106	129	116.3	7.30	6.2
		RAMH	13	146	170	156.6	8.31	5.3

Subgroup	N	Variable	N	Min	Max	Mean	S.D.	C.V.
ZAIS1M	1	ANGD	1	232	232	232.0		
		ANGW	1	26	26	26.0		
		BDBR	1	57	57	57.0		
		BDM1	1	120	120	120.0		
		BDHT	1	87	87	87.0		
		CNM3	1	200	200	200.0		
		LM1L	1	46	46	46.0		
		LM1W	1	31	31	31.0		
		MNMD	1	166	166	166.0		
		RAMD	1	196	196	196.0		
		RAMH	1	257	257	257.0		
ZAIS2M	1	ANGD	1	225	225	225.0		
		ANGW	1	16	16	16.0		
		BDBR	1	33	33	33.0		
		BDM1	1	119	119	119.0		
		BDHT	1	98	98	98.0		
		CNM3	1	202	202	202.0		
		LM1L	1	52	52	52.0		
		LM1W	1	32	32	32.0		
		MNMD	1	182	182	182.0		
		RAMD	1	170	170	170.0		
		RAMH	1	271	271	271.0		

APPENDIX 6.

SAS-IML PROGRAMS

Statistical programs written in SAS Interactive Matrix Language (SAS Institute, 1988). Program comments are bracketed by slashes and stars (/*comment*/).

PRINCIPAL COMPONENTS ANALYSIS, GENERALIZED DISTANCES, Q-Q PLOTS, NORMALITY TESTING, AND ANGULAR DIFFERENCES ROUTINES.

```
/* MULTIVAR.IML VER. 5-23-93 */
/* MULTIVARIATE ANALYSIS PROGRAM IN SAS IML */
/*----------------- SET WORKING ENVIRONMENT -------------------------*/
     OPTIONS NOSOURCE; /*EXCLUDE PROGRAM LINES FROM OUTPUT*/
     LIBNAME SASDAT 'C:\ZBALES\INPUT\SAS';
     LIBNAME FLOPDAT 'B:\';
     PROC PRINTTO LOG = 'PRN';         /* SET OUTPUT DESTINATION */
     PROC IML WORKSIZE = 210; /* SET SPACE FOR MATRIX OPERATIONS */
     RESET LINESIZE = 175 PAGESIZE = 35;
     TWELVE = {12};
     NEWPAGE = BYTE(TWELVE); /* PAGE BREAK CONTROL CODE */
/*SET*/  TRUNCLEV = 96;
/*--SET--*/ AXISPERC = {5}; /* PERCENTAGE CUTOFF FOR PC AXES */
/*--SET--*/ PLOTTYPE = "GRPSYMB"; /* "SEX"  "GRPNAME" "GRPSYMB" "LOC" "IND" */
/*--SET--*/ ANALYSE = "AS";  /* [AG] ALL GENERA   [AS] ALL SUBGROUPS */
                             /* [SG] SOME GENERA  [SS] SOME SUBGROUPS */
     IF ANALYSE = "AG" THEN DO;
        PRINT "------------- ANALYSIS OF ALL GENERA ----------------";
        PRINT "----------------------------------------------------";
     END;
     IF ANALYSE = "AS" THEN DO;
        PRINT "------------- ANALYSIS OF ALL SUBGROUPS --------------";
        PRINT "----------------------------------------------------";
     END;
     IF ANALYSE = "SG" | ANALYSE = "SS" THEN DO;
         DOGRPS = {MENO};
     /*   DOGRPS = {UNICN JAVAN}; */
       /*  DOGRPS = {TELE};  */
      /*   DOGRPS = {UNICN JAVAN}; */
       /*  DOGRPS = {AMYN DICE FORS HYCO LOPS MENO PERA QACE RIGO TELE
                                                      WSUB YRAN}; */
       /*  BOGRPS = {ACER DICE FORS HYCO LOPS MENO PERA RIGO SUBN TELE  */
     /*  DOGRPS = {TELE1S TELE2S TELE3S TELE4S TELE5S TELE6S}; */
```

```
      /*   DOGRPS =  {TELE1M TELE2M TELE3M TELE4M
                     TELE5M TELE6M TELE7M TELE8M TELE9M};     */
    /*  DOGRPS = {BICOS TELE1S TELE2S TELE3S TELE4S TELE5S TELE6S}; */
    /*  DOGRPS = {BICOM TELE1M TELE2M TELE3M TELE4M
                     TELE5M TELE6M TELE7M TELE8M TELE9M};  */
    /*    BOGRPS = {BICOM CERAM UNICM JAVAM SUMAM};  */
    /*      DOGRPS = {BICOS CERAS UNICS JAVAS SUMAS};  */
    /*    DOGRPS = {ACER1M ACER2M APHE1M APHE2M APHE3M APHE4M
                     APHE5M DICE1M DICE2M DICE3M DICE4M DICE5M
                     FORS1M FORS2M HYCOM HYRA1M HYRA2M MENO1M
                     MENO2M PERA1M PERA2M PERA3M SUBH1M SUBH2M
                     SUBH3M SUBH4M TELE1M TELE2M TELE3M TELE4M
                     TELE5M TELE6M TELE7M TELE8M TELE9M TRIGM
                     ZAIS1M ZAIS2M};  */
    /*    DOGRPS = {ACER1S ACER2S AMYNS APHE1S APHE2S DICE1S
                       DICE2S DICE3S DICE4S DICE5S DICE6S FORSS
                       HYCOS HYRA1S HYRA2S HYRA3S MENOS PERA1S
                       PERA2S SUBH1S SUBH2S SUBH3S SUBH4S SUBH5S
                       TELE1S TELE2S TELE3S TELE4S TELE5S TELE6S
                       TRIG1S TRIG2S XAMYS}; */

      PRINT "------- FOLLOWING GROUPS SPECIFIED FOR ANALYSIS ---------";
      PRINT "---------------------------------------------------------";
      PRINT DOGRPS;
      PRINT "---------------------------------------------------------";
      END;
/*SET*/      REPEAT = "Y";   /* BYPASS "CREATE" STATMENTS [Y]es  [N]o   */
/*SET*/      RUN = "M"; /* [S]kull    [M]andible  */
             IF RUN = "S" THEN DO;
                PCLIMITS = {280 125, -280 -125};
                BLANKS = {" "," "};
                PRINT "---------------->> SKULL <<--------------------";
             END;
             IF RUN = "M" THEN DO;
                PCLIMITS = {100 40, -100 -40};
                BLANKS = {" "," "};

                PRINT "--------------->> MANDIBLE <<------------------";
             END;
/*SET*/    TFORM = {"N"}; NO = {"N"}; YES = {"Y"};    /* TRANSFORMATION */
/*SET*/    PLEV = "MED";  /* PRINT LEVEL [MIN]imum  [MED]ium  [MAX]imum */
/*SET*/    USE SASDAT.MANOSUBS; /* DATA SET FOR ANALYSIS*/
      READ ALL INTO TEMPDATA [ROWNAME=ID COLNAME=VARNAME];
      IF TFORM = YES THEN DATA = LOG(TEMPDATA)#0.43429448;
      IF TFORM = NO THEN DATA = TEMPDATA;
 FREE TEMPDATA;
      CASES = NROW(DATA);   /* NUMBER OF CASES */
      NVAR = NCOL(DATA);  /* NUMBER OF VARIABLES */
      ROWVAR = VARNAME`;    /* Column of variable names */
```

```
/*-------------------- SET GROUPINGS AND LABELS ------------------*/
     READ ALL VAR(LOCAL) INTO LOCSEX;
     SEXCOL = SUBSTR(LOCSEX,2,1);
     LOCALCOL = SUBSTR(LOCSEX,1,1);
 FREE LOCSEX;
     IF ANALYSE = "AG" | ANALYSE = "SG" THEN DO;
        READ ALL VAR(GENUS) INTO GRPLABLS;
     END;
     IF ANALYSE = "AS" | ANALYSE = "SS" THEN DO;
        IF RUN = "N" THEN DO;
           READ ALL VAR(SUBS) INTO GRPLABLS;
        END;
        IF RUN = "S" THEN DO;
           READ ALL VAR(SUBG) INTO GRPLABLS;
        END;
     END;
     IF ANALYSE = "AG" | ANALYSE = "AS" THEN DO;
        GRPSROW = UNIQUE(GRPLABLS);   /* ROW VECTOR *//* Row of unique group names */
        GRPSCOL = GRPSROW`;    /* COLUMN VECTOR */    /* unique group names */
     END;


     IF ANALYSE = "SG" | ANALYSE = "SS" THEN DO;
        GRPSROW = DOGRPS;  /* ROW VECTOR */
        GRPSCOL = GRPSROW`;   /* COLUMN VECTOR */
     END;
     NGRPINIT = NROW(GRPSCOL);
        VARCOL = VARNAME`;              /* COLUMN OF VARIABLE NAMES */
        PRINT "NUMBER OF VARIABLES " NVAR;
        PRINT "VARIABLE NAMES ", VARCOL;

        IF ANALYSE = "AG" | ANALYSE = "SG" THEN DO;
           PRINT "NUMBER OF STARTING GENERA " NGRPINIT;
           PRINT "GENERA NAMES ", GRPSCOL;
        END;
         IF ANALYSE = "AS" | ANALYSE = "SS" THEN DO;
           PRINT "NUMBER OF STARTING SUBGROUPS " NGRPINIT;
           PRINT "SUBGROUP NAMES  ", GRPSCOL;
        END;
     NROOTS = NVAR; /* NUMBER OF PRINCIPAL COMPONENT ROOTS */
     PCLAB0 = {PC}; /* PC AXIS LABELS ROUTINES */
     PCLAB1 = REPEAT(PCLAB0,1,NROOTS);
     PCLAB2 = DO(1,NROOTS,1);
     PCLAB2A = CHAR(PCLAB2,2);
        CALL CHANGE(PCLAB2A," 1","1");
        CALL CHANGE(PCLAB2A," 2","2");
        CALL CHANGE(PCLAB2A," 3","3");
        CALL CHANGE(PCLAB2A," 4","4");
        CALL CHANGE(PCLAB2A," 5","5");
```

```
      CALL CHANGE(PCLAB2A," 6","6");
      CALL CHANGE(PCLAB2A," 7","7");
      CALL CHANGE(PCLAB2A," 8","8");
      CALL CHANGE(PCLAB2A," 9","9");
    PCLABL = CONCAT(PCLAB1, PCLAB2A);

/*------------ SUB-GENERIC GROUP ROUTINES ---------------------- */
/*---------------------------------------------------------------*/
    CNTSKIP = {0};
    CNTGRPS = {0};
    GRPNUM = {0};
DO ITERA = 1 TO NGRPINIT BY 1; /* CYCLE THROUGH GROUPS */
  CNTCASES = {0};
  GRPNUM = GRPNUM+{1};
  GRPNAME = GRPSCOL[GRPNUM];
     DO ITERB = 1 TO CASES;      /* COLLECT GROUP INFO */
        IF GRPLABLS[ITERB] =  GRPNAME THEN DO; /* FIND DATA FOR GROUP */
          CNTCASES = CNTCASES + {1};
          ROWDAT = DATA[ITERB,1];  /* SPECIMEN DATA */
          IF RUN = "S" THEN DO;
             SIZEDAT1 = DATA[ITERB,13];
          END;
          IF RUN = "M" THEN DO;
             SIZEDAT1 = DATA[ITERB,6];
          END;
          ROWID = ID[ITERB];   /* SPECIMEN ID */
          SEXCHAR = SEXCOL[ITERB];   /* SPECIMEN SEX */
          LOCALCHAR = LOCALCOL[ITERB];   /* SPECIMEN LOCALITY */
          IF CNTCASES = 1 THEN DO; /* SETUP MATS FOR THIS GROUP  */
             SUBDAT = ROWDAT;
             SIZEDAT2 = SIZEDAT1;
             SUBGRPID = GRPNAME;
             SUBINDID = ROWID;
             SUBSEXS = SEXCHAR;
             SUBLOCS = LOCALCHAR;

          END;
