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A MORPHOMETERIC ANALYSIS OF THE FIVE
SUBSPECIES OF SUS BARBATUS, THE BEARDED PIG

presented by

KAREN MARI MUDAR

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Donald L. Straney
Major professor

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A MORPHOMETERIC ANALYSIS OF THE FIVE SUBSPECIES OF SUS BARBATUS, THE BEARDED PIG

by

Karen Mari Mudar

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ABSTRACT

A MORPHOMETRIC ANALYSIS OF THE FIVE SUBSPECIES OF SUS BARBATUS, THE BEARDED PIG

By

Karen Mari Mudar

Cranial variation among the five subspecies of the bearded pig *Sus barbatus* is an interesting problem of morphological diversity. Multivariate statistics are employed to explore the degree of diversity and characterize patterns of morphology among the populations. Measurements taken using a truss scheme are subjected to discriminant analysis. It was shown that size differences are present between three of the five subspecies. Standard principal component analysis added little new information. However, the shear procedure (Humphries et al. 1981) demonstrated that shape discrimination between three of the five subspecies was also possible.

Patterns of shape and size differences are discussed with reference to the effects of island size on body size of artiodactyls, and geological reconstruction of dispersal patterns. The smallest sub-species were found on the oceanic islands of the Philippines, the largest on the Malaysian mainland and the large islands of Sumatra and Borneo. The populations on Palawan were larger than expected, based on island size. Size of this population may be influenced by genetic relationships with the largest subspecies on the next island, Borneo.

Shape differences were most pronounced in the ventral region of the skull pertaining to the tooth row. It is suggested that these subspecies may be adapting to local ecological conditions.

This study indicates that *Sus barbatus barbatus* and *Sus barbatus oi* should be combined as *Sus barbatus barbatus* and that *Sus barbatus philippensis* and *Sus barbatus cebifrons* should be combined as *Sus barbatus philippensis*.

ACKNOWLEDGEMENTS

Like a tale that grew in the telling, this thesis has expanded greatly since its first inception. Initially it was a study of the interactions between human predators and suid prey in northeastern Luzon, Philippines. By the time of submission and defence, the thesis consisted of a morphometric analysis of the five subspecies of *Sus barbatus*. The people who have aided in the completion of this thesis deserve most of the credit; I was primarily a catalyst. I have been honored by the assistance that these people have given me, and am grateful for the opportunity to thank them here.

Dr. Karl Huttter first introduced me to the Philippines in 1979, as a member of the Bais Anthropological Project. He provided financial support in 1981, when the suid sample from northeastern Luzon was collected, and again in 1983, when the museum collections were examined. He has also been an important source of emotional support. Dr. P. Bion Griffin provided accomodations in the field in northeastern Luzon in 1981, and initiated trading relationships between myself and the local hunters. He continued to collect skulls in 1982, and made arrangements to ship them to the United States. Both of these men have been primary support, and deserve a very special thanks. This thesis would have been logistically impossible without them.

Thanks goes to the Agta hunters, especially Tatayan, Sinebu, Galpong, and the hunters at Sapinet for cooperating in trading arrangements. Employees of Acme, Southern Plywood, and Cagayan Lumber Company provided transportation, and receive my thanks, especially Pete Galimba. My traveling companions, Marcus Griffin and Melinda Allen, deserve special recognition for their tolerance and patience.

After returning from the Philippines in 1981, I attended the University of Michigan for one semester. During this time, Dr. Lawrence Heaney found working space for me at the Museum of Zoology, and provided a sounding board for ideas. His comments have been instrumental in the formation of the thesis topic and are acknowledged here.

After my admittance to Michigan State University and the formation of my committee, the thesis began to take shape. I would like to thank my committee, Dr. Donald Straney, Dr. Alan Holman, and Dr. Norman Sauer for their patience and assistance. I owe a special debt to Dr. Alan Holman for arranging office space for me. Dr. Straney has been particularly helpful, both as an advisor and a friend. The office staff at the Zoology Department, especially Anne Tanner and Charmane Corcoran, have handled much paperwork and found financial support for me for three years, for which I am very grateful.

In 1984 I was able to visit museum collections in Southeast Asia and Europe. Support for this trip came from the University of Michigan, (through Dr. Karl Hutterer), Michigan State University, and Michigan State University Museum, (through Dr. Kurt Dewhurst, and Dr. A. Chris Carmichael). Their assistance is acknowledged here.

I would also like to thank the following people for assistance while woking in their countries: National Museum of the Philippines, Manila: Dr. Pedro Gonzales, Dr. Jess Peralta, Roger Sission, and Raymundo Esquerra; National University Museum, Singapore, Mrs. Yung; Jabatan Museum, Kuching, Lucas Chin and Charles Leh; Muzium Sabah, Kota Kinabalu, Anwar Sullivan, Judith John Baptist; Muzeum Zoologici Bogoriense, Bogor, Indonesia,Mr. Bogadi; British Museum, London, Dr. Juliet Jewell; Cambridge Museum, Cambridge, Dr. Joysey; U.S. Museum of Natural History, Washington, D.C., Dr. Thorrington, David Schmidt; Field Museum of Natural History, Chicago, Dr. Bruce Patterson, Dr. Robert Timm. I also would like to thank C.H. Diong, who showed me the only live bearded pigs I ever saw, Napoleon and Petunia, at the Singapore Zoo.

My woefully small sample of *Sus barbatus cebifrons* was augmented through the efforts of Paula Heideman, who took the time from his dissertation fieldwork to collect several specimens. I greatly appreciate the effort he made, and thank him here.

My fellow students are gratefully acknowledged for their tolerance and support. Frank Knight spent many hours discussing thesis writing, Dan Bennack helped proof numbers, and Dean and Bette Premo opened their house to me while in Indonesia. Ken Creighton and Barb Lundrigen loaned me their apartments while in Washington D.C. Alan Jaslow was a thoughtful host while working in Chicago. I also benefitted from class discussions with Miriam Zeldich, Don Swidersky, Sergio Dos Rey, and Jim Zablotney.

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There is also a group of people who deserve a special thanks. These people had no interest in the thesis topic, but provided help and encouragement nonetheless. Mr. Alfonso Lim allowed me to work in his timber concessions, and arranged for logistical support. The Bombay to Borneo Bushbashers, Mr. Nick Cerra and Mr. Pat Jackson, opened their home to me on several occasions. Dr. Alice Dewey was a wonderful guide while staying in Jogyakarta. My sister Charlotte spent numerous hours proofreading data sheets, and my brothers Joe and Marc lent equipment and money. The support of this special group has been essential to finishing this thesis, and I thank them.

There is also a group of people who believed I would finish even when I didn't, for whom any measure of thanks is inadequate: Joe, Mary, and Tim.