          IF CNTCASES > 1 THEN DO;  /* ACCUM FOR THIS GRP */
             SUBDAT = SUBDAT//ROWDAT;
             SIZEDAT2 = SIZEDAT2//SIZEDAT1;
             SUBGRPID = SUBGRPID//GRPNAME;
             SUBINDID = SUBINDID//ROWID;
             SUBSEXS = SUBSEXS//SEXCHAR;
             SUBLOCS = SUBLOCS//LOCALCHAR;
          END;
        END; /* GRPLABLS = GRPNAME LOOP */
     END; /* END ITERB */
    SUBSIZE = NROW(SUBDAT);
    PRINT " SIZE OF GROUP" ITERA SUBSIZE;
```

```
      IF SUBSIZE > 1 THEN DO;     /* ACCUM ACROSS GRPS FOR POOLED */
         CNTGRPS = CNTGRPS+{1};
         IF ITERA = 1 THEN DO;
            GRPSKEPT = GRPNAME;
            GSIZECOL = SUBSIZE;
            ACCGRPID = SUBGRPID;
            ACCINDID = SUBINDID;
            SEXIDS = SUBSEXS;
            LOCALIDS = SUBLOCS;
            SIZEDAT3 = SIZEDAT2;
         END;
         IF ITERA > 1 THEN DO;
            GRPSKEPT = GRPSKEPT//GRPNAME;
            GSIZECOL = GSIZECOL//SUBSIZE;
            ACCGRPID = ACCGRPID//SUBGRPID;
            ACCINDID = ACCINDID//SUBINDID;
            SEXIDS = SEXIDS//SUBSEXS;
            LOCALIDS = LOCALIDS//SUBLOCS;
            SIZEDAT3 = SIZEDAT3//SIZEDAT2;
         END;
      END; /* SUBSIZE > 1 LOOP */
 FREE ROWDAT;

         IF SUBSIZE = 1 THEN DO;        /* KEEP TRACK OF SKIPPED GROUPS */
            NAMESKIP = GRPNAME||ROWID;
       CNTSKIP = CNTSKIP + {1};

              IF CNTSKIP = 1 THEN DO;
                 SKIPMAT = NAMESKIP;
              END;
              IF CNTSKIP > 1 THEN DO;   /* MORE THAN ONE SKIPPED GROUP */
                 SKIPMAT = SKIPMAT//NAMESKIP;
              END;
         END;
         IF ITERA = NGRPINIT THEN DO;
            IF CNTSKIP > 0 THEN DO;
               PRINT "SUMMARY OF SKIPPED 1-SPECIMEN GROUPS ";
               PRINT SKIPMAT;
            END;
         END;
      IF SUBSIZE = 1 THEN GOTO LEAPFROG;   /* NO ANALYSIS FOR ONE SPECIMEN */
         IF PLEV = "MAX" THEN DO;
          PRINT NEWPAGE;
          PRINT, GRPNAME;
          PRINT, SUBSIZE[FORMAT=2.0];
          PRINT, SUBDAT[FORMAT=3.0 ROWNAME = SUBINDIDS  COLNAME = VARNAME];
        END;
      SUBMEANS = SUBDAT[:,];                  /* ROW OF VARIABLE MEANS */
```

```
    MEANMAT = REPEAT(SUBMEANS,SUBSIZE,1);   /* MEAN MATRIX */
    SUBDEVS = SUBDAT - MEANMAT;             /* DEVIATIONS FROM MEAN */
    SUBSSCP = SUBDEVS` * SUBDEVS;           /* SUMS-OF-SQUARES AND CROSS-PRODUCTS */
    SUBCOV = SUBSSCP * ((SUBSIZE-(1))**-1.0);/* GROUP COVARIANCE MATRIX */
      IF PLEV = "MAX" THEN DO;
      PRINT NEWPAGE;
       PRINT "COVARIANCE MATRIX FOR  " GRPNAME;
       PRINT SUBCOV[FORMAT=5.2 ROWNAME =  ROWVAR  COLNAME = VARNAME];
      END;
        IF PLEV = "MAX" THEN DO;
          VARIANCE = VECDIAG(SUBCOV);  /* COLUMN VECTOR OF VARIANCES */
          STDDEV = SQRT(VARIANCE);
          STDINVRS = STDDEV##-1.0;
          STDMAT = DIAG(STDINVRS);
          CORREL = STDMAT * SUBCOV * STDMAT; /* CORRELATION MATRIX FROM COVARIANCE MATRIX */
          PRINT NEWPAGE;
          PRINT CORREL[FORMAT=3.1 ROWNAME = ROWVAR COLNAME = VARNAME];
        END;
FREE MEANMAT SUBMEANS SUBSSCP CORREL;
    IF ITERA = 1 THEN DO;      /* SAVE MEAN-CORRECTED DATA FOR POOLED-WITHIN PCA */
       POOLDAT = SUBDEVS;
    END;
    IF ITERA ^= 1 THEN DO;
       POOLDAT = POOLDAT//SUBDEVS;
    END;
FREE PCLAB0 PCLAB1 PCLAB2 PCLAB2A;
    CALL EIGEN(SUBEIGVAL, SUBEIGVEC, SUBCOV);
    SUBVALS=SUBEIGVAL[1:NROOTS,1];          /* COLUMN OF EIGENVALUES */
    SUBEIGS=SUBEIGVEC[,1:NROOTS];           /* COLUMN OF EIGENVECTORS */
FREE SUBEIGVAL SUBEIGVES;
    IF ITERA = 1 THEN DO;
       PCS = SUBEIGS[,1];       /* ACCUMULATE PC 1'S FOR ANGLE CALCS */
       VALSUMM = SUBVALS;   /* ACCUMULATE EIGENVALUES FOR SUMMARY */
    END;
    IF ITERA ^= 1 THEN DO;
       PCS = PCS||SUBEIGS[,1];
       VALSUMM = VALSUMM||SUBVALS;
    END;
    ADDVALS = SUBVALS[+,];    /* SUMMATE EIGENVALUES */
    PERCENT = (SUBVALS * ADDVALS**-1.0) * 100;  /* EIGENVALUE PERCENT OF TOTAL */

     CNTSUB = {0};
       ITVAL = NROW(SUBVALS);
       DO ITERO = 1 TO ITVAL;
          PERCVAL = SUBVALS[ITVAL];
             IF PERCVAL > 1 THEN DO;
                CNTSUB = CNTSUB + 1;
             END;
       END;
```

```
     IF ITERA = 1 THEN DO;

         PERCS = PERCENT;     /* ACCUMULATE PERCENTAGES FOR SUMMARY */
         ADDSUMM = ADDVALS;
     END;
     IF ITERA ^=1 THEN DO;
        PERCS = PERCS||PERCENT;
        ADDSUMM = ADDSUMM||ADDVALS;
     END;

     VALMAT = SUBVALS||PERCENT;
     NAMECOL = {EIGENVALUE PERCENT};
FREE PERCENT;

          IF PLEV = "MED" THEN DO;
           PRINT "GROUP SIZE " SUBSIZE;
           PRINT "GROUP IS " GRPNAME;
           PRINT "GROUP EIGENVALUES" , VALMAT[FORMAT=7.3 ROWNAME=PCLABL COLNAME=NAMECOL],;
           PRINT "SUM OF THE EIGENVALUES " ADDVALS[FORMAT=7.3];
           PRINT NEWPAGE;
           PRINT "GROUP EIGENVECTORS FOR " GRPNAME;
           PRINT SUBEIGS[FORMAT=6.3 ROWNAME = ROWVAR COLNAME = PCLABL];
          END;
          VLABS1 = ROWVAR;     /* SORTING ROUTINES */
          EIGS1 = SUBEIGS[,1];
          ABEIGS = ABS(EIGS1);
          R1 = RANK(ABEIGS);

          SORTPC1 = EIGS1;
                   DO ITERQ = 1 TO NVAR BY 1;
                      RJ1 = R1[ITERQ];
                      SORTPC1[RJ1,] = EIGS1[ITERQ,];
                      VLABS1[RJ1,] = ROWVAR[ITERQ,];
                   END;
          PRINT NEWPAGE;
          PRINT "SORTED EIGENVECTORS FOR FIRST PRINCIPAL AXIS";
          PRINT VLABS1 SORTPC1[FORMAT=4.2];
FREE ADDVALS PERCENT VALMAY NAMECOL;
     IF SUBSIZE > 2 THEN DO;  /* CORRELATIONS OF VARIABLES WITH PCS */
     DO FIRSTIT = 1 TO NVAR BY 1;
        DO SECONDIT = 1 TO NROOTS BY 1;
                  EIG = SUBEIGS[FIRSTIT, SECONDIT];
                  VAL = SUBVALS[SECONDIT,];
                  VAR = SUBCOV[FIRSTIT, FIRSTIT];
                  IF  VAL > 1 THEN
                  CORRPC = EIG * SQRT(VAL)/SQRT(VAR);
                  ELSE CORRPC = 0;
                IF SECONDIT = 1 THEN DO;/* CONSTRUCT ROW MATRIX */
                  ROWCORR = CORRPC;
```

```
               END;
               IF SECONDIT ^=1 THEN DO;
                  ROWCORR = ROWCORR||CORRPC;
               END;
            END; /* SECONDIT */

                IF FIRSTIT = 1 THEN DO;    /* APPEND ROWS TO MATRIX */
                  CORRMAT = ROWCORR;
               END;
               IF FIRSTIT ^=1 THEN DO;

                  CORRMAT = CORRMAT //ROWCORR;
               END;
         END; /* FIRSTIT */
FREE SUBVALS SUBCOV CORRPC ROWCORR;
            IF PLEV = "MAX" THEN DO;
               PRINT NEWPAGE;
               PRINT "CORRELATIONS OF VARIABLES WITH PRINCIPAL COMPONENTS ";
               PRINT CORRMAT[FORMAT = 4.3 ROWNAME =  VARNAME COLNAME = PCLABL];
            END;
         END; /* END VARIABLE-CORRELATION ROUTINES */
FREE CORRMAT;
      SUBSCOR = SUBDEVS * SUBEIGS;  /* INDIVIDUAL SCORES */
FREE SUBDAT SUBEIGS;
FREE SUBDAT SUBEIGS SCORMEAN SCORMDES;
   IF SUBSIZE = 2 THEN DO;
      NPLOTS = 1;
   END;
   IF SUBSIZE > 2 THEN DO;
      IF CNTSUB < 3 THEN DO;
         NPLOTS = 1;
      END;
      IF CNTSUB > 2 THEN DO;
         NPLOT1 = CNTSUB/2 + 3/4;
         NPLOTS = INT(NPLOT1);
         IF RUN = "M" THEN IF NPLOTS = 6 THEN NPLOTS = 5;
         IF RUN = "S" THEN IF NPLOTS = 10 THEN NPLOTS = 9;
      END;
   END; /* SUBSIZE > 2 LOOP */
      XAX = {1};
      YAX = {2};
 IF PLEV = "MED" THEN DO;
          DO ITERC = 1 TO NPLOTS BY 1; /* SORT SCORES FOR EACH PLOT */
                XYMAT = SUBSCOR[,XAX:YAX];
                 PCX = SUBSCOR[,XAX];  /* SORT ON X-AXIS PCS */
                 RS = RANK(PCX);
                 SORTIDS = SUBINOID;
                 SORTVALS = XYMAT;
                    DO ITERG = 1 TO SUBSIZE BY 1;
```

```
                    RJ = RS[ITERQ];
                    SORTIDS[RJ,] = SUBINDID[ITERQ,];
                    SORTVALS[RJ,] = XYMAT[ITERQ,];
                  END;
                PRINT NEWPAGE;
                PRINT "SORTED SCORES FOR PC " YAX[FORMAT=2.0] "VS" XAX[FORMAT=2.0];
                PRINT SUBINDID XYMAT[FORMAT=4.1] SORTIDS SORTVALS[FORMAT = 4.1];
                PRINT NEWPAGE;
            IF PLOTTYPE = "SEX" THEN PLOTLABL = SEXIDS;
            IF PLOTTYPE = "LOC" THEN PLOTLABL = LOCALIDS;
            IF PLOTTYPE = "GRPNAME" THEN PLOTLABL = SUBGRPID;
            IF PLOTTYPE = "IND" THEN PLOTLABL = SUBINDID;
            IF PLOTTYPE = "GRPSYMB" THEN DO;
               PLOYLABL = SUBSTR(SUBGRPIDS,1,1);
            END;
                PLOTLABL = PLOTLABL//BLANKS;
                XYMAT = XYMAT//PCLIMITS;
                CALL PGRAF(XYMAT, PLOTLABL, PCLABL[XAX], PCLABL[YAX]);
             OLDXAX = XAX;
             OLDYAX = YAX;
             XAX = OLDYAX+(1);
             YAX = OLDXAX+(3);
          END;
   END;  /* PLEV LOOP */
LEAPFROG:;
END;  /* END ITERA */
          NGRPKEPT = CNTGRPS;
          NIDS = NROW(ACCINDID);
          PRINT "GROUPS SKIPPED IN ANALYSIS " SKIPMAT;
          PRINT "NUMBER OF GROUPS REMAINING", NGRPXEPT;
          PRINT "REMAINING GROUPS & SIZES", GRPSKEPT GSIZECOL;
/* ---------------- TOTAL VARIANCE VS SAMPLE SIZE -----------------*/
/* ---------------------------------------------------------------*/
   IF NGRPKEPT > 1 THEN DO;
        XYMAT1 = GSIZECOL||ADDSUMM`;

      IF PLEV = "MED" THEN DO;
        PRINT NEWPAGE;
        CALL PGRAF(XYMAT1, GRPSKEPT, 'SAMPLE SIZE', 'TOTAL VARIANCE');
      END;
   END;
FREE XYMAT1;
/* -------------- PC1 EIGENVALUE VS SAMPLE SIZE ------------------*/
/* ---------------------------------------------------------------*/
    IF PLEV = "MED" THEN DO;
      IF NGRPKEPT > 1 THEN DO;
         PRINT NEWPAGE;
         PC1VALR = VALSUMM[1,];
         PC1VALC = PC1VALR`;
```

```
         XYMAT2 = GSIZECOL||PC1VALC;
         CALL PGRAF(XYMAT2, GRPSKEPT, 'SAMPLE SIZE', 'PC1 VARIANCE');
      END;
   END;
FREE XYMAT2 PC1VALR PC1VALC;
/*---------------- POOLED-WITHIN GROUP ROUTINES --------------------*/
/*------------------------------------------------------------------*/
      POOLNUM = NROW(POOLDAT);
      PRINT "NUMBER OF POOLED DATA CASES " POOLNUM;
      POOLSSCP = POOLDAT` * POOLDAT;
      POOLCOV  = POOLSSCP * ((POOLNUM-NGRPKEPT)**-1.0); /* POOLED COVARIANCE MATRIX*/
    /*  NROOTS = MIN(NVAR,POOLNUM-(1)); */
         NROOTS = NVAR;
       PRINT " NUMBER OF ROOTS FOR POOLED ANALYSIS " NROOTS;
      PCLAB0 = {PC}; /* PC AXIS LABEL ROUTINES */
      PCLAB1 = REPEAT(PCLAB0,1,NROOTS);
      PCLAB2 = DO(1,NROOTS,1);
      PCLAB2A = CHAR(PCLAB2,2);
         CALL CHANGE(PCLAB2A," 1","1");
         CALL CHANGE(PCLAB2A," 2","2");
         CALL CHANGE(PCLAB2A," 3","3");
         CALL CHANGE(PCLAB2A," 4","4");
         CALL CHANGE(PCLAB2A," 5","5");
         CALL CHANGE(PCLAB2A," 6","6");
         CALL CHANGE(PCLAB2A," 7","7");
         CALL CHANGE(PCLAB2A," 8","8");
         CALL CHANGE(PCLAB2A," 9","9");
      PCLABL = CONCAT(PCLAB1, PCLAB2A);
FREE WSSCP;
      CALL EIGEN(PCEIGVAL, PCEIGVEC, POOLCOV);
      POOLEVAL = PCEIGVAL[1:NROOTS,];
      ADPOOVAL = POOLEVAL[+,];  /* SUMMATE EIGENVALUES */
      POOLPERC = (POOLEVAL * ADPOOVAL**-1.0) * 100; /* EIGENVALUE PERCENT OF TOTAL */
      CUMUPERC = CUSUM(POOLPERC);
      NPS = NROW(CUMUPERC);
            DO ITER = 1 TO NPS;
/*SET*/         IF CUMUPERC[ITER,] < TRUNCLEV THEN DO;  /* SET TRUNCATION LEVEL*/
                    TRUNCROW = ITER;
                END;
            END;

          /*  DO ITER = 1 TO NPS WHILE(POOLEVAL[ITER,] > 0.00001);
                    TRUNCLEV = ITER;
            END;
            IF TRUNCLEV < NVAR THEN DO;
               PRINT " ZERO EIGENVALUE TRUNCATION LEVEL " TRUNCLEV;
            END;    */
        COUNTVAL = {0};
          DO ITER = 1 TO NROOTS BY 1;
```

```
            IF POOLPERC[ITER] > AXISPERC THEN DO;
               COUNTVAL = COUNTVAL + {1};
            END;
         END;

      FIRSTCOL = PCEIGVEC[,1];      /* SAVE FIRST PC */
      POOLSCOR = POOLDAT * PCEIGVEC;
      FREE PCEIGVEC;
         MAX1SCOR = MAX(POOLSCOR[,1]);  /* SETUP FOR FIXING AXES */
         MIN1SCOR = MIN(POOLSCOR[,1]);
         MAX2SCOR = MAX(POOLSCOR[,2]);
         MIN2SCOR = MIN(POOLSCOR[,2]);
         MAXVALS = MAX1SCOR||MAX2SCOR;
         MINVALS = MIN1SCOR||MIN2SCOR;
         BLANKS = {" ", " "};
   FREE MAX1SCOR MIN1SCOR MAX2SCOR MIN2SCOR;
      VALMAT = POOLEVAL||POOLPERC||CUMUPERC;
      COLNAM = {EIGENVALUE POFTOTAL CUMULATIVE};
      PRINT NEWPAGE;
      PRINT, "SUMMARY OF EIGENVALUES FOR POOLED-WITHIN PCA ";
      PRINT VALMAT[FORMAT = 9.6 ROWNAME = PCLABL COLNAME = COLNAM];
IF REPEAT = "N" THEN DO; /* SAVE POOLED SCORES IF RUN IS NOT REPEAT */
   IF RUN = "M" THEN DO;
      CREATE SASDAT.POOLSCOR VAR { PC1 PC2 PC3 PC4 PC5 PC6 PC7 PC8 PC9 PC10 PC11 };
   END;
   IF RUN = "S" THEN DO;
      CREATE SASDAT.POOLSCOR VAR { PC1 PC2 PC3 PC4 PC5 PC6 PC7 PC8 PC9

                                   PC10 PC11 PC12 PC13 PC14 PC15 PC16

                                   PC17 PC18 PC19 };
   END;
   APPEND FROM POOLSCOR;
   CLOSE SASDAT.POOLSCOR;
END; /* END REPEAT IF */

FREE PCLABL1 PCLABL2 PCLABL3 PCLABL4
       KEEPEIG PCEIGMAT PCEIGVAL PCEIGVEC;
      NPLOTS1 = COUNTVAL/2 + 3/4;
      NPLOTS = INT(NPLOTS1);
      PRINT "NUMBER OF PLOTS FOR POOLED-WITHIN PCA " NPLOTS;
       XAX = {1};
       YAX = {2};
  DO ITERZ = 1 TO NPLOTS BY 1;
        XYMAT = POOLSCOR[,XAX:YAX];
                 PCX = POOLSCOR[,XAX];  /* SORT ON X-AXIS PCS */
                 RS = RANK(PCX);
                 SORTIDS = ACCINDID;
                 SORTVALS = XYMAT;
```

```
                SORTSIZE = SIZEDAT3;
                   DO ITERQ = 1 TO POOLNUM BY 1;
                      RJ = RS[ITERQ];
                      SORTIDS[RJ,] = ACCINDID[ITERQ,];
                      SORTVALS[RJ,] = XYMAT[ITERQ,];
                      SORTSIZE[RJ,] = SIZEDAT3[ITERQ,];
                   END;
              PRINT NEWPAGE;
              PRINT "POOLED SCORES FOR PC " YAX[FORMAT=2.0] "VS" XAX[FORMAT=2.0];
              PRINT ACCINDID XYMAT[FORMAT = 4.1] SORTIDS SORTVALS[FORMAT = 4.1]
SORTSIZE[FORMAT=3.0];
              PRINT NEWPAGE;
 FREE SORTSIZE;

           IF PLOTTYPE = "SEX" THEN PLOTLABL = SEXIDS;
           IF PLOTTYPE = "LOC" THEN PLOTLABL = LOCALIDS;
           IF PLOTTYPE = "GRPNAME" THEN PLOTLABL = ACCGRPID;
           IF PLOTTYPE = "GRPSYMB" THEN DO;
              PLOTLABL = SUBSTR(ACCGRPID,1,1);
           END;
           IF PLOTTYPE = "IND" THEN PLOTLABL = ACCINDID;
           IF ITERZ = 1 THEN DO;
             CALL PGRAF(XYMAT, PLOTLABL, PCLABL[XAX], PCLABL[YAX]);  /*PC SCATTER*/
           END;
          IF ITERZ > 1 THEN DO;
             XYFIXEDA = XYMAT//MAXVALS;
             XYFIXED = XYFIXEDA//MINVALS;
             PLOTLABL = PLOTLABL//BLANKS;
             CALL PGRAF(XYFIXED, PLOTLABL, PCLABL[XAX], PCLABL[YAX]);
          END;
 FREE PCX PCXY RS SORTIDS SORTVALS XYMAT XYFIXEDA XYFIXED;
        OLDXAX = XAX;
        OLDYAX = YAX;
        XAX = OLDYAX+(1);
        YAX = OLDXAX+(3);
 END; /* PLOT LOOP */
 FREE PLOTLABL XYFIXEDA XYFIXED;
/*-------- SUMMARY OF GROUP AND POOLED EIGENVALUES ----------*/
/*---------------------------------------------------------------*/

 IF NGRPKEPT > 1 THEN DO;  /* SPLIT LARGE TABLE INTO TWO*/
     LEFTNUM = NGRPKEPT/2;
     RITENUM = LEFTNUM + (1);
     LEFTLABL = GRPSKEPT`[,1:LEFTNUM];
     LPOOLAB = "  POOL";
     LABLLEFT = LEFTLABL||LPOOLAB;
     RITELABL = GRPSKEPT`[,RITENUM:NGRPKEPT];
     PRINT NEWPAGE;
     PRINT "SUMMARY OF SUBGROUP EIGENVALUES ";
```

```
/* LEFT HALVES OF EIGENVALUE & SUM-OF-EIGENVALUES MATRICES */
     LEFTEVAL = VALSUMM[,1:LEFTNUM];
     LFTPOOL = LEFTEVAL||POOLEVAL;  /* POOLED APPENDED TO LEFT HALF */
        PRINT, LFTPOOL[FORMAT=6.4 ROWNAME = PCLABL COLNAME = LABLLEFT];
     LEFTADD = ADDSUMM[1,1:LEFTNUM];
     ADDPOOL = LEFTADD||ADPOOVAL;  /* POOLED APPENDED TO LEFT HALF */
        PRINT "SUM OF THE EIGENVALUES";
        PRINT, ADDPOOL[FORMAT = 6.4 COLNAME = LABLLEFT];
FREE LEFTEVAL LEFTADD ADPOOVAL;
/* RIGHT HALVES OF EIGENVALUE & SUM-OF-EIGENVALUES MATRICES */
     RITEEVAL = VALSUMM[,RITENUM:NGRPKEPT];
        PRINT, RITEEVAL[FORMAT=6.4 ROWNAME = PCLABL COLNAME = RITELABL];
     RITEADD = ADDSUMM[,RITENUM:NGRPKEPT];
        PRINT, RITEADD[FORMAT=6.4 COLNAME = RITELABL];
FREE RITEEVAL ADDSUMM RITEADD;
        PRINT NEWPAGE;
        PRINT "SUMMARY OF PERCENTAGE CONTRIBUTIONS OF EIGENVALUES FOR SKUL VARIABLES";
     LEFTPERC = PERCS[,1:LEFTNUM];  /* LEFT HALF OF PERCENTAGES MATRIX */
     LPERPOO = LEFTPERC||POOLPERC;  /* POOLED APPENDED TO LEFT HALF */
        PRINT, LPERPOO[FORMAT=6.4 ROWNAME = PCLABL COLNAME = LABLLEFT];
FREE LEFTNUM LEFTPERC LEFTLADL;
     /* RIGHT HALF OF PERCENTAGE MATRIX */
     RITEPERC = PERCS[,RITENUM:NGRPKEPT];
        PRINT, RITEPERC[FORMAT= 6.4 ROWNAME = PCLABL COLNAME = RITELABL];

END;