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INTRODUCTION

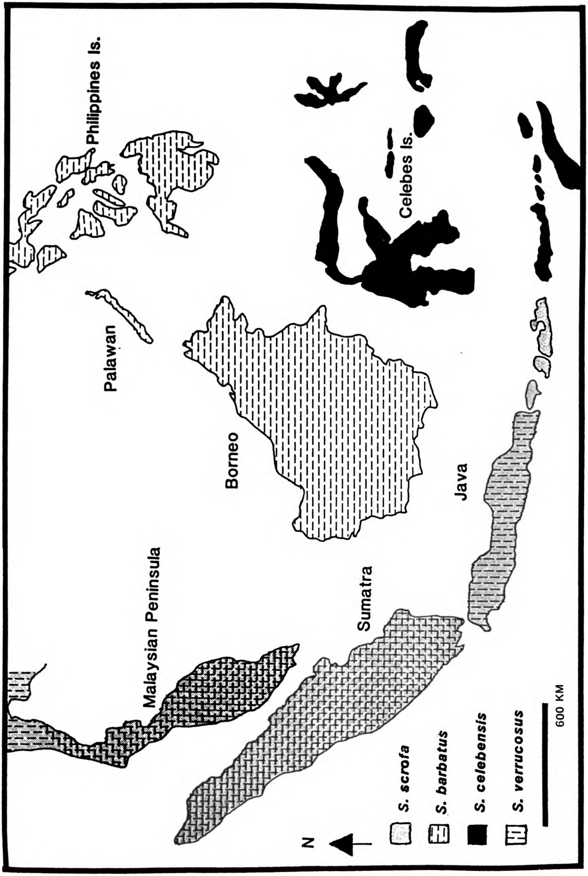
Four species of wild pig occur in Southeast Asia: *Sus barbatus* Muller (bearded pig), *S. scrofa* Linnaeus (domestic pig), *S. celebensis* Muller (Celebes pig), and *S. verrucosus* Miller (Javanese warty pig). *S. verrucosus* is found on Java and the adjacent islands of Bawean and Madura (see Figure 1). *S. celebensis* occurs on the Celebes islands of Sulawesi, Flores, and Halmahera. *S. scrofa* has been introduced to all of Southeast Asia inhabited by humans, but occurs indigenously on the Malaysian peninsula and Sumatra. Populations of *S. barbatus* occur sympatrically with wild *Sus scrofa* in Malaysia and Sumatra, but are the only wild pig on Borneo, Palawan, and the Philippines.

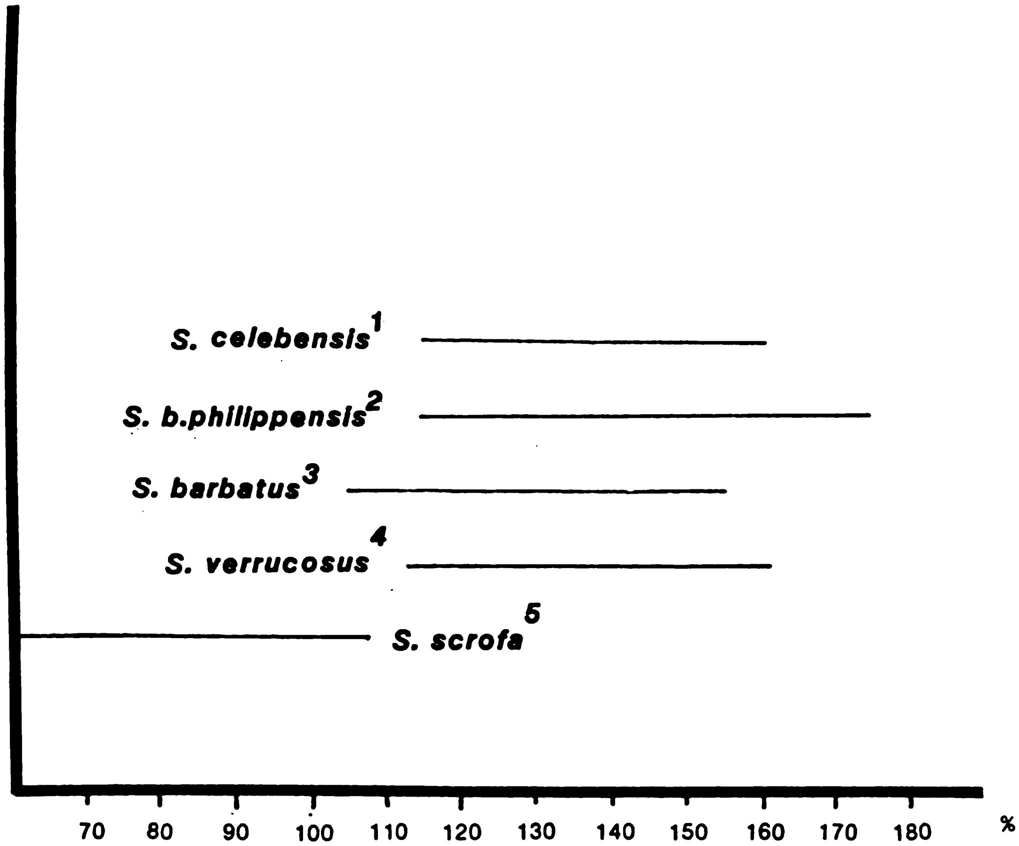
Groves (1981) recently proposed a taxonomic revision of *S. barbatus* as part of a revision of the genus, recognizing five subspecies. Although they exhibit intra-spcific differences in size and occupy disjunct geographical areas, these five subspecies are distinct from sympatric *S. scrofa* in at least one characteristic. Ratios of the width of the inferior surface to width of the posterior surface of the male lower canine for all subspecies of *S. barbatus* fall outside the range for the same ratio in *S. scrofa* (see Figure 2). For the purposes of this study, I accept the taxonomy proposed by Groves.

These subspecific assignments appear to be partly a function of size differences between populations, and partly based on geographical considerations. All wild pigs on Borneo were assigned to *S. b. barbatus*, while all non-*scrofa* wild pigs on Sumatra and the Malaysian mainland were classified as *S. b. oi* (see Figure 3). Reasons for uniting geographically discontinuous populations in subspecies *oi* were not given. Groves indicates that *S. b. barbatus* and *S. b. oi* may be separated on the basis of the length of the molar row as a percentage of the total tooth row, as the molar row is relatively smaller in *S. b.*

Figure 1

Distribution of wild pigs in Southeast Asia.


Philippines Is.
Palawan
Borneo
Celebes Is.
Java
Sumatra
Malaysian Peninsula
N
S. scrofa
S. barbatus
S. celebensis
S. verrucosus
600 KM



1. N=4 (Groves;1981)
2. N=22 (Groves;1981,Mudar,n.d.)
3. N=21 (Groves;1981)
4. N=19 (Groves;1981)
5. N=54 (Groves;1981)

Figure 2

Width of inferior surface as a percentage of width of posterior surface in lower canines of adult male *Sus*, by species and subspecies. surface in lower canines of adult male *Sus*, by species and subspecies.

oi. This is interpreted as an example of character displacement (Groves 1981;51), as *S. b. oi* occurs sympatrically with *S. scrofa*. He also noted that *oi* has shorter whiskers and a shorter molar row in relation to total tooth row size than *barbatus*. Mohr (in Groves 1981) noted that the body of *oi* is more bilaterally flattened than *barbatus*. There appears to be no difference in size between the two subspecies.

All populations found in Palawan and adjacent islands were assigned to *S. b. ahoenobarbus*. This subspecies is smaller than *barbatus* and *oi*. Sanborn (1952) also noted that this form exhibits a particularly short palate.