FREE PERCS LEFTNUM RITENUM LEFTPERC RITEPERC LEFTLADL RITELABL LABLLEFT;
/*-------------------- POOLED-WITHIN NORMALITY CHECKS ---------------*/
/*-----------------------------------------------------------------*/
       PRINT " DEGREES OF FREEDOM ADJUSTMENT ";

        DFT = POOLNUM - {1};
        DFW = POOLNUM - NGRPKEPT;
        FACTOR = DFT/DFW;
        PRINT "TOTAL DF ", DFT;
        PRINT "POOLED W/I DF ", DFW;
        PRINT "-------DEGREES OF FREEDOM TRANSFORMATION FACTOR-----";
        PRINT FACTOR;
 FREE DFT DFW;

/* ----- MAHALANOBIS DISTANCES ----- */
       PRINT " USED TRUNCATED PC SCORES & LAMBDAS FOR DSQ CALCULATION";
       PRINT "NUMBER OF LAMBDAS RETAINED " TRUNCROW;
       LAMBDIAG = DIAG(POOLEVAL);
       LAMBDAS = LAMBDIAG[1:TRUNCROW,1:TRUNCROW];
       INVPCOV = INV(LAMBDAS);
       DDAT = POOLSCOR[,1:TRUNCROW];
 FREE LAMBDIAG LAMBDAS POOLSCOR;
   DEESQ = J(POOLNUM,1); /* BEGIN Q-Q PLOT ROUTINE */
```

```
    DO ITERD = 1 TO POOLNUM BY 1;
       DEESQ[ITERD,] = DDAT[ITERD,]*INVPCOV*DDAT[ITERD,]`;/* D-SQUAREDS*/
    END;
   ROOTDSQ = SQRT(DEESQ);   /* COLUMN OF SQUARE ROOTS */
   ADJROOTS = ROOTDSQ*FACTOR;
   RANKS = RANK(ADJROOTS);
   LONGDEES = CHAR(ADJROOTS);
      DIDS = ACCINDID;
      LABLDEES = DIDS||LONGDEES;
 FREE LONGDEES;
      SORTED = LABLDEES;
      DO ITER = 1 TO POOLNUM BY 1;
         R = RANKS[ITER,];
         SORTED[R,] = LABLDEES[ITER,];
      END;
   SORTDIDS = SORTED[,1];
   SORTDSQ = NUM(SORTED[,2]);
        CHISQ = CINV(DO(.5,POOLNUM-.5,1)/POOLNUM,TRUNCROW,0);
     ROOTCHI = SQRT(CHISQ);
FREE CHISQ;
     CHICOL = ROOTCHI`;
     DELTAS = SORTDSQ-CHICOL;
     PRINT DIDS ROOTDSQ[FORMAT=4.2] SORTDIDS SORTDSQ[FORMAT=4.2]
               CHICOL[FORMAT=4.2] DELTAS[FORMAT=4.2];
FREE DIDS DELTAS;
     XYQQ = SORTDSQ||CHICOL;
FREE SORTDSQ CHICOL;
            ROOTROWS = NROW(XYQQ);  /* SETUP FOR QQ PLOT */
            ADDROWS = ROOTROWS/2;
            MAXD = MAX(XYQQ);
            MIND = MIN(XYQQ);
            INCREM = (MAXD-MIND)/ADDROWS;
            ROWSEQ = DO(MIND, MAXD, INCREM);
            COLSEQ = ROWSEQ`;
            DOUBCOL = REPEAT(COLSEQ,1,2);
     FULLXYQQ = XYQQ//DOUBCOL;
FREE XYQQ DOUBCOL;
            SYMB1 = "*";
            SYMB2 = REPEAT(SYMB1, ADDROWS ,1);
FREE SYMB1;
            SORTDLAB = SORTED[,1];
            SPECI = SUBSTR(SORTDLAB,1,1);
            PLOTSYMB = SPECI//SYMB2;
FREE SORTDLAB SPECI;
PRINT NEWPAGE;
      CALL PGRAF(FULLXYQQ, PLOTSYMB,"SQRTDSQ","SQRTCHI-SQ","Q-Q PLOT");
FREE FULLXYQQ;
          ND = NROW(ROOTDSQ);
          DLAB = 1;
```

```
         DCOL = REPEAT(DLAB,ND);
         DD = DCOL||ROOTDSQ;
         NC = NROW(ROOTCHI`);
         CLAB = 2;
         CCOL = REPEAT(CLAB,NC);
         CC = CCOL||ROOTCHI`;
         BARQQ = DB//CC;
FREE BD CC QQPLOT CHISQ;
      IF REPEAT = "N" THEN DO;
         CREATE SASDAT.BARQQ VAR ( LABS VALS );
         APPEND FROM BARQQ;
         CLOSE SASDAT.BARQQ;
      END;
FREE BARQQ PLDTMAT1 POOLSSCP INVPCOV QQPLOT;
/*----------- MULTIVARIATE KURTOSIS AFTER MARDIA IN MARCUS ----------*/
   AVEDSQSQ = SUM(BEESQ#Z)/POOLNUM;
   Z = (AVEDSQSQ - NVAR*(NVAR+2))/SQRT(8*NVAR*(NVAR+2)/POOLNUM);
   PROB = 1 - PROBNORM(Z);
      PRINT "MULTIVARIATE POOLED-WITHIN KURTOSIS =" AVEDSQSQ;
      PRINT "Z = " Z "WITH PROBABILITY = " PROB;
FREE DEESQ AVEBSQSQ;
/*------------ SUBGROUP VS POOLED-WITHIN PC1 ANGULAR DIFFERENCES -----*/
/*------------------------------------------------------------------*/
IF NGRPKEPT > 1 THEN DO;
      PCMAT = FIRSTCOL||PCS;
FREE FIRSTCOL PCS;
      NPLUSONE = NGRPKEPT+(1);
      DO ITERONE = 1 TO NPLUSONE BY 1;
          DO ITERTWO = 1 TO NPLUSONE BY 1;
             IF ITERONE = ITERTWO THEN DO;       /* ANGLE WITH SELF */
                ANGLE = (0);
             END;
             IF ITERONE ^= ITERTWO THEN DO;       /* ANGLES BETWEEN GROUPS */
                CROSSPS = PCMAT[,ITERONE]#PCMAT[,ITERTWO];
                KOSYNE = SUM(CROSSPS);
                RADS = ARCOS(KOSYNE);
                ANGLE = RADS#57.296;
                IF ANGLE > 90 THEN DO;
                   ANGLE = (180) - ANGLE;
                END;
             END;
             IF ITERONE = ITERTWO THEN DO;
                ANGROW = ANGLE;                /* ACCUMULATE ANGLES */
             END;
             IF ITERONE ^= ITERTWO THEN DO;
                ANGROW = ANGROW||ANGLE;
             END;
          END; /* END ITERTWO */
FREE ANGLE CROSSPS KOSYNE RADS;
```

```
            IF ITERONE = 1 THEN DO;
               ANGMAT = ANGROW;
            END;
            IF ITERONE ^= 1 THEN DO;
               SPACER = {0};
               REPSPACE = REPEAT(SPACER,1,(ITERONE-{1}));
               ROWMAT = REPSPACE||ANGROW;
               ANGMAT = ANGMAT//ROWMAT;  /* UPPER TRIANGULAR */
            END;
FREE ANGROW ROWMAT REPSPACE;
      END; /* END ITERONE */
      DO ITERATE = 1 TO NPLUSONE BY 1;    /* CONVERT TO SYMMETRIC */
         ROWTOCOL = ANGMAT[ITERATE,]`;
         SUBSYM = ROWTOCOL + ANGMAT[,ITERATE];
         IF ITERATE = 1 THEN DO;
            SYMMAT = SUBSYM;
         END;
         IF ITERATE ^= 1 THEN DO;
            SYMMAT = SYMMAT||SUBSYM;
         END;
      END;
      POOL = {"AAAA"};
      COLLAB = UNION(POOL,GRPSKEPT);
      CALL CHANGE(COLLAB, "AAAA", "POOL");
      ROWLAB = COLLAB`;
         PRINT NEWPAGE;
         PRINT / "ANGULAR DIFFERENCES BETWEEN SUBGROUP PC1 & POOLED PC1";
      FIRSTNUM = NPLUSONE/2;
      SECONUMB = FIRSTNUM +{1};
      LEFTSYMM = SYMMAT[,1:FIRSTNUM];
      RITESYMM = SYMMAT[,SECONUMB:NPLUSONE];
         LCOLLAB = COLLAB[,1:FIRSTNUM];
         RCOLLAB = COLLAB[,SECONUMB:NPLUSONE];
         PRINT LEFTSYMM[FORMAT=3.0 ROWNAME = ROWLAB COLNAME = LCOLLAB];
         PRINT NEWPAGE;
         PRINT RITESYMM[FORMAT=3.0 ROWNAME = ROWLAB COLNAME = RCOLLAB];
         XYMAT = GSIZECOL||SYMMAT[2:NPLUSONE,1];
         SAMPSIZE = {"SAMPLE SIZE"};
         ANGLEDIF = {"ANGULAR DIFFERENCE WITH TOTAL"};
            PRINT NEWPAGE;
            CALL PGRAF(XYMAT, ROWLAB[2:NPLUSONE,], "SAMPLE SIZE", "ANGULAR DIFFERENCE");
```

CANONICAL VARIATES, LINEAR REGRESSION, VECTOR PROJECTION, AND SIZE REMOVAL ROUTINES

```
/*----------------- SET WORKING ENVIRONMENT -------------------------*/
     OPTIONS NOSOURCE;  /* NO PROGRAM LINES IN OUTPUT*/
     PROC PRINTTO LOG = 'PRN'; /*OUTPUT DESTINATION*/
     PROC IML WORKSIZE = 220;  /*SPACE AVAILABLE FOR MATRIX OPERATIONS*/
RESET LINESIZE = 165 PAGESIZE = 35;
TWELVE = {12};
NEWPAGE = BYTE(TWELVE); /*PAGE BREAK CONTROL CODE*/
/*SET*/   USE SASDAT.MANDSUBS; /* DATA SOURCE*/
/*SET*/   RUN = "MAND"; /* ---> SKULL  MAND-IBLE  */
/*SET*/   NEWPOOL = "YES"; /* CALCULATE NEW POOLED W/IN GROUP COV */
/*SET*/   INDRICO = "YES";   /* INCLUDE-EXCLUDE INDRICOTHERIUM */
/*SET*/   DROPTAX = "NO"; /* USE SUBSET FOR TARGET VECTOR ? */
     IF DROPTAX = "YES" THEN DO;
        IF RUN = "MAND" THEN ELIMTAX = {"INDRM"}; /* INDRICOTHERIUM DROPPED FROM ANALYSIS*/
        IF RUN = "SKULL" THEN ELIMTAX = {"INDRS"};
     END;
/*SET*/   BIVARIAT = "NO"; /* INCLUDE BIVARIATE MEAN VAR-SIZE PLOTS */
/*SET*/   FINDVECT = "YES";/* FIND TARGERT VECTOR OF INTEREST*/
/*SET*/   VECTTARG = "SHAPE"; /* SIZE SHAPE *//*TARGET VECTOR TYPE*/
/*SET*/   REMOVECT = "NO";      /* NO ISO BURN */ /*REMOVE VECTOR*/
/*SET*/   ISOSZVAR = "SIZE1";    /* SCALE DATA ISOMETRICALLY TO WHICH VARIABLE ? */
/*SET*/   CORRSIZE = "NO";    /* FIND CORRELATIONS AMONG SIZE VARIABLES */
/*SET*/   CANSTO3D = "NO"; /* SAVE DATA TO FILE FOR 3D */
/*SET*/   PLOTTYPE = "GRPSYMB"; /* ---> GRPNAME   GRPSYMB   IND  */
/*SET*/   PLOTSET = "ARB"; /* --->  ARB-ITRARY   FIND   ALL  *//* # OF PLOTS*/
/*SET*/   PLOTNUM = "2";  /* ---> [#] */
/*SET*/   WEIGHT = "NO"; /* --->  YES    NO  */ /* WEIGHTED CANAONICAL VARIATES*/
/*SET*/   TFORM = "NO"; /* --->   YES    NO  */
/*SET*/   PLEV = "MIN"; /* PRINT LEVEL MIN MED MAX *//*AMOUNT OF OUTPUT*/
/*SET*/   POOL = "ALL"; /* --->  SOME     ALL  *//* POOL HOW MANY GROUPS*/
/*SET*/   DISCRIM = "ALL"; /* --->  SOME   ALL  *//*HOW MANY CANONICAL GROUPS*/
/*SET*/   AXES = "MAX"; /* --->  MAX   ARB  */ /*AXIS RANGES*/
/*SET*/   ANALYSIS = "SUB"; /* --->  GEN-ERA   SUB-GROUPS  */
/* ---------------------------------------------------------------- */
/*SET*/   IF POOL = "SOME" THEN DO; /* DEFINE SUBSET FOR POOLONG*/
          POOLGRPS =  {BICO};
          POOLCOL = POOLGRPS`;
          NGPOOLED = NROW(POOLGCOL);
     END;
/*SET*/   IF DISCRIM = "SOME" THEN DO; /* DEFINE GROUPS FOR CANONICAL ANALYSIS*/
        /*  BISCGRPS = {BICOM CERAM JAVAM UNICM XUMAM}; */
        /*  DISCGRPS = {BICOS CERAS JAVAS UNICS XUMAS}; */
            DISCGRPS = {YRAH1M YRAH2M FORS1M FORS2M INDRM HYCOM};
        /*  DISCGRPS = {FORSS INDRS HYCOS}; */
        /*  DISCGRPS = {DICE1S DICE2S DICE3S FORSS LOPS1S
                        LOPS2S MENOS PERA1S PERA2S QACE1S
                        QACE2S RIGO1S RIGO2S SUBH1S SUBH2S
                        SUBH3S SUBH4S TELE1S TELE2S TELE3S
```

```
                        TELE4S TELE5S YRAN1S YRAN2S); */
        /*   DISCGRPS = (ACER1M ACER2M DICE1M DICE2M DICE3M DICE4M LOPS1M LOPS2M LOPS3M
LOPS4M
                        MENO1M MENO2M PERA1M PERA2M PERA3M
                        RIGOM SUBH1M SUBH2M SUBH3M TELE1M
                        TELE2M TELE3M TELE4M YRAN1M YRAN2M); */
    DISCCOL = D[SCGRPS`;
          NGDISC = NROW(DISCCOL);
     END;
     IF AXES = "ARB" THEN DO; /* SET AXIS RANGES*/
/*SET*/      IF RUN = "MAND"  THEN DO;
          IF DISCRIM = "ALL" THEN RANGESXY = (40 15, -40 -15);
          IF DISCRIM = "SOME" THEN RANGESXY = (16 6, -16 -6);
        END;
/*SET*/      IF RUN = "SKULL" THEN DO;
          IF DISCRIM = "ALL" THEN RANGESXY = (40 20, -40 -20);
          IF DISCRIM = "SOME" THEN RANGESXY = (28 15, -28 -15);
        END;
     END;  /* ---> AXES = ARB */

PRINT " ---------------- CONFIGURATION FOR THIS RUN --------------- ";
PRINT "";
PRINT  RUN "" ANALYSIS "" POOL "" DISCRIM "" WEIGHT "" INDRICO;
PRINT "";
PRINT  TFORM "" PLOTNUM "" PLOTSET "" AXES "" PLOTTYPE "" PLEV;
PRINT "";
PRINT NEWPOOL "" RANGESXY "" FINDVECT "" REMOVECT "" ISOSZVAR;
PRINT VECTTARG "";
PRINT "-------------------------------------------------------------";
/* ---------------------- READ DATA ------------------------------*/
/* GET DATA - INCLUDE-EXCLUDE INDRICOTHERIUM - TRANSFORM DATA OPTION*/
 IF INDRICO = "YES" THEN DO;
    READ ALL INTO TEMPDATA [ROWNAME=ID COLNAME=VARNAME];
   IF TFORM = "YES" THEN DATA = LOG(TEMPDATA)#0.43429448;
   IF TFORM = "NO" THEN DATA = TEMPDATA;
   PRINT "--- DATA READ ---";
 END; /* INDRICO = YES LOOP */
 IF INDRICO = "NO" THEN DO;
    IF RUN = "SKULL" THEN DO;

   READ ALL WHERE(SUBG^="INDRS") INTO TEMPDATA [ROWNAME=ID COLNAME=VARNAME];
   IF TFORM = "YES" THEN DATA = LOG(TEMPDATA)#0.43429448;
   IF TFORM = "NO" THEN DATA = TEMPDATA;
   PRINT "--- DATA & SUBG READ, INDRICO EXCLUDED ---";
    END;
    IF RUN = "MAND" THEN DO;
   READ ALL WHERE(SUBS^="INDRM") INTO TEMPDATA [ROWNAME=ID COLNAME = VARNAME];
   IF TFORM = "YES" THEN DATA = LOG(TEMPDATA)#0.43429448;
   IF TFORM = "NO" THEN DATA = TEMPDATA;
```

```
   PRINT "--- DATA & SUBS READ, INDRICO EXCLUDED ---";
    END;
 END; /* ---> INDRICO = NO LOOP */
 FREE TEMPDATA;
CASES = NROW(DATA);          /* NUMBER OF CASES */
VARCOL = VARNAME`;           /* Column of variable names */
NVAR = NROW(VARCOL);
/*-------------------------------------------------------------------*/

/*------------- READ AND/OR SETUP LABELLING MATRICES --------------*/
   IF POOL = "ALL" | DISCRIM = "ALL" THEN DO;
IF ANALYSIS = "GEN" THEN DO;
   READ ALL VAR(GENUS) INTO GRPLABLS;
END;
IF ANALYSIS = "SUB" THEN DO;
      IF RUN = "MAND" THEN DO;
 IF INDRICO = "NO" THEN DO;
            READ ALL VAR(SUBS) WHERE(SUBS^="INDRM") INTO GRPLABLS;
         END;
         IF INDRICO = "YES" THEN DO;
            READ ALL VAR(SUBS) INTO GRPLABLS;
         END;
     END; /* ---> RUN = M LOOP */
      IF RUN = "SKULL" THEN DO;
         IF INDRICO = "NO" THEN DO;
            READ ALL VAR(SUBG) WHERE(SUBG^="INDRS") INTO GRPLABLS;
         END;
         IF INDRICO = "YES" THEN DO;
            READ ALL VAR(SUBG) INTO GRPLABLS;
         END;
      END; /* ---> RUN = S LOOP */
  END; /* ---> ANALYSIS = SUB */
  END; /* ---> POOL OR DISCRIM = ALL */
   IF DISCRIM = "ALL" THEN DO;
 DISCGRPS = UNIQUE(GRPLABLS);
 DISCCOL = DISCGRPS`;
 NGDISC = NROW(DISCCOL);
   END; /* ---> ALL-ALL LOOP */
   IF POOL = "ALL" THEN DO;
 POOLGRPS = UNIQUE(GRPLABLS);
 POOLCOL = POOLGRPS`;
 NGPOOLED = NROW(POOLCOL);
  END;
/*-------------- STARTING PARAMETERS ----------------------------*/
 PRINT " TOTAL CASES READ " CASES;
 PRINT " NUMBER OF VARIABLES " NVAR;
 PRINT " LIST OF VARIABLES ", VARCOL;
 IF POOL ^= "ALL" | DISCRIM ^= "ALL" THEN DO;
    PRINT " NUMBER OF GROUPS DISCRIMINATED " NGDISC;
```

```
   PRINT " LIST OF GROUPS SPECIFIED FOR DISCRIMINATION ", DISCCOL;
   PRINT "";
   PRINT " NUMBER OF GROUPS POOLED " NGPOOLED;
   PRINT " LIST OF GROUPS SPECIFIED FOR POOLED ", POOLCOL;
 END;
 IF POOL = "ALL" & DISCRIM = "ALL" THEN DO;
   PRINT "NUMBER OF POOLED AND DISCRIMINATED GROUPS " NGDISC;
   PRINT " LIST OF ALL GROUPS FOR BOTH POOLED AND BETWEEN", DISCCOL;
 END;
/* ------------------- FURTHER SETUP ROUTINES ----------------------*/
NROOTS = NVAR; /* SET NUMBER OF ROOTS FOR CANONICAL VARIATES*/
CVLABO = {CV}; /* SETUP CANONICAL AXIS LABELLING */
CVLAB1 = REPEAT(CVLABO,1,NROOTS);
CVLAB2 = DO(1,NROOTS,1);
CVLAB2A = CHAR(CVLAB2,2);
  CALL CHANGE(CVLAB2A," 1","1");
  CALL CHANGE(CVLAB2A," 2","2");
  CALL CHANGE(CVLAB2A," 3","3");
  CALL CHANGE(CVLAB2A," 4","4");
  CALL CHANGE(CVLAB2A," 5","5");
  CALL CHANGE(CVLAB2A," 6","6");
  CALL CHANGE(CVLAB2A," 7","7");
  CALL CHANGE(CVLAB2A," 8","8");
  CALL CHANGE(CVLAB2A," 9","9");
CVLABROW = CONCAT(CVLAB1, CVLAB2A);
CVLABCOL = CVLABROW`;
CNTSKIP = {0};
CNTGRPS = {0};
GRPNUM = {0};
 /*---------- SIZE VARIABLE ROUTINES -------------------------*/
  TESTDAT = DATA[1:2,]; /* TEST DATA FOR CHECKING ROUTINES */
  PRINT " FIRST TWO DATA ROWS FOR TESTING CALCULATIONS";
  SPECNAMS = GRPLABLS[1:2,];
  PRINT TESTDAT[FORMAT=4.0 ROWNAME =  SPECNAMS COLNAME = VARNAME];
 /*  SIZE1 = GREATEST LENGTH  */
PRINT "SIZE1 = GREATEST LENGTH ";
IF RUN = "MAND" THEN DO;
  RAMD = DATA[, 10 ];
  MNMD = DATA[,  9 ];
  SIZE1 = RAMD + MNMD;

 END;
    IF RUN = "SKULL" THEN DO;
  SIZE1 = DATA[,13];     /* OCP2 */
    END;
 /* SIZE2 = SQUARE ROOT OF SUMS OF SQUARES */
    PRINT "SIZE2 = SQUARE ROOT OF SUM OF SQUARES";
    SIZE2A = DATA[,##];
    SIZE2  = SQRT(SIZE2A);
```

```
FREE SIZE2A PRNTEST2;
 /* SIZE3 = GEOMETRIC MEAN (NTH ROOT OF PRODUCT) */
PRINT "SIZE3 = GEOMETRIC MEAN";
SIZE3A = DATA[,#];
ROOT  = 1/NVAR;
SIZE3 = SIZE3A ## ROOT;
FREE SIZE3A;
/* SIZE4 = CUBE ROOT OF VOLUME */
   PRINT "SIZE4 = CUBE ROOT OF VOLUME";
   IF RUN = "MAND" THEN DO;
 RAMH = DATA[, 11 ];
 BDBR = DATA[,  3 ]; BDHT = DATA[,  4 ];
 RAMD = DATA[, 10 ];
 SIZE4A = RAMH # BDBR # SIZE1;
 SIZE4 = SIZE4A##0.3333333;
   END;  /* MAND LOOP */
FREE RAMH BDBR RAMD MNMO BDHT ;
   IF RUN = "SKULL" THEN DO;
 BIZY = DATA[, 5 ]; LFHT = DATA[, 6 ];
 SIZE4A = SIZE1 # BIZY # LFHT;
 SIZE4 = SIZE4A##0.3333333;
   END; /* SKULL LOOP */
FREE BIZY LFHT PRNTEST4;
/* SIZE5 = AVERAGE VARIABLE SIZE */
   SIZE5 = DATA[,:];
 PRINT "SIZE5 = AVERAGE VARIABLE SIZE";
 IF CORRSIZE = "YES" THEN DO;
 /* ACCUMULATE SIZE COLUMNS INTO MATRIX */
   SIZEMAT = SIZE1||SIZE2||SIZE3||SIZE4||SIZE5;
 /* CORRELATIONS BETWEEN SIZE VARIABLES */
    /* ACROSS ALL SPECIMENS */
  SIZEMEAN = SIZEMAT[:,];
  MEANMAT = REPEAT(SIZEMEAN, CASES, 1);
  MEANDEVS = SIZEMAT - MEANMAT;
FREE SIZEMEAN MEANMAT SIZEMAT;
  SIZESSCP = MEANDEVS` * MEANDEVS;
  SIZECOV = SIZESSCP * ((CASES - {1})** -1.0);
FREE MEANDEVS SIZESSCP;
  SZVARIANC = VECDIAG(SIZECOV);
  SZSTDEV = SQRT(SZVARIANC);
  STDEVINV = SZSTDEV ## -1.0;
  SZSTDMAT = DIAG(STDEVINV);
FREE SZSTDEV STDEVINV SZVARIANC;
  SZCORREL = SZSTDMAT * SIZECOV * SZSTDMAT;
FREE SZSTDMAT SIZECOV;
SZCOLNAM = {S1 S2 S3 S4 S5 };
SZROWNAM = {S1,S2,S3,S4,S5 };
PRINT NEWPAGE;
PRINT "SIZE VARIABLES CORRELATION MATRIX";
```

```
PRINT SZCORREL[FORMAT = 5.2 ROWNAME = SZROWNAM COLNAME = SZCOLNAM];
FREE SZCOLNAM SZROWNAM SZCORREL;
END; /* SIZE VARIABLE CORRELATIONS LOOP */
IF REMOVECT = "ISO" THEN DO;
/* ------------- REMOVE ISOMETRIC SIZE FROM DATA ----------------- */
   IF ISOSZVAR = "SIZE1" THEN DO;
TARGETSZ = MIN(SIZE1);      /* ARBITRARY */
TARGCOL = REPEAT(TARGETSZ, CASES, 1);
RATIOS = SIZE1##-1.0#TARGCOL;
TARGMAT = REPEAT(RATIOS,1,NVAR);
SCALEDAT = DATA#TARGMAT;
   END; /* SIZE1 REMOVAL */
FREE TARGMAT DATA TARGINV TARGETSZ TARGCOLRATIOS ISOSZVAR;
    IF RUN = "MAND" THEN DO;
  TEMP1 = SCALEDAT[,1:8];
  TEMP2 = SCALEDAT[,11];
  SCALEDAT = TEMP1||TEMP2;
  NVAR = NCOL(SCALEDAT);
  LABTEMP1 = VARNAME[,1:8];  LABTEMP2 = VARNAME[,11];
  VARNAME = LABTEMP1||LABTEMP2;  VARCOL = VARNAME`;
    END;
 IF RUN = "SKULL" THEN DO;
    TEMP1 = SCALEDAT[,1:12];