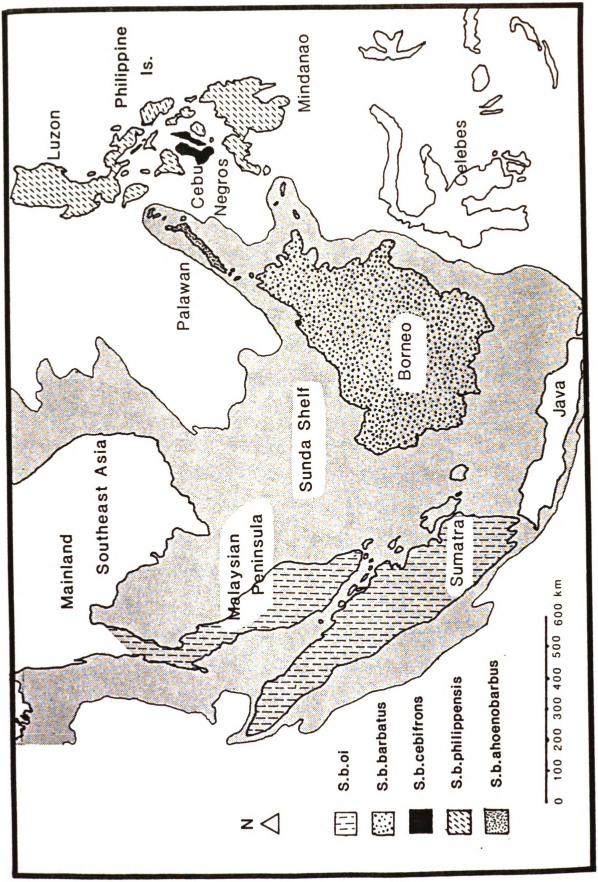
All wild pigs in the Philippine archepelago with the exception of Negros and Cebu were placed in *S. b. philippensis*. This subspecies has a shorter maxillary diastema and a smaller body size than the three preceeding subspecies (Groves 1981). Populations of bearded pigs from the islands of Negros and Cebu were recognized by Heude (1888) as a separate species because of their small size. This distinction is maintained by Groves, who assigned the populations of these islands to a separate subspecies, *S. b. cebifrons*. He placed the Philippine pigs in *S. barbatus*, but suggested that they may be a separate species, most closely related to *S. barbatus* (1981;50).

Species such as the bearded pig are particularly problematic to distinguish taxonomically because populations which are, potentially, closely related are allopatrically distributed. An important question concerning this species is how much variation between the populations is likely to be ecological in origin, and how much is likely to be genetic. Pervasive differences in size and shape between the populations may be a result of long isolation, or adaptation to specific ecological conditions.

The objective of this study is to assess intra-specific variation in cranial morphology through an exploration of shape as well as size differences. I wish to address the following questions: What is the pattern of size differences between the different subspecies? Can the subspecies be separated on the basis of shape differences? Do these shape differences correspond in groupings to those isolated by size differences? Do shape differences consist

Figure 3

Geographical distribution of the five subspecies of *Sus barbatus*.


Luzon
Philippine Is.
Mindanao
Cebu
Negros
Celebes
Palawan
Borneo
Sunda Shelf
Java
Sumatra
Mainland Southeast Asia
Malaysian Peninsula
N
S.b.oi
S.b.barbatus
S.b.cebifrons
S.b.philippensis
S.b.ahoenobarbus
0 100 200 300 400 500 600 km

of single characters or character complexes? Can these differences be explained in biological terms? What is the nature of the shape and size differences between the populations? To accomplish these objectives, multivariate analysis of cranial characteristics of all five subspecies were performed. Consideration of geographical distribution of the populations was used as a source for explanation in discussion of the results.

MATERIALS AND METHODS

All specimens measured were from museum collections with the exception of a sample of *S. b. philippensis* which I collected (see Appendix A). This sample, from northeastern Luzon (see Figure 4), was the only one in which most of the specimens were from a restricted geographical area and a potentially interbreeding population. Use of samples from geographically restricted areas would reduce inter-population variation which may obscure intra-species differences. Unfortunately, most museum collections consisted of specimens from a number of localities, and it was not possible to eliminate specimens from consideration and maintain an adequate sample size for statistical purposes. Forty-five total individuals of *S. b. philippensis* were measured from one locality in Luzon, one from Catanduanis, and five from Mindanao. *S. b. cebifrons* was represented by five individuals from two localities on Negros Island. The sample of 12 *S. b. ahoenobarbus* is from three islands between Borneo and Mindoro (Palawan, Culion, and Balabec). Very few of the 76 specimens of *S. b. barbatus* from Borneo are from the same locality, while the 24 specimens of *S. b. oi* are from localities on Sumatra, the Rhio Archepelago, and Malaysia.

Comparison of standard deviations of *S. b. philippensis* with *S. b. barbatus*, the other subspecies sample of comparable size, suggests that inter-population variation was minimal (see Tables 1 and 2). Standard deviations as a percentage of the mean measurement were comparable for both samples; the largest for *barbatus* was 25% (female M6), the largest for *philippensis* was 22% (male M4). Ratios of standard deviations to mean measurement for other samples were consistantly higher, presumably as a function of the smaller sample sizes. OTUs (Operational Taxonomic Units) were chosen on the