    TEMP2 = SCALEDAT[,14:19];
    SCALEDAT = TEMP1||TEMP2;
    NVAR = NCOL(SCALEDAT);
    LABTEMP1 = VARNAME[,1:12];
    LABTEMP2 = VARNAME[,14:19];
    VARNAME = LABTEMP1||LABTEMP2;
    VARCOL = VARNAME`;
 END;
FREE TEMP1 TEMP2 LABTEMP1 LABTEMP2;
PRINT " SPECIMENS HAVE BEEN SCALED ISOMETRICALLY TO AN ARBITRARY";
PRINT " VALUE OF THE SIZE VARIABLE (SIZE1 ONLY)";
END;  /* REMOVE ISOMETRIC SIZE LOOP */
/* SET SIZE VARIABLE FOR FURTHER COMPUTATIONS */
   SIZEVAR = SIZE4;
FREE SIZE1 SIZE2 SIZE3 SIZE4;
FREE SIZE5 SIZE92;
PRINT "SIZE VARIABLE USED FOR  SIZE ROUTINES";
SIZETEST = SIZEVAR[1:10,];
NAMSTEST = GRPLABLS[1:10,];
PRINT NAMSTEST SIZETEST;
FREE SIZETEST;
/*----- SHAPE AND OTHER DERIVED VARIABLES ------------------------*/
 PRINT "SHAPE1 = ORIG. VARIABLES DIVIDED BY SIZE";
 IF RUN = "MAND" THEN DO;
    PRINT "SHAPE2M = REL. HT. OF MANDIB. CONDYLE ABOVE TOOTH ROW";
   SHAPE2M = DATA[,4]#DATA[,11]##-1.0;
```

```
PRINT "SHAPE3M = RELATIVE ANGLE EXPANSION";
SHAPE3M = DATA[,1]#DATA[,10]##-1.0;
PRINT "SHAPE4M = WORN M1 CROWN HEIGHT";
SHAPE4M = DATA[,5]#DATA[,3]##-1.0;
PRINT "SHAPE5M = POS. CONDYLE REL. TO M3";
DENOM5M = DATA[,11]-DATA[,4];
SHAPE5M = DATA[,6]#DENOM5M##-1.0;
END;
IF RUN = "SKULL" THEN DO;
  PRINT "SHAPE2S = RELATIVE DIVERGENCE OF TOOTH ROW";
    SHAPE2S = DATA[,8]#DATA[,9]##-1.0;
  PRINT "SHAPE3S = OBLIQUENESS OF EXTERNAL MASSETER FIBERS";
    SHAPE3S = DATA[,5]#DATA[,9]##-1.0;
  PRINT "SHAPE4S = RELATIVE DEPTH OF TEMPORAL FOSSA";
    SHAPE4S = DATA[,5]#DATA[,16]##-1.0;
  PRINT "SHAPE5S = RELATIVE DOLICHOCEPHALY";
    SHAPE5S = DATA[,5]#DATA[,13]##-1.0;
END;
/*--------------------- SET TARGET VECTOR -----------------------*/
  IF VECTTARG = "SIZE" THEN DO;
 TARGVAR = SIZEVAR;
FREE SIZEVAR;
  END;
  IF VECTTARG = "SHAPE" THEN DO;
 TARGVAR = SHAPE5M;
  END;

SORTTARG = TARGVAR; /* SORT TARGET VECTOR ROUTINES */
SORTLABS = GRPLABLS;
RANKTARG = RANK(TARGVAR);
  DO ITERB = 1 TO CASES BY 1;
     RT = RANKTARG[ITERB];
     SORTTARG[RT,] = TARGVAR[ITERB,];
     SORTLABS[RT,] = GRPLABLS[ITERB,];
  END;  /* ---> ITERB LOOP */
 PRINT "TARGET VECTOR OF INTEREST" SORTLABS SORTTARG;
 FREE SORTTARG SORTLABS RANKTARG;
/*-------------------------------------------------------------*/
/*-----------POOLED WITHIN-GROUP COVARIANCE ROUTINE ---------------*/
/*-------------------------------------------------------------*/
IF NEWPOOL = "YES" THEN DO; /* FIND NEW WITHIN-GROUP COVARIANCE */
  DO ITERA = 1 TO NGPOOLED BY 1; /* CYCLE THROUGH GROUPS */
 CNTCASES = {0};
 GRPNUM = GRPNUM+{1};
 GRPNAME = POOLCOL[GRPNUM];
  DO ITERB = 1 TO CASES; /* CYCLE THROUGH CASES */
     IF GRPLABLS[ITERB] = GRPNAME THEN DO; /* SELECT CASES */
        CNTCASES = CNTCASES+{1};
        IF REMOVECT = "NO" | REMOVECT = "BURN" THEN DO;
```

```
            ROWDAT = DATA[ITERB,];
         END;
         IF REMOVECT = "ISO" THEN DO;
            ROWDAT = SCALEDAT[ITERB,];
         END;
           ROWID = ID[ITERB];
           IF CNTCASES = 1 THEN DO;
                   SUBDAT = ROWDAT;
            END;
            IF CNTCASES > 1 THEN DO;
                   SUBDAT = SUBDAT//ROWDAT;
            END;
       END; /* ---> GRPNAME = GRPLABLS LOOP */
    END; /* ---> ITERB LOOP */
  SUBSIZE = NROW(SUBDAT); /* SIZE OF EXTRACTED GROUP */
  SUBMEANS = SUBDAT[:,];/* VARIABLE MEANS OF GROUP */
  MEANMAT = REPEAT(SUBMEANS,SUBSIZE,1);
  SUBDEVS = SUBDAT-MEANMAT; /* DEVIATIONS FROM GROUP MEAN*/
           IF ITERA = 1 THEN DO; /* SETUP POOLED DATA SET */
              POOLDAT = SUBDEVS;
              POOLGNS = SUBSIZE;
           END;
           IF ITERA ^= 1 THEN DO;
              POOLDAT = POOLDAT//SUBDEVS;
              POOLGNS = POOLGNS//SUBSIZE;
           END;
   END; /* ---> ITERA LOOP */
 POOLNUM = NROW(POOLDAT);
 PRINT "NUMBER OF POOLED DATA CASES " POOLNUM;
 POOLSSCP = POOLDAT` * POOLDAT; /* POOLED  SUMS OF SQUARES AND CROSS PRODUCTS*/
 POOLCOV  = POOLSSCP * ((POOLNUM-NGPOOLED)**-1.0); /*NEW POOLED COVARIANCE*/
  IF RUN = "MAND" THEN DO; /* SAVE POOLED COVARIANCE*/
    CREATE SASDAT.MPOOLCOV FROM POOLCOV;
    APPEND FROM POOLCOV;
    CREATE SASDAT.MPOOLGNS FROM POOLGNS;
    APPEND FROM POOLGNS;
    CREATE SASDAT.MPOOLCOL FROM POOLCOL;
    APPEND FROM POOLCOL;
    PRINT " NEW POOLED COVARIANCE MATRIX CALCULATED FOR MANDIBLE";
  END; /*---> RUN = MAND */
  IF RUN = "SKULL" THEN DO;
    CREATE SASDAT.SPOOLCOV FROM POOLCOV;
    APPEND FROM POOLCOV;
    CREATE SASDAT.SPOOLGNS FROM POOLGNS;
    APPEND FROM POOLGNS;
    CREATE SASDAT.SPOOLCOL FROM POOLCOL;
    APPEND FROM POOLCOL;
    PRINT "NEW POOLED COVARIANCE MATRIX CALCULATED FOR SKULL";
  END; /*---> RUN = MAND */
```

```
END; /* ---> NEWPOOL = "YES" */
  IF  NEWPOOL = "NO" THEN DO; /* USE OLD POOLED COVARIANCE */
 IF RUN = "MAND" THEN DO;
    USE SASDAT.MPOOLCOV;
    READ ALL INTO POOLCOV;
    PRINT "POOLED COVARIANCE MATRIX READ FROM MPOOLCOV";
    USE SASDAT.MPOOLGMS;
    READ ALL INTO POOLGMS;
    USE SASDAT.MPOOLCOL;
    READ ALL VAR(COL1) INTO POOLCOL;
 END;
   IF RUN = "SKULL" THEN DO;
       USE SASDAT.SPOOLCOV;        READ ALL INTO POOLCOV;
       PRINT "POOLED COVARIANCE MATRTIX READ FROM SPOOLCOV";
       USE SASDAT.SPOOLGMS;
       READ ALL INTO POOLGMS;
       USE SASDAT.SPOOLCOL;
       READ ALL VAR(COL1) INTO POOLCOL;
 END;
  END; /* ---> NEWPOOL = "NO" */
POOLROWS = NROW(POOLCOV);
POOLCOLS = NCOL(POOLCOV);
 FREE POOLSSCP;
 IF PLEV = "MAX" THEN DO;
 PRINT NEWPAGE;
    PRINT "POOLED-WITHIN GROUPS COVARIANCE MATRIX", POOLCOV[FORMAT=6.1 ROWNAME = VARCOL
COLNAME = VARNAME];
  PRINT "POOLCOV MATRIX IS " POOLROWS "BY " POOLCOLS;
 END;
 FREE POOLROWS POOLCOLS;
CNTSKIP = {0};
CNTGRPS = {0};
GRPNUM = {0};
/*-------------------------------------------------------------------*/
/*----------- GROUP MEANS ------------*/
/*-------------------------------------------------------------------*/
DO ITERA = 1 TO NGDISC BY 1; /* CYCLE THROUGH GROUPS */
   CNTCASES = {0};
   GRPNUM = GRPNUM+{1};
   GRPNAME = DISCCOL[GRPNUM];
  DO ITERB = 1 TO CASES; /* CYCLE THROUGH CASES*/
     IF GRPLABLS[ITERB] = GRPNAME THEN DO;
        CNTCASES = CNTCASES+{1};
        IF FINDVECT = "NO" THEN DO; /* SETUP REQUIRED DATA SETS AND LABELS*/
           ROWDAT = DATA[ITERB,];
        END;
        IF REMOVECT = "ISO" THEN DO;
           ROWDAT = SCALEDAT[ITERB,];
        END;
```

```
IF FINDVECT = "YES" & REMOVECT ^= "ISO" THEN DO;
   ROWDAT = DATA[ITERB,];
   TARGDAT = TARGVAR[ITERB,];
END;
  ROWID = ID[ITERB];
  IF CNTCASES = 1 THEN DO;
        SUBDAT = ROWDAT;
        SUBGRPID = GRPNAME;
        SUBINDID = ROWID;
    IF FINDVECT = "YES" & REMOVECT ^= "ISO" THEN DO;
       SUBTARDT = TARGDAT;
      END;
   END;
   IF CNTCASES > 1 THEN DO;
        SUBDAT = SUBDAT//ROWDAT;
        SUBGRPID = SUBGRPID//GRPNAME;
        SUBINDID = SUBINDID//ROWID;
        IF FINDVECT = "YES" & REMOVECT ^= "ISO" THEN DO;
        SUBTARDT = SUBTARDT//TARGDAT;
        END;
   END;
 END; /* GRPNAME = GRPLABLS LOOP */
END; /* ITERB LOOP */
SUBSIZE = NROW(SUBDAT);
SUBMEANS = SUBDAT[:,]; /* GROUP MEANS*/
IF FINDVECT = "YES" & REMOVECT ^= "ISO" THEN DO;
GPTARMEA = SUBTARDT[:,];
END;
      IF ITERA = 1 THEN DO;
         DISCDAT = SUBDAT;
         BETGNS = SUBSIZE;
         ACCGRPID = SUBGRPID;
         ACCINDID = SUBINDID;
         GRPMEANS = SUBMEANS;
         GSIZEROW = SUBSIZE;
         IF FINDVECT = "YES" & REMOVECT ^= "ISO" THEN DO;
         TARMEANS = GPTARMEA;
         END;
      END;
      IF ITERA ^= 1 THEN DO;
         DISCDAT = DISCDAT//SUBDAT;
         ACCGRPID = ACCGRPID//SUBGRPID;
         ACCINDID = ACCINDID//SUBINDID;
         BETGNS = BETGNS//SUBSIZE;
         GRPMEANS = GRPMEANS//SUBMEANS;
         IF FINDVECT = "YES" & REMOVECT ^= "ISO" THEN DO;
         TARMEANS =  TARMEANS//GPTARMEA;
         END;
   END;
```

```
END; /* ITERA LOOP */
    PRINT NEWPAGE;
    PRINT "GROUPS AND SIZES USED IN ANALYSIS";
    PRINT  POOLCOL  POOLGNS "     " DISCCOL  BETGNS;
    PRINT "GROUP MEANS OF ORIGINAL VARIABLES";
    PRINT GRPMEANS[FORMAT=4.1 ROWNAME = DISCCOL  COLNAME = VARNAME];
/*---------------- BIVARIATE ROUTINES -------------------------*/
 IF BIVARIAT = "YES" THEN DO; /* LINEAR REGRESSION VARIABLES AGAINST SIZE*/
    DO ITERQ = 1 TO NVAR;
  MEASCOL = GRPMEANS[,ITERQ];
  NMEANS = NROW(MEASCOL);
  LOGMEAS =  LOG(MEASCOL)#0.43429448; /* BASE TEN LOGS*/
  LOGTARMS = LOG(TARMEANS)#0.43429448;
  NMEANS = NROW(MEASCOL);
  RANKLOGS = LOGTARMS;
  RANKNAMS = DISCCOL;