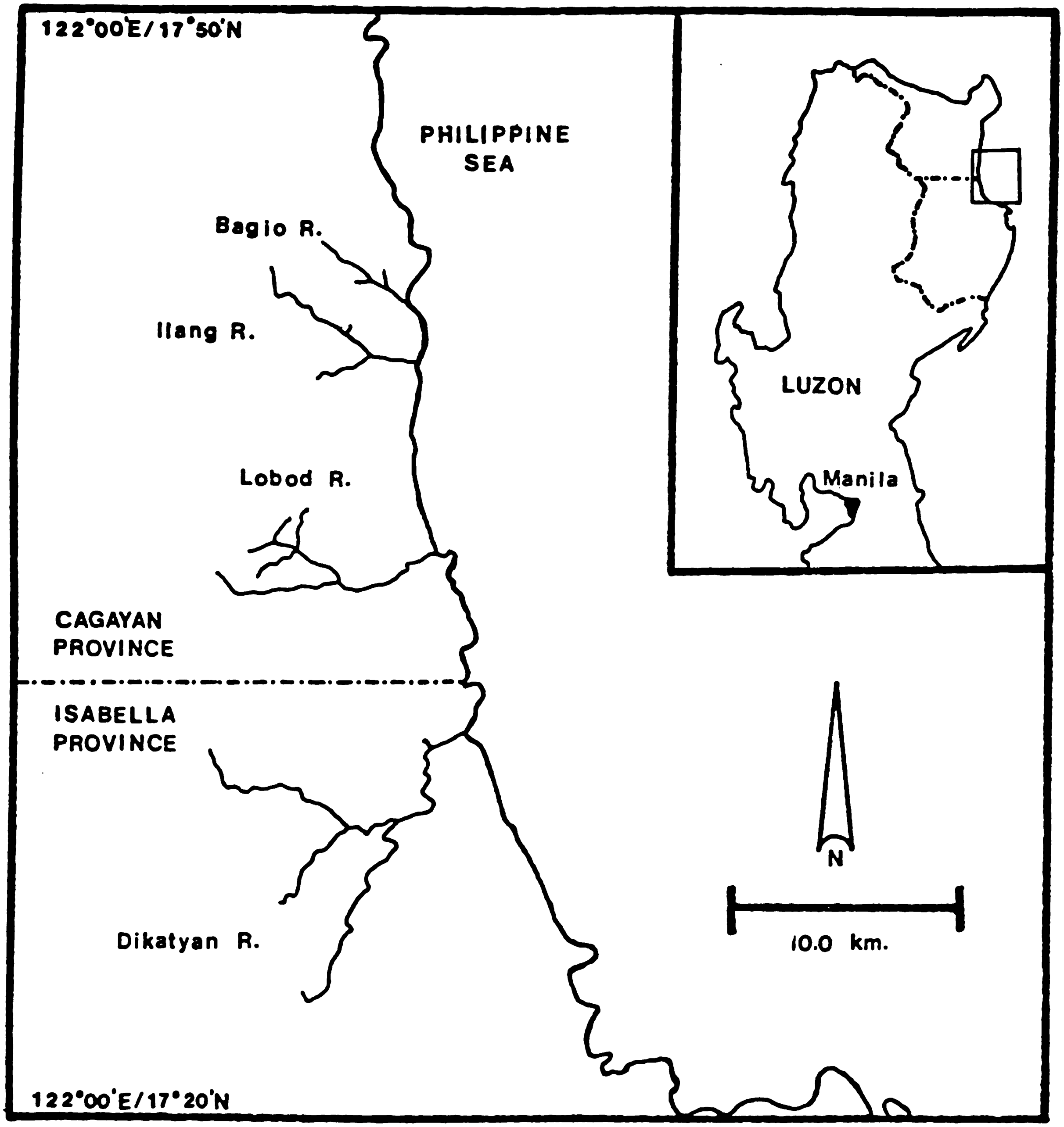


Figure 4

Map of the major river valleys in northeastern Luzon, where sample of *S. b. philippensis* was collected.

basis of current taxonomy, *barbatus* (BARB), *oi* (OI), *ahoenobarbus* (AHO), *philippensis* (FIL), and *cebifrons* (CEBI).

To minimize the effects of allometric variations associated with growth, only adults were measured. Adult status was defined by the eruption of the third molar. A total of 173 mandibles and 186 skulls were measured. All five subspecies are represented, although two, *ahoenobarbus* and *cebifrons*, are represented by few individuals.

Young individuals of *philippensis* were also measured to assess ontogenetic changes in morphology. Unfortunately, no tooth eruption schedule has been developed for *S. barbatus*. I used one developed for *S. scrofa* (Matsche 1967) as a guide for aging these specimens (Table 3). Although the absolute age at eruption may be different in the two species, the order of eruption is the same. The schedule thus provides a standardizing set of relative age criteria.

The measurement scheme used in this analysis was modeled after the box truss method (Strauss and Bookstein 1982). The truss is a geometric template for retrieving information on specimen shape that relies on the recognition of homologous points between specimens. This data collection method has a number of advantages over more traditional measurement schemes. It emphasizes recognition of landmarks which are biologically meaningful; it provides a more complete and even coverage of the specimen; it specifies measurements which are oblique to the long axis of the specimen and it breaks up long distances into shorter units. In addition, the truss scheme is extremely flexible, and can be used in conjunction with standard statistical procedures as well as other analytical techniques.

The truss measurement scheme I used resulted in a total of 48 measurements per specimen, 39 on the crania and 9 on the mandible (see Appendix B). Measurements were taken of distances between 23 landmarks (see Figure 5). Landmarks were chosen to represent morphological features on the major portions of the skull, and that could be located in both adult and immature skulls. I avoided landmarks from the basicranial

Table 1

Means, standard deviations, and sample sizes for female *Sus barbatus*.

Variable	FIL (32,23)[1]	CEBI (2,3)	AHO (6,6)	BARB (23,28)	OI(8,5)
			Crania		
M1	2.221±.178	1.967±.314	2.989±.301	3.851±.513	3.801±.304
M2	7.711±.524	6.727±.067	8.751±.769	11.728±.901	11.897±1.152
M3	9.817±.605	8.526±.357	11.586±.799	15.254±.982	15.523±1.229
M4	12.889±.938	11.662±.144	14.854±1.242	19.066±1.239	19.104±1.
M5	3.464±.612	2.985±.049	5.900±.932	7.294±.968	7.370±1.288
M6	3.535±.436	3.325±.530	3.990±.534	4.294±1.095	4.246±1.531
M7	1.857±.217	1.595±.219	3.256±.731	4.285±1.053	4.534±1.144
M8	8.618±.685	8.644±.000	12.024±1.238	15.680±1.446	16.821±1.149
M9	8.726±.779	9.072±.477	10.202±.936	12.713±.948	13.606±1.007
M10	4.454±.836	3.880±.148	4.995±.688	5.802±.750	6.071±.657
M11	6.762±.671	6.957±.201	7.250±.489	9.193±.725	9.568±.408
M12	6.313±.342	4.935±2.276	7.347±.386	9.196±.550	9.029±.661
M13	6.083±.377	5.690±.360	6.170±.293	7.488±.361	7.231±.822
M14	3.715±.450	3.252±.159	3.497±.238	4.023±.341	4.181±.549
M15	4.242±.511	4.157±.639	4.661±.323	5.924±.408	5.311±.445
M16	7.660±.459	6.897±.413	8.602±.388	10.920±.765	10.784±.875
M17	6.120±.371	5.790±.212	6.702±.191	8.358±.316	8.411±.518
M18	7.933±.487	7.177±.350	9.202±.612	11.961±.514	12.319±.766
M19	5.058±.379	4.872±.258	6.750±.583	9.215±.505	9.497±1.037
M20	4.972±.211	4.595±.120	6.245±.247	7.448±.301	7.233±.238
M21	6.197±.284	5.912±.130	6.416±.302	7.637±.397	7.648±.433
M22	4.828±.413	4.232±.074	6.260±.502	8.099±.523	7.915±.748
M23	3.090±.255	2.982±.159	3.918±.487	4.328±.188	4.101±.188
M24	4.084±.337	4.13±.240	4.527±.255	5.725±.302	5.815±.587
M25	3.872±.291	3.435±.127	4.238±.462	5.525±.628	5.085±.730

Table 1 (continued)

Variable	FIL (32,23)[1]	CEBI (2,3)	AHO (6,6)	BARB (23,28)	OI(8,5)
			Crania		
M26	2.756±.290	2.435±.197	3.318±.342	5.033±.398	5.338±.704
M27	5.336±.492	4.547±.067	6.256±.704	8.678±.747	8.219±.972
M28	5.288±.337	5.192±.194	6.296±.552	7.807±.359	8.858±1.004
M29	3.019±.193	2.745±.049	3.844±.316	4.815±.248	5.184±.567
M30	3.582±.225	3.677±.180	4.269±.301	5.948±.413	6.335±.559
M31	2.140±.229	1.950±.289	2.528±.440	2.622±.300	3.209±.549
M32	4.485±.627	4.040±.296	5.546±.560	7.043±.448	8.120±1.277
M33	9.347±.622	8.117±.498	11.357±1.26	14.254±1.177	15.246±1.371
M34	5.199±.394	4.502±.279	6.420±.794	7.897±.931	7.826±.722
M35	2.910±.318	2.512±.201	3.476±.509	4.335±.656	4.669±.413
M36	3.610±.364	3.530±.459	6.049±.419	7.836±1.008	7.789±1.205
M37	3.451±.305	3.530±.021	4.405±.622	4.756±.921	4.427±.780
M38	1.983±.193	1.755±.098	3.131±.446	4.510±.551	4.790±1.082
M39	4.798±.227	4.782±.130	4.883±.247	6.092±.500	6.050±.450
			Mandibles		
M1	5.147±.600	4.536±.052	6.259±.569	8.732±.531	9.245±.840
M2	5.704±.463	5.636±.215	7.047±.847	9.298±.588	9.752±.903
M3	3.451±.237	3.228±.179	3.940±.414	4.758±.337	5.068±1.00
M4	4.596±.251	3.873±.280	5.462±.272	6.587±.328	6.701±.608
M5	10.824±.676	9.276±.336	13.305±.642	16.257±.755	16.005±.753
M6	4.342±.408	4.888±.271	5.507±.372	7.245±.544	7.735±.626
M7	10.314±.489	10.102±.084	12.959±.732	16.502±.784	16.434±1.125
M8	7.406±.467	6.551±.199	9.084±.558	11.091±.702	10.888±.553
M9	3.191±.157	2.850±.073	4.032±.338	4.405±.389	4.463±.251

[1]Numbers in parentheses refer to sample sizes. First number is crania, second number is mandibles.

Table 2

Means, standard deviations, and sample sizes for male *Sus barbatus*.

Variable	FIL (11,13)[1]	CEBI (2,2)	AHO (4,6)	BARB (48,31)	OI (18,16)
			Crania		
M1	2.554±.298	2.290±.141	3.263±.232	4.117±.414	4.278±.329
M2	8.596±.722	7.427±.922	11.159±1.786	13.417±1.398	12.979±.772
M3	11.011±.932	9.705±.933	14.234±1.888	17.335±1.529	17.068±.895
M4	13.633±3.109	13.510±.537	17.701±1.235	22.048±1.733	21.903±1.307
M5	3.527±.663	4.300±.155	4.832±1.94	7.827±1.248	8.335±1.070
M6	3.951±.483	4.087±.420	3.795±.847	5.198±1.100	5.476±1.107
M7	2.042±.192	2.002±.406	2.662±.616	4.186±.991	4.261±.812
M8	9.931±.957	10.305±1.131	13.500±1.167	17.102±1.443	16.837±1.631
M9	10.434±1.144	10.605±.947	12.606±1.996	14.680±1.349	14.231±1.085
M10	5.009±.567	5.672±1.000	5.821±.963	6.610±.918	6.344±.923
M11	7.395±.489	7.460±.551	8.716±.903	10.042±.992	10.054±.565
M12	7.101±.411	6.455±.417	8.527±.585	10.298±1.552	9.854±.689
M13	6.619±.295	7.160±.438	6.682±.454	7.987±.693	8.254±.624
M14	4.273±.306	4.295±.275	3.895±.609	4.755±.532	4.911±.479
M15	4.322±.489	5.450±.947	4.980±.667	6.188±.697	6.598±.746
M16	8.971±.854	9.020±.742	10.294±.807	12.525±1.064	11.977±.938
M17	6.991±.488	7.810±.586	7.756±.566	9.532±.713	9.648±1.223
M18	8.928±.575	9.640±.127	10.664±.846	13.423±1.637	13.075±1.027
M19	5.266±.264	5.377±.477	7.908±.662	10.117±.645	10.126±1.143
M20	5.112±.315	5.012±.031	6.771±.166	7.632±.412	7.836±.843
M21	6.675±.383	6.530±.042	6.872±.468	8.476±.516	8.379±.469
M22	5.026±.348	5.140±.141	6.782±.221	8.864±.837	8.580±.694
M23	3.234±.169	2.967±.060	3.868±.100	4.418±.379	4.544±1.098
M24	4.593±.375	4.782±.045	5.107±.352	6.371±.490	6.495±.744
M25	4.413±.828	3.972±.137	5.563±1.236	6.014±.615	5.758±.487

Table 2 (continued)

Variable	FIL (11,13)[1]	CEBI (2,2)	AHO (4,6)	BARB (48,31)	OI (18,16)
			Crania		
M26	3.317±.510	2.875±.134	4.336±.998	5.919±.557	6.342±1.097
M27	5.881±.522	5.045±.395	8.601±.874	9.516±1.363	8.882±1.270
M28	6.100±.397	6.265±.212	7.640±1.345	9.229±.575	9.374±.862
M29	3.450±.234	3.625±.212	4.608±.725	5.507±.661	5.589±1.260
M30	4.053±.289	4.612±.300	5.241±1.656	6.713±.670	6.863±1.005
M31	2.643±.332	2.262±.060	3.052±.286	3.372±.650	3.665±1.089
M32	5.532±.776	4.682±.074	6.898±.805	8.347±1.121	8.560±1.578
M33	10.505±.823	8.752±1.064	13.291±1.385	15.302±1.582	15.411±1.922
M34	5.495±.261	5.112±.378	7.116±.923	7.963±1.239	8.198±2.209
M35	3.061±.192	2.910±.304	3.943±.599	4.450±.720	4.487±.998
M36	3.765±.267	3.610±.240	6.981±1.384	8.738±1.161	8.285±1.360
M37	3.548±.409	3.462±.434	4.476±.844	5.080±.591	5.204±1.150
M38	2.124±.308	1.930±.035	3.833±.592	5.247±.895	4.831±.739
M39	5.028±.179	5.112±.166	5.793±.737	6.303±.859	6.343±.930
			Mandibles		
M1	6.269±.843	5.547±.081	7.445±.369	10.556±1.020	11.183±.798
M2	7.042±.877	6.360±.091	8.205±.487	11.083±1.113	11.432±.902
M3	3.960±.382	3.865±.113	4.347±.249	5.867±.638	5.779±.495
M4	5.018±.405	4.930±.289	6.179±.517	7.786±.715	7.736±.586
M5	11.269±.569	10.447±.342	13.855±1.525	17.634±1.378	17.657±1.030
M6	4.975±.552	5.745±.289	5.804±.683	8.202±.718	7.864±.931
M7	11.119±.528	11.155±.452	13.451±1.677	17.807±1.015	17.347±1.013
M8	7.707±.464	7.402±.088	9.266±1.244	11.897±1.032	11.845±.462
M9	3.318±.186	3.687±.583	3.792±.331	4.623±.347	4.514±.237

[1]Numbers in parentheses refer to sample sizes. First number is crania, second number is mandibles.