  RANKMEAS = LOGMEAS;

  RANKLS =  RANK(LOGTARMS); /* SORT DATA */
     DO ITERB = 1 TO NMEANS BY 1;
        RJ1 = RANKLS[ITERB];
        RANKLOGS[RJ1,] = LOGTARMS[ITERB,];
        RANKNAMS[RJ1,] = DISCCOL[ITERB,];
        RANKMEAS[RJ1,] = LOGMEAS[ITERB,];
     END;  /* ---> ITERB LOOP */
  DUMMYA = {1}; /* SETUP DUMMY VARIABLE */
  DUMMY = REPEAT(DUMMYA, NMEANS,1);
  DUMXX = DUMMY||RANKLOGS;
  LXXPROD = DUMXX`*DUMXX;
  LXYPROD = DUMXX`*RANKMEAS;
  LXXPROIN = INV(LXXPROD);
  PARAMETR = LXXPROIN*LXYPROD;
  PREDYS = DUMXX*PARAMETR; /* PREDICTED Y'S*/
  RESIDS = RANKMEAS - PREDYS; /* RESIDUALS*/
  PRINT NEWPAGE;
  PRINT RANKNAMS RANKLOGS RANKMEAS PREDYS RESIDS;
      DO ITERW = 1 TO NMEANS BY 1; /* FIND RESIDUAL SIGNS */
         IF RESIDS[ITERW] < 0.0 THEN SIGN = "-";
         IF RESIDS[ITERW] = 0.0 THEN SIGN = "0";
         IF RESIDS[ITERW] > 0.0 THEN SIGN = "+";
         IF ITERW = 1 THEN DO;
            SIGNROW = SIGN;
         END;
         IF ITERW > 1 THEN DO;
            SIGNROW = SIGNROW||SIGN;
         END;
      END; /* ITERW LOOP */

 IF ITERQ = 1 THEN DO; /* ACCUMULATE RESIDUAL SIGNS */
```

```
   SIGNMAT = SIGNROW;
END;
IF ITERQ ^=1 THEN DO;
   SIGNMAT = SIGNMAT//SIGNROW;
END;
ABSCISSA = RANKLOGS//RANKLOGS;
ORDINATE = RANKMEAS//PREBYS;
BIVARMAT = ABSCISSA||ORDINATE;
  /*         IF RUN = "KAND" THEN DO;
         XMAXYMAX = {2.4 2.65};         XMINYMIN = {1.65 0.75};         SETSCALE =
XMAXYMAX//XMINYMIN;
      END;
      IF RUN = "SKULL" THEN DO;
         XMAXYMAX = {2.75 3.5};         XMINYMIN = {1.85 1.15};         SETSCALE =
XMAXYMAX//XMINYMIN;
      END;
      BIVARMAT = BIVARMAT//SETSCALE;
 */
PREDSYMB = "*";
SYMBPRED = REPEAT(PREDSYMB, NMEANS, 1);
SYMBCOL = SUBSTR(RANKNAMS, 1, 1);
PLOTMARK = SYMBCOL//SYMBPRED;
      NOPOINT = " ";
      PLOTMARK = PLOTMARK//NOPOINT;
YLAB = VARCOL[ITERQ];
  SYMBROW = SYMBCOL`;
 PRINT NEWPAGE;
    CALL PGRAF(BIVARMAT, PLOTMARK, "CUBE ROOT OF VOLUME", YLAB);
    PRINT "SUBGROUPS" SYMBROW[FORMAT=3.0];
    PRINT "RESIDUALS" SIGNROW[FORMAT=3.0] ;
   END; /* ITERQ LOOP */
 PRINT NEWPAGE;
 PRINT SYMBROW[FORMAT= 3.0];
 PRINT SIGNMAT[FORMAT = 3.0];
 END; /* BIVARIATE BLOCK */
 FREE SIGNMAT;
 FREE MEASCOL NMEANS PARAMETR PREDYS;
 FREE ABSCISSA ORDINATE BIVARMAT PREDSYMB SYMBPRED PLOTMARK;
 FREE YLAB SYMBCOL LXXPROD LXYPROD LXXPROIN PARAMETR SIGNROW RESIDS;
 FREE LOGTARMS LOGMEAS RANKLOGS RANKMEAS RANKNAMS;

 /*-------------------- BETWEEN GROUPS COVARIANCES ------------------*/
    DISCASES = NROW(DISCDAT);
    GRNDMEAN = GRPMEANS[:,]; /* GRANDMEANS */
    GRNDMAT1 = REPEAT(GRNDMEAN,DISCASES,1);
    GRNDMAT2 = REPEAT(GRNDMEAN, GRPNUM,1);
    GRNDDEVS = DISCDAT-GRNDMAT1; /* DEVIATIONS OF SPECS FROM GRAND MEANS */
 FREE GRNDMAT1;
    BETDEVS = GRPMEANS-GRNDMAT2; /* DEVIATIONS OF GROUP MEANS FROM GRNAD MEANS*/
```

```
FREE GRNDMAT2;
 IF WEIGHT = "NO" THEN DO; /* UNWEIGHTED ANALYSIS */
    BSSCP = BETDEVS`*BETDEVS; /* BETWEEN GROUPS SUMS OF SQUARES AND CROSS PRODUCTS*/
    BETCOV = BSSCP*((NGDISC-1)**-1.0); /* BETWEEN GROUPS COVARIANCES */
    PRINT NEWPAGE;
    PRINT "BETWEEN GROUPS COVARIANCE BASED ON BSSCP (UNWEIGHTED)";
 END;
  IF WEIGHT = "YES" THEN DO; /* WEIGHTED ANALYSIS */
       GSIZEMAT = REPEAT(BETGNS,1,NVAR);
       WBETDEVS = BETDEVS#GSIZEMAT;
       WBSSCP = WBETDEVS`*WBETDEVS;
       BETCOV = WBSSCP*((NGDISC-1)**-1.0);
       PRINT NEWPAGE;
       PRINT "BETWEEN-GROUPS COVARIANCE BASED ON WBSSCP (WEIGHTED)";
  END;
FREE GSIZEMAT GRNDMAT2 GRNDMAT1 BETDEVS;
FREE  WBETDEVS WBSSCP BSSCP BETDEVS ;
 IF PLEV = "MAX" THEN DO;
 PRINT BETCOV[FORMAT=4.1];
 END;
/*---------------------------------------------------------------------*/
/*---------------- CANONICAL VARIATES ANALYSIS -----------------------*/
/*---------------------------------------------------------------------*/
XAX = {1};
YAX = {2};
CALL GENEIG(CVEIGVAL, CVEIGVEC, BETCOV, POOLCOV); /* CALCULATE EIGENVECTORS,VALUES*/
FREE POOLCOV BETCOV;
ADDVALS = CVEIGVAL[+,];
VALPERCS = (CVEIGVAL*ADDVALS**-1.0)*100;
CUMUPERC = CUSUM(VALPERCS);
VALSUM = CVEIGVAL||VALPERCS||CUMUPERC;
VALSLAB = {EIGENVALUE POFTOTAL CUMULATIVE};
PRINT NEWPAGE
PRINT "EIGENVALUES";
PRINT VALSUM[FORMAT=5.3 ROWNAME = CVLABCOL COLNAME = VALSLAB];
PRINT "SUM OF THE EIGENVALUES";
PRINT ADDVALS[FORMAT = 5.2];
PRINT NEWPAGE;
PRINT "EIGENVECTORS";
PRINT  CVEIGVEC[FORMAT=7.4 ROWNAME = VARNAME COLNAME = CVLABROW];
CANSCORS = GRNDDEVS*CVEIGVEC; /* SPECIMENS SCORES */
CANMEANS = (GRPMEANS-J(NGDISC,1)*GRNDMEAN)*CVEIGVEC; /* CANONICAL MEANS */
FREE CVEIGVEC GRNDDEVS GRNDMEAN;
PRINT NEWPAGE;
PRINT CANMEANS[FORMAT = 4.2 ROWNAME =  DISCCOL COLNAME = CVLABCOL];
 /*----------------- SAVE CANONICAL MEANS FOR GRAPHICS -----------*/
  IF CANSTO3D = "YES" THEN DO;
 IF RUN = "MAND" THEN DO;
   CREATE SASDAT.MANDCV3D FROM CANMEANS;   /* FRO PROC G3D */
```

```
   APPEND FROM CANMEANS;
END;
IF RUN  = "SKULL" THEN DO;
   CREATE SASDAT.SKULLCV3D FROM CANMEANS;
   APPEND FROM CANMEANS;
END;
  END; /* SAVE TO 3D LOOP */
 /*---------------------------------------------------------*/
 /*  CORREL. OF CANONICAL MEANS TO OTHER MEANS (ORIG.,SHAPE,ETC) */
 /*---------------------------------------------------------*/
 /* CORRELATIONS TO ORIGINAL VARIABLES */
GLUEMEAN = GRPMEANS||CANMEANS; /* APPEND TWO SETSA OF MEANS */
ENNS = NROW(GLUEMEAN);
MEANMEAN = GLUEMEAN[:,];
  MEANMAT = REPEAT(MEANMEAN, ENNS, 1);
  MEANDEVS = GLUEMEAN - MEANMAT;
FREE GLUEMEAN MEANMEAN MEANMAT;
  MEANSSCP = MEANDEVS` * MEANDEVS;
  MEANCOV = MEANSSCP * ((ENNS - (1))** -1.0);
FREE MEANDEVS MEANSSCP;
  MEANVARI = VECDIAG(MEANCOV);
  MEANSD = SQRT(MEANVARI);
  SDINV = MEANSD ## -1.0;
  MEANSDS = DIAG(SDINV);
  MEANCORR = MEANSDS * MEANCOV * MEANSDS; /* CORRELATIONS OF GROUP TO CANONICAL MEANS*/
  IF RUN = "MAND" THEN DO;
     LLBLOCK = MEANCORR[NVAR+(1):NVAR*2,1:NVAR];
  END;
  IF RUN = "SKULL" THEN DO;
     LLBLOCK = MEANCORR[NVAR+(1):NVAR*2,1:NVAR];
  END;
 IF PLEV = "MED" | PLEV = "MAX" THEN DO;
 PRINT NEWPAGE;
 PRINT "CORRELATIONS BETWEEN ORIGINAL VARIABLES AND CANONICAL MEANS";
 PRINT LLBLOCK[FORMAT=4.2 ROWNAME = CVLABCOL COLNAME = VARNAME];
 END;
 FREE  MEANCOV MEANVARI MEANSD MEANSDS SDINV LLBLOCK;
 IF VECTTARG = "SIZE" & REMOVECT ^= "ISO" THEN DO;
 /* CORRELATIONS TO SHAPE1 (ORIG. \ SIZE) */
    PRINT NEWPAGE;
    PRINT "SHAPE1 = ORIGINAL VARIABLE MEANS DIVIDED BY SIZE4 MEANS";
    IF RUN = "MAND" THEN DO;
  SHAPEBAR = REPEAT(TARMEANS, 1, NVAR);
    END;
    IF RUN = "SKULL" THEN DO;
  SHAPEBAR = REPEAT(TARMEANS, 1, NVAR);
    END;
    SHAPEVAR = GRPMEANS#SHAPEBAR##-1.0;
    STIKMEAN = SHAPEVAR||CANMEANS; /* APPEND SHAPE VARIABLE MEANS TO CANONICAL MEANS */
```

```
    BARBAR = STIKMEAN[:,];
    BARMAT = REPEAT(BARBAR, ENNS, 1);
    STIKDEVS = STIKMEAN - BARMAT;
FREE SHAPEBAR STIKMEAN BARBAR BARMAT;
  STIKSSCP = STIKDEVS` * STIKDEVS;
  STIKCOV = STIKSSCP * ((ENNS - {1})** -1.0);
FREE STIKDEVS STIKSSCP;
  STIKVARI = VECDIAG(STIKCOV);
  STIKSD = SQRT(STIKVARI);
  STIKINV = STIKSD ## -1.0;
  SDSTIK = DIAG(STIKINV);
 FREE STIKVARI STIKSD;
  STIKCORR = SDSTIK * STIKCOV * SDSTIK; /* CORRELATIONS OF SHAPE TO CANONICAL MEANS */
FREE SDSTIK STIKCOV;
  IF RUN = "MAND" THEN DO;
     LLBLOCK = STIKCORR[12:22,1:NVAR];
  END;
  IF RUN = "SKULL" THEN DO;
     LLBLOCK = STIKCORR[20:38,1:NVAR];
  END;
 FREE STIKCORR;
 PRINT "CORRELATIONS BETWEEN SHAPE1 MEANS AND CANONICAL MEANS";
 PRINT LLBLOCK[FORMAT=4.2 ROWNAME = CVLABCOL COLNAME = VARNAME];
 FREE  MEANCOV MEANVARI MEANSD SDINV LLBLOCK;
END;  /* VECTTARG - REMOVECT LOOP */
 IF FINDVECT = "YES" & VECTTARG ^= "SIZE" THEN DO;
 /*---------------------------------------------------------------*/
 /* ---- FIND DIRECTION COSINES OF VECTOR OF INTEREST --- */
 /*---------------------------------------------------------------*/

 /*    I.E., FIND MAXIMAL ASSOCIATION BETWEEN CRITERION VARIABLE AND */
 /*    MULTIPLE UNCORRELELATED PREDICTOR VARIABLES (CV'S) */
IF DROPTAX = "NO" THEN DO;/* DROP SELECTED TAXA FROM VECTOR DIRECTION */
   PRINT " TARGET VECTOR MEANS";
   PRINT DISCCOL  BETGNS  TARMEANS;
   PREDTARG = CANMEANS||TARMEANS;  /* PREDICTOR(S) = ALL CV'S */
END;
IF DROPTAX = "YES" THEN DO;
   DO ITERF = 1 TO NGDISC BY 1;
      IF DISCCOL[ITERF,] = ELIMTAX THEN DO;
         INDEX = ITERF;
      END;
   END;  /* ITERF LOOP */
   NEWCANS = CANMEANS[1:INDEX-{1},]//CANMEANS[INDEX+{1}:NGDISC,];
   NEWTARS = TARMEANS[1:INDEX-{1},]//TARMEANS[INDEX+{1}:NGDISC,];
   NEWBTGNS = BETGNS[1:INDEX-{1},]//BETGNS[INDEX+{1}:NGDISC,];