Table 3

Criteria used for aging individuals of *Sus barbatus*
(from Matsche 1967)

Age	Temporary teeth	Permanent teeth
0–6 days	$i\frac{3}{3}, c\frac{1}{1}$	
7–22 days	$i\frac{3}{3}, c\frac{1}{1}, p\frac{3}{4}$	
23–40 days	$i\frac{13}{13}, c\frac{1}{1}, p\frac{3}{34}$	
6–7 weeks	$i\frac{13}{13}, c\frac{1}{1}, p\frac{34}{34}$	
7–19 weeks	$i\frac{123}{123}, c\frac{1}{1}, p\frac{234}{234}$	
20–33 weeks	$i\frac{123}{123}, c\frac{1}{1}, p\frac{234}{234}$	$P\frac{1}{1}, M\frac{1}{1}$
30–51 weeks	$i\frac{12}{12}, p\frac{234}{234}$	$I\frac{3}{3}, C\frac{1}{1}, P\frac{1}{1}, M\frac{1}{1}$
12–15 months	$i\frac{2}{2}, p\frac{234}{234}$	$I\frac{1\ 3}{1\ 3}, C\frac{1}{1}, P\frac{1}{1}, M\frac{12}{12}$
14–18 months	$i\frac{2}{2}$	$I\frac{1\ 3}{1\ 3}, C\frac{1}{1}, P\frac{1234}{1234}, M\frac{12}{12}$
18–22 months	$i\frac{2}{-}$	$I\frac{1\ 3}{123}, C\frac{1}{1}, P\frac{1234}{1234}, M\frac{12}{12}$
21–26 months		$I\frac{123}{123}, C\frac{1}{1}, P\frac{1234}{1234}, M\frac{12}{123}$
+26 months		$I\frac{123}{123}, C\frac{1}{1}, P\frac{1234}{1234}, M\frac{123}{123}$

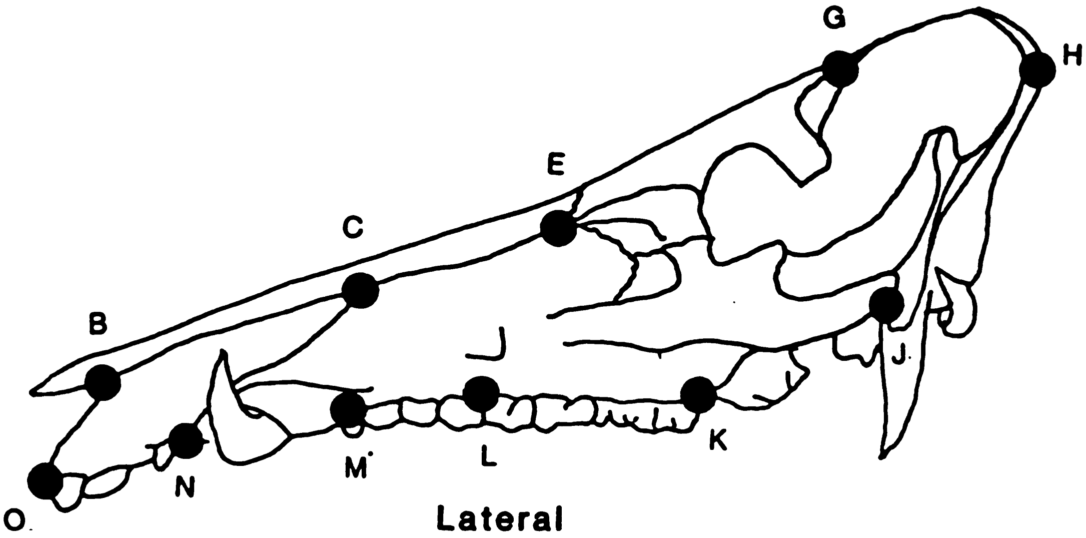
region of the skull because this was frequently missing in the *philippensis* skulls. A verbal description of the distances measured is presented in Appendix C.

A greater number of variables than specimens will result in a singular covariance matrix, which cannot be used for subsequent multivariate analysis. The sample sizes were small; therefore it was necessary to divide into subsets corresponding to dorsal, lateral, and ventral views of skull, and lateral view of the mandible (see Figure 6). It decreased the number of variables utilized in each analysis while maintaining biological coherence. Variables 1 (mandible), 20, 23, 29, 35, which were highly correlated with others, were removed from analysis to further avoid a singular covariance matrix.

Patterns of discrimination between a priori defined OTUs were examined by discriminant function analysis using SPSS (Nie et al. 1979). Canonical variates were computed and individual scores were plotted in the canonical variate space for all populations in the analysis.

Both principal components analysis and the shear principal components analysis developed by Humphries et al. (1981) were used to evaluate size and shape differences between taxa. These procedures differ from discriminanat analysis in several fundamental ways. Discriminant analysis finds linear combinations of variables which maximally separate groups. It relies on correct identification of specimens. Multi-group principal component analysis does not require correct identification of specimens beforehand, and is more appropriate as an exploratory tool in separating groups and assessing the validity of the OTUs. The statistical package used, BMDP (Dixon et al. 1983), provided for the extraction of three axes. The purpose of performing principal component analysis was to isolate contrasts between sets of variables. Contrasts are negatively correlated, that is, as one set increases the other decreases. I examined patterns of contrast to isolate portions of the skull where variability among samples was present.

The shear procedure is a modification of the standard principal component analysis, which standardizes variables to a zero mean, and removes the effects of size through



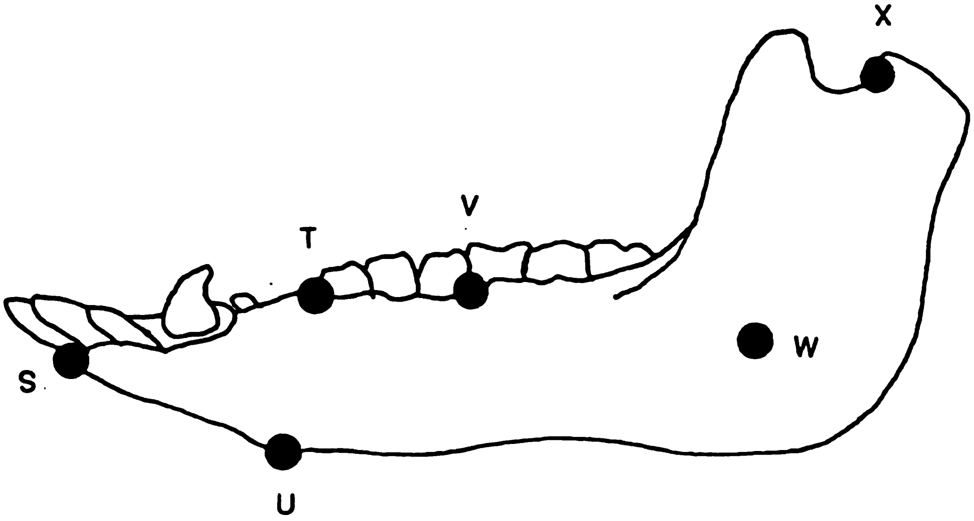


Figure 5 a,b

Landmarks chosen for measurement on crania of *Sus barbatus*.

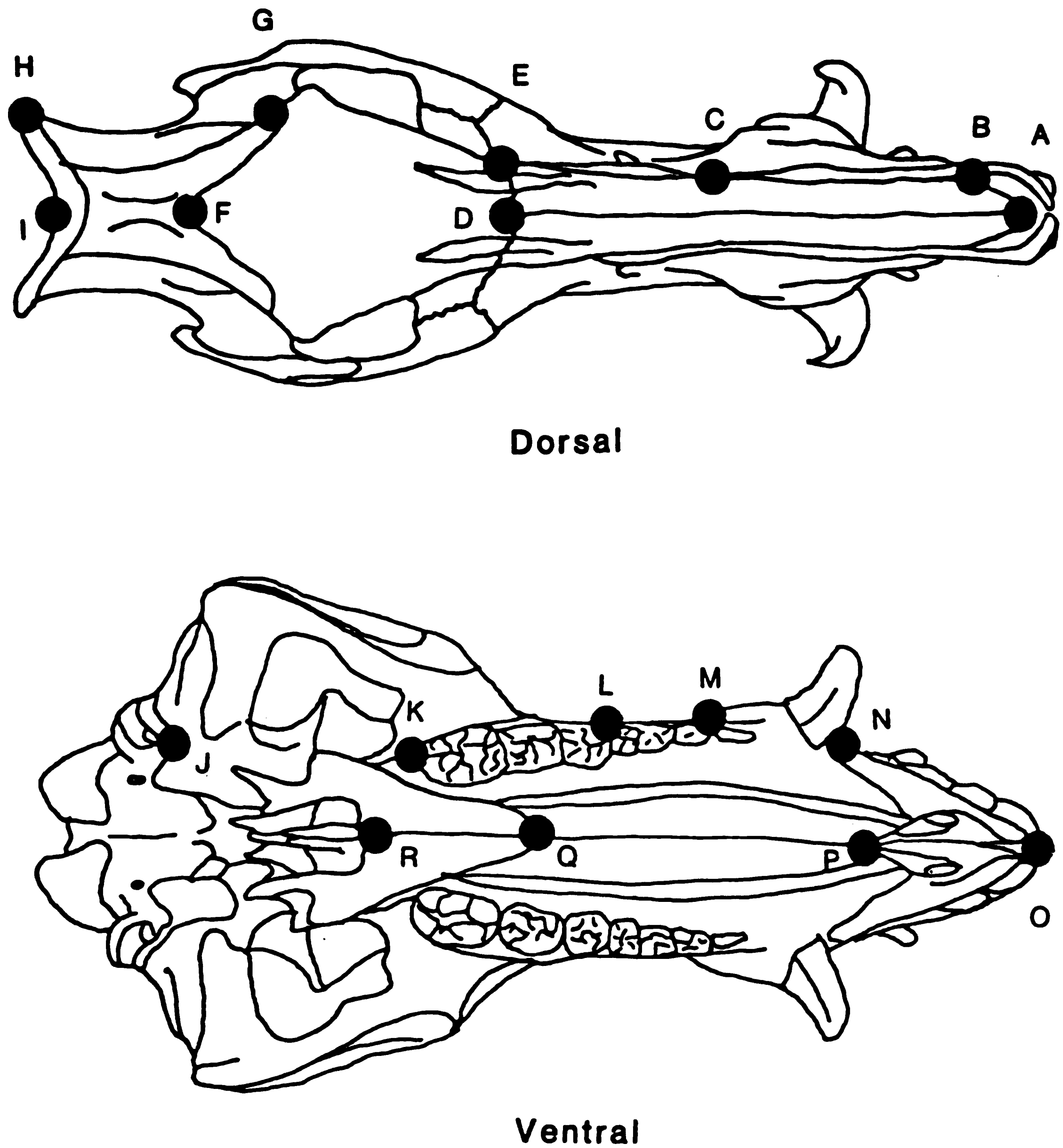


Figure 5 c,d

Landmarks chosen for measurement on crania of *Sus barbatus*.