   NEWDCOL =  DISCCOL[1:INDEX-{1},]//DISCCOL[INDEX+{1}:NGDISC,];
   PRINT "TARGET VECTOR MEANS ";
```

```
   PRINT NEWDCOL  NEWBTGNS  NEWTARS[FORMAT = 6.2];
   PREDTARG = NEWCANS||NEWTARS;  /* PREDICTOR(S) = ALL CV'S */
FREE NEWCANS NEWTARS NEWBTGNS ;
   NGDISC = NGDISC - (1);
END; /* DROPTAX LOOP */
TARLABL = VECTTARG;
NEWRLABL = CVLABCOL//TARLABL;NEWCLABL = NEWRLABL`;
NEWNVAR = NVAR+(1);
FREE TARMEANS;
COLMEANS = PREDTARG[:,];
MEANMAT = REPEAT(COLMEANS, NGDISC,1);
DEVSMAT = PREDTARG-MEANMAT;
FREE MEANMAT;
PTARSSCP = DEVSMAT`*DEVSMAT;
FREE DEVSMAT;
PTARGCOV = PTARSSCP*((NGDISC-1)**-1.0); /* PREDICTOR-TARGET VARIANCE COVARIANCE MATRIX*/
FREE PTARSSCP;
PRINT NEWPAGE;
PRINT " TARGET-PREBICTORS VARIANCE-COVARIANCE MATRIX";
NEWCLABL = NEWRLABL`;
PRINT PTARGCOV[FORMAT= 6.2 ROWNAME = NEWRLABL COLNAME = NEWCLABL];
FREE GRUPROW;
TARGVAR = PTARGCOV[NEWNVAR, NEWNVAR];
TARGSTD = SQRT(TARGVAR);
TARSDCOL = REPEAT(TARGSTD,NVAR,1);
PREDVARA = PTARGCOV[1:NVAR,1:NVAR];
PREDVARI = VECDIAG(PREDVARA);        /* PREDICTOR VARIANCES */
FREE PREDVARA;
PTARCOV = PTARGCOV[NEWNVAR,1:NVAR];
PTCOVCOL = PTARCOV`;                 /*TARGET-PREDICTOR COVARIANCES */
  PTVARS = VECDIAG(PTARGCOV);
  PTARSTD = SQRT(PTVARS);
  PTSTDINV = PTARSTD ## -1.0;
  PTSTDMAT = DIAG(PTSTDINV);
  PTARCORR = PTSTDMAT * PTARGCOV * PTSTDMAT; /*PREDICTOR-TARGET CORRELATION MATRIX*/
 FREE PTARCOV PTVARS PTSTDMAT PTSTDINV;
  PTCORRS = PTARCORR[NEWNVAR,1:NVAR];
 FREE PTARCORR;
  PTCORRCOL = PTCORRS`;
FREE PTCORRS;
  PTCORRSQ = PTCORRCOL##2;
 REGCOEFF = PTCORRCOL # TARSDCOL##-1.0 # PTARSTD[1:NVAR,];
   SSQCOEFF = REGCOEFF[##,];
   ROOTSSQC = SQRT(SSQCOEFF);
   INVRTSSQ = ROOTSSQC##-1.0;
   DIRECCOS = REGCOEFF#INVRTSSQ; /* DIRECTION COSINES */
   RADIANS  = ARCOS(DIRECCOS);
   ANGLES = RADIANS#57.295779;
 PRINT NEWPAGE;
```

```
PRINT CVLABCOL
 PREDVARI[FORMAT=5.2]
 PTCOVCOL[FORMAT =5.2]
 PTCORRCOL[FORMAT=5.2]
 PTCORRSQ[FORMAT=5.2]
 REGCOEFF[FORMAT=6.4]
 DIRECCOS[FORMAT=6.5]
 ANGLES[FORMAT=4.1];
FREE PTCORRSQ PTCORRCOL PTARGCOV PTCORRS SSQCOEFF ROOTSSQC INVRTSSQ PREDVAR PTCOVCOL;
COEFCV12 = REGCOEFF[1:2,];
FREE REGCOEFF;
SSQCV12 = COEFCV12[##,];
ROOTCV12 = SQRT[SSQCV12);
INVCV12 = ROOTCV12##-1.0;
CV12COS = COEFCV12#INVCV12;
CV12RADS = ARCOS(CV12COS);
CV12ANGL = CV12RADS # 57.295779;
PRINT"";
PRINT "PROJECTED ANGLE OF TARGET VECTOR WITH CV1 AND CV2";
PRINT  CV12ANGL[FORMAT=4.1];
SMALLANG = CV12ANGL[1,1];
RADANGLE = SMALLANG # 0.017453293;
THETATAN = TAN(RADANGLE);        /* FIND DUMMY MARKERS FOR PLOTTING*/
PRINT THETATAN;
C1 = {5};
C2 = {10};
HEIGHT1 = C1 # THETATAN;
HEIGHT2 = C2 # THETATAN;
POS1 = C1||HEIGHT1;
POS2 = C2||HEIGHT2;
POSMARKS = POS1//POS2;
NEGMARKS = - POSMARKS;
PRINT POSMARKS NEGMARKS;
FREE SINTEMP SINTHETA C1 C2 HYPOT1 HTPOT2 HTTEMP1 HTTEMP2 HEIGHT1 HEIGHT2;
END; /* SIZE VECTOR COSINES LOOP */
IF PLEV = "MED" | PLEV = "MAX" THEN DO;
/*---- PLOTTING ROUTINES - ORIGINAL CANONICAL VARIATES -----------*/

    IF AXES = "MAX" THEN DO;
       MAX1SCOR = MAX(CANSCORS[,1]);
       MIN1SCOR = MIN(CANSCORS[,1]);
       MAX2SCOR = MAX(CANSCORS[,2]);
       MIN2SCOR = MIN(CANSCORS[,2]);
       MAXXYS = MAX1SCOR||MAX2SCOR;
       MINXYS = MIN1SCOR||MIN2SCOR;
       RANGESXY = MAXXYS//MINXYS;
    END; /*---> AXES = MAX */

     BLANKS = {" ", " "};
```

```
FREE MAX1SCOR MIN1SCOR MAX2SCOR MIN2SCOR MAXXYS MINXYS MAXMEANS MINMEANS;
 IF PLOTSET = "ARB" THEN NPLOTS = NUM(PLOTNUM);
 IF PLOTSET = "FIND" THEN DO;
 END;
 IF PLOTSET = "ALL" THEN DO;
    POSCOUNT = {0};
    ITVAL = NROW(CVEIGVAL);
    DO ITERY = 1 TO ITVAL BY 1;
       IF CVEIGVAL[ITERY] > 0 THEN DO;
          POSCOUNT = POSCOUNT + {1};
       END;
    END;
    NPLOT1 = POSCOUNT/2 + 3/4;
    NPLOTS = INT(NPLOT1);
    IF RUN = "HAND" THEN IF NPLOTS = 6 THEN NPLOTS = 5;
    IF RUN = "SKULL" THEN IF NPLOTS = 10 THEN NPLOTS = 9;
 END; /* ---> PLOTSET = ALL */
DO ITERA = 1 TO NPLOTS BY 1;
XYMAT = CANSCORS[,XAX:YAX]; /* SORT ROUTINES FOR EACH PLOT */
CVBARS = CANMEANS[,XAX:YAX];
CVX = XYMAT[,1];
CVB = CVBARS[,1];
RNKS1 =  RANK(CVX);
RNKS2 = RANK(CVB);
SORTIDS = ACCINDIB;
SORTSCOR = XYMAT;
SORTMEAN = CVBARS;
SORTGLAB = DISCCOL;
  DO ITERB = 1 TO DISCASES BY 1;
     RJ1 = RNKS1[ITERB];
     SORTIDS[RJ1,] = ACCINDID[ITERB,];
     SORTSCOR[RJ1,] = XYMAT[ITERB,];
  END;  /* ---> ITERB LOOP */
  DO ITERC = 1 TO NGDISC BY 1;
     RJ2 = RNKS2[ITERC];
     SORTGLAB[RJ2,] = DISCCOL[ITERC,];
     SORTMEAN[RJ2,] = CVBARS[ITERC,];
  END; /* ---> ITERC LOOP */
  SCORPRNT = SORTSCOR;
  MEANPRNT = SORTMEAN;
 FREE CHARSCOR CHARMEAN CHOPSCOR CHOPMEAN;
    PLOTSYM1 = SUBSTR(SORTIDS,1,1);
    PLOTSYM2 = SUBSTR(SORTGLAB,1,1);
    PLOTSYM1 = PLOTSYM1//BLANKS;
    PLOTSYM2 = PLOTSYM2//BLANKS;
    SORTSCOR = SORTSCOR//RANGESXY;
    SORTMEAN = SORTMEAN//RANGESXY;
  PRINT NEWPAGE;
  PRINT "SORTED SCORES FOR " YAX "VS" XAX, SORTIDS SCORPRNT;
```

```
 PRINT NEWPAGE;
   CALL PGRAF(SORTSCOR, PLOTSYM1, CVLABCOL[XAX], CVLABCOL[YAX]);
 PRINT NEWPAGE;
   PRINT "SORTED CANONICAL MEANS FOR " YAX "VS" XAX, SORTGLAB MEANPRNT;
 PRINT NEWPAGE;
  CALL PGRAF(SORTMEAN, PLOTSYM2, CVLABCOL[XAX], CVLABCOL[YAX]);
OLDXAX = XAX;
OLDYAX = YAX;
XAX = OLDYAX+{1};
YAX = OLDXAX+{3};
   END; /* ---> NPLOTS  LOOP */
 END; /* PLEV MED MAX BLOCK */
IF PLEV = "MAX" THEN DO;
/*-- AMONG-GROUPS GENERALIZED DISTANCES WITHOUT VECTOR REMOVEL----*/
 D = J(NGDISC,NGDISC);
 DO ITERONE = 1 TO NGDISC BY 1;
    DO ITERTWO = ITERONE TO NGDISC BY 1;
   IF ITERTWO = ITERONE THEN DO;
      D[ITERONE, ITERTWO] = {0};
   END;
   IF ITERTWO ^= ITERONE THEN DO;
      DIFFS = CANMEANS[ITERONE,]-CANMEANS[ITERTWO,];
      SUMDSQR = SSQ(DIFFS);
      D[ITERONE, ITERTWO] = SQRT(SUMDSQR);
      D[ITERTWO, ITERONE] = SQRT(SUMDSQR);
   END;
    END; /*ITERTWO*/
END; /*ITERONE*/
  MINISUB1 = SUBSTR(DISCGRPS,1,1);
  MINISUB2 = SUBSTR(DISCGRPS,5,1);
  NEWGROW = CONCAT(MINISUB1, MINISUB2);
  NEWGCOL = NEWGROW`;
PRINT NEWPAGE;
PRINT D[FORMAT=3.0 ROWNAME=NEWGCOL COLNAME = NEWGROW];
END; /* PLEV BLOCK */
 IF REMOVECT = "BURN" THEN DO;
/*---------------- BURNABY'S METHOD FOR VECTOR(S) REMOVAL ----------*/
/* P=LO L = I - F(FtF)-1Ft WHERE F = DIRECTION COSINES IN CV SPACE */
 IDENTMAT = I(NVAR);
 ELIMVECT = DIRECCOS; /* VECTOR TO ELIMINATE IS DIRECTION COSINES OF SIZE VARIABLE */
FREE DIRECCOS;
    ELIMMAT = ELIMVECT` * ELIMVECT;
    ELIMINV = INV(ELIMMAT);
FREE ELIMMAT;
    ALLVECT = ELIMVECT * ELIMINV * ELIMVECT`;
FREE ELIMINV ELIMVECT;
    PROJMAT = IDENTMAT - ALLVECT;
FREE IDENTMAT ALLVECT;
    PROJDAT = CANMEANS * PROJMAT; /* PROJECT CANONICAL MEANS TO ORTHOGONAL PLANE */
```

```
FREE CANMEANS;
BURNLABL = SUBSTR(DISCCOL, 1,1);
BLANKS =(" "," ");
CANMLABL = BURNLABL//BLANKS;
PRINT NEWPAGE;
PRINT "TARGET VECTOR-FREE DATA BASED ON BURNABY'S METHOD";
PRINT PROJDAT[FORMAT=4.1 ROWNAME = DISCCOL COLNAME = CVLABROW];
MAXVAL = MAX(PROJDAT);
MINVAL = MIN(PROJDAT);
 PRINT MAXVAL MINVAL;
 MAXIS = REPEAT(MAXVAL, 1, 2);
 MINIS = REPEAT(MINVAL, 1, 2);
 COLS12 = PROJDAT[,1:2];
 PLOT12 = COLS12//MAXIS//MINIS;
 COLS34 = PROJDAT[,3:4];
 PLOT34 = COLS34//MAXES//MINIS;
PRINT NEWPAGE;
CALL PGRAF(PLOT12, CANMLABL, "SIZE-FREE CV1", "SIZE-FREE CV2");
PRINT NEWPAGE;
CALL PGRAF(PLOT34, CANMLABL, "SIZE-FREE CV3", "SIZE-FREE CV4");
/* ----- REORTHOGONALIZE BURNABY DATA USING PCA --------------*/
PCMEANS = PROJDAT[:,];
MEANMAT = REPEAT(PCMEANS, NGDISC,1);
PCDEVS = PROJDAT - MEANMAT; /* DEVIATIONS OF PROJECTED DATA FROM MEANS */
FREE MEANMAT;
PCSSCP = PCDEVS` * PCDEVS;
PCCOV = PCSSCP * (NGDISC-(1))**-1.0; /* COVARIANCE MATRIX OF PROJECTED DATA */
CALL EIGEN(PCEIGVAL, PCEIGVEC, PCCOV);
ADDVALS = PCEIGVAL[+,];
VALPERCS = (PCEIGVAL*ADDVALS**-1.0)*100;
CUMUPERC = CUSUM(VALPERCS);
VALSUM = PCEIGVAL||VALPERCS||CUMUPERC;
VALSLAB = {EIGENVALUE POFTOTAL CUMULATIVE};
PRINT NEWPAGE
PRINT "EIGENVALUES";
PRINT VALSUM[FORMAT=5.3 ROWNAME = CVLABCOL COLNAME = VALSLAB];
PRINT "SUM OF THE EIGENVALUES";
PRINT ADDVALS[FORMAT=6.1];
PRINT NEWPAGE;
PRINT PCEIGVAL[FORMAT=6.2];
PRINT PCEIGVEC[FORMAT=6.4];
NOVECSC = PROJDAT * PCEIGVEC;
SCORMEAN = NOVECSC[:,];
MEANMAT = REPEAT(SCORMEAN, NGDISC,1);
NOVECCEN = NOVECSC - MEANMAT;          /* MEAN-CENTERED SCORES */
PRINT NEWPAGE;
PRINT NOVECCEN[FORMAT=4.1 ROWNAME = DISCCOL COLNAME = CVLABROW];
MAXSCOR = MAX(NOVECCEN);
MINSCOR = MIN(NOVECCEN);
```

```
PRINT MAXSCOR MINSCOR;
REPMAX = REPEAT(MAXSCOR, 1, 2);
REPMIN = REPEAT(MINSCOR, 1, 2);
PC1PC2 = NOVECCEN[,1:2];
PCPLOT12 = PC1PC2//REPMAX//REPMIN;
PC3PC4 = NOVECCEN[,3:4];
```