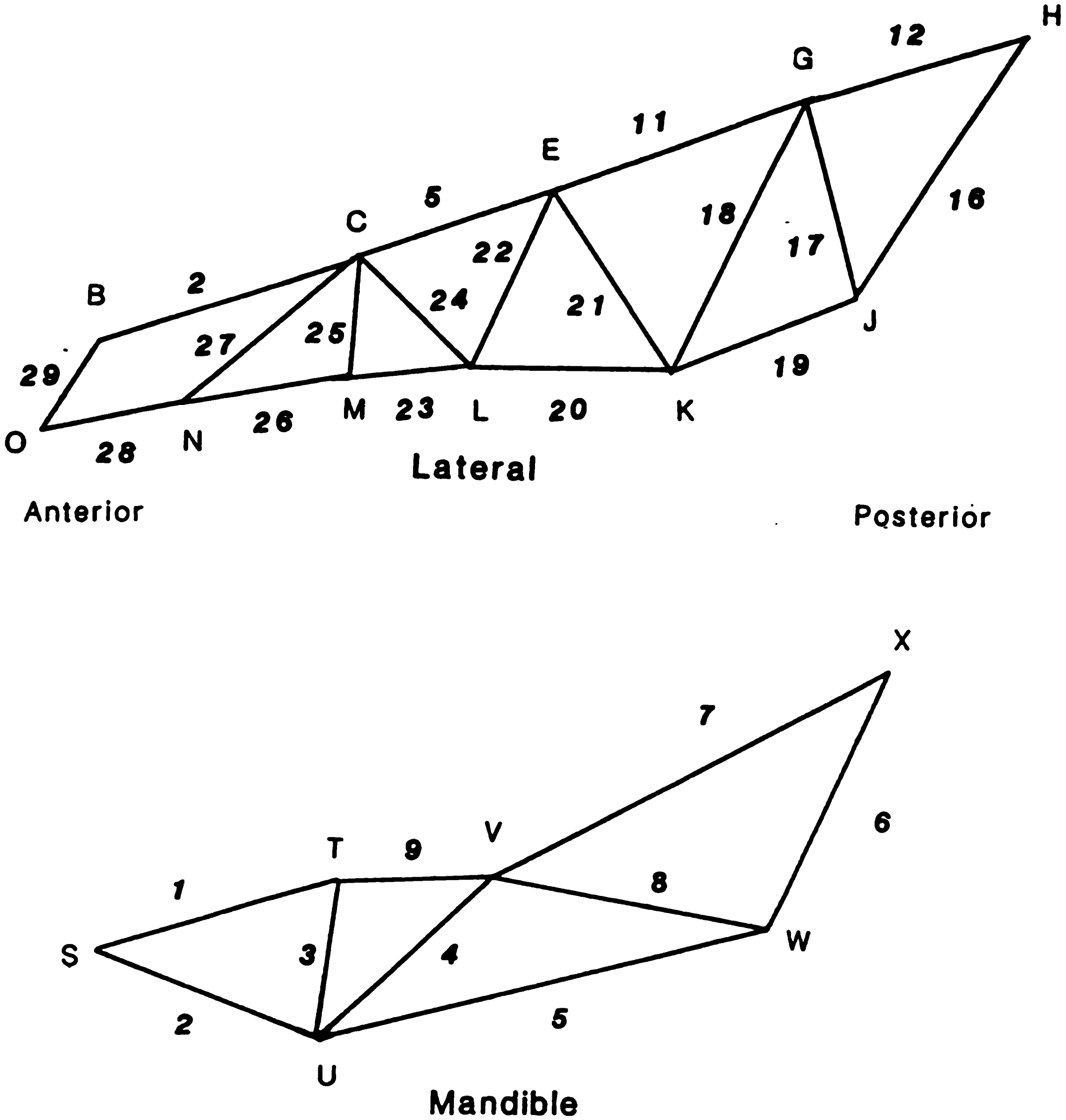


Figure 6 a,b

Box truss schemes for *Sus barbatus*, lateral view and mandible

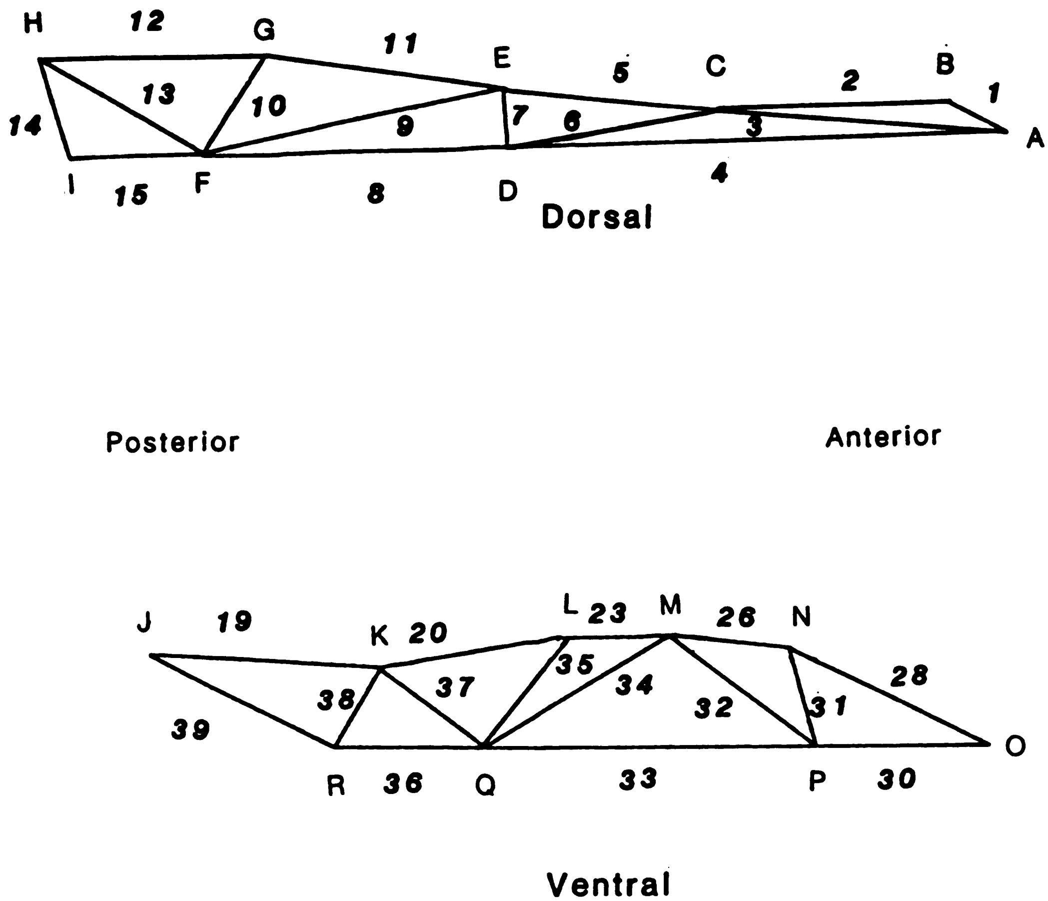


Figure 6 c,d

Box truss schemes for *Sus barbatus*, lateral view and mandible regression analysis. It was particularly useful in this study, where there was a substantial range in size between OTUs. I performed the shear procedure using a list of commands for MIDAS (Fox and Guire 1976) provided by R. E. Strauss (pers. comm.)

RESULTS

Measurement Error

To minimize and assess changing perceptions of landmarks, one specimen was repeatedly measured at periodic intervals during the study. Descriptive statistics associated with these measurements are presented in Table 4. The largest coefficient of variation is 15.886% for M26, and the smallest is 0.251%, for M20. The average coefficient of variation is 3.5%, suggesting that measurement error within the data set is reasonably low.

Discriminant Analysis

I performed discriminant analyses on subsets of variables and on all variables combined. These analyses, performed on sexes separately, established that, for both sexes, differences in morphology between subspecies samples were present. Plots of centroids and computation of Mahalanobis distances in analyses of data from each sex indicated three groups, one consisting of BARB-OI, one of FIL-CEBI, with AHO in an intermediate position (see Figure 7 for representative result). For all analyses performed, AHO was plotted more closely to BARB-OI than to FIL-CEBI. Average correct classifications of OI and CEBI were 75%. Average correct classifications of FIL and BARB were 91 and 92%, respectively, while classification of AHO was 100% correct.

Plots of canonical variate 1 against canonical variate 2 showed no overlap of OTUs along 1, but extensive overlap along 2. Separation of groups along canonical variate 1 indicates that this axis represents the effects of size, as the first variate is thought to reflect a size vector (Humphries et al. 1981:293). Whatever size independent shape

Table 4

Descriptive statistics associated with measurements repeatedly taken from one specimen during data collection as an accuracy check (N=5).

Measurement	Mean	C.V. Pct.	Maximum	Minimum
M1	2.420	.901	2.445	2.395
M2	7.931	.618	7.980	7.875
M3	10.158	.687	10.260	10.110
M4	12.808	10.004	13.455	10.520
M5	3.917	3.969	4.075	3.750
M6	3.553	1.475	3.640	3.505
M7	2.016	5.915	2.150	1.870
M8	9.155	1.370	9.350	9.035
M9	9.060	1.817	9.240	8.895
M10	4.409	1.333	4.480	4.330
M11	6.888	2.070	7.125	6.750
M12	6.551	1.264	6.560	6.480
M13	6.489	.878	6.540	6.425
M14	3.926	5.785	4.220	3.590
M15	4.340	7.337	4.635	3.935
M16	8.124	1.319	8.290	8.035
M17	6.457	.527	6.505	6.425
M18	8.373	.566	8.410	8.300
M19	5.272	.427	5.305	5.250
M20	5.159	.251	5.175	5.140
M21	6.605	.704	6.680	6.565
M22	5.219	3.595	5.350	4.910
M23	3.969	11.694	4.370	3.240
M24	4.602	2.759	4.735	4.395
M25	4.344	5.187	4.610	4.100
M26	2.126	15.886	2.700	1.865
M27	5.515	3.968	5.660	5.130
M28	5.652	4.730	6.120	5.475
M29	3.285	1.811	3.345	3.220
M30	3.958	1.467	4.010	3.890
M31	2.275	10.883	2.700	2.110
M32	4.052	11.531	4.590	3.505
M33	9.844	.567	9.905	9.765
M34	6.632	5.626	6.990	6.120
M35	3.422	1.883	3.490	3.335
M36	3.655	.580	3.680	3.625
M37	3.210	1.145	3.260	3.170
M38	2.152	3.672	2.255	2.065
M39	4.728	.355	4.755	4.710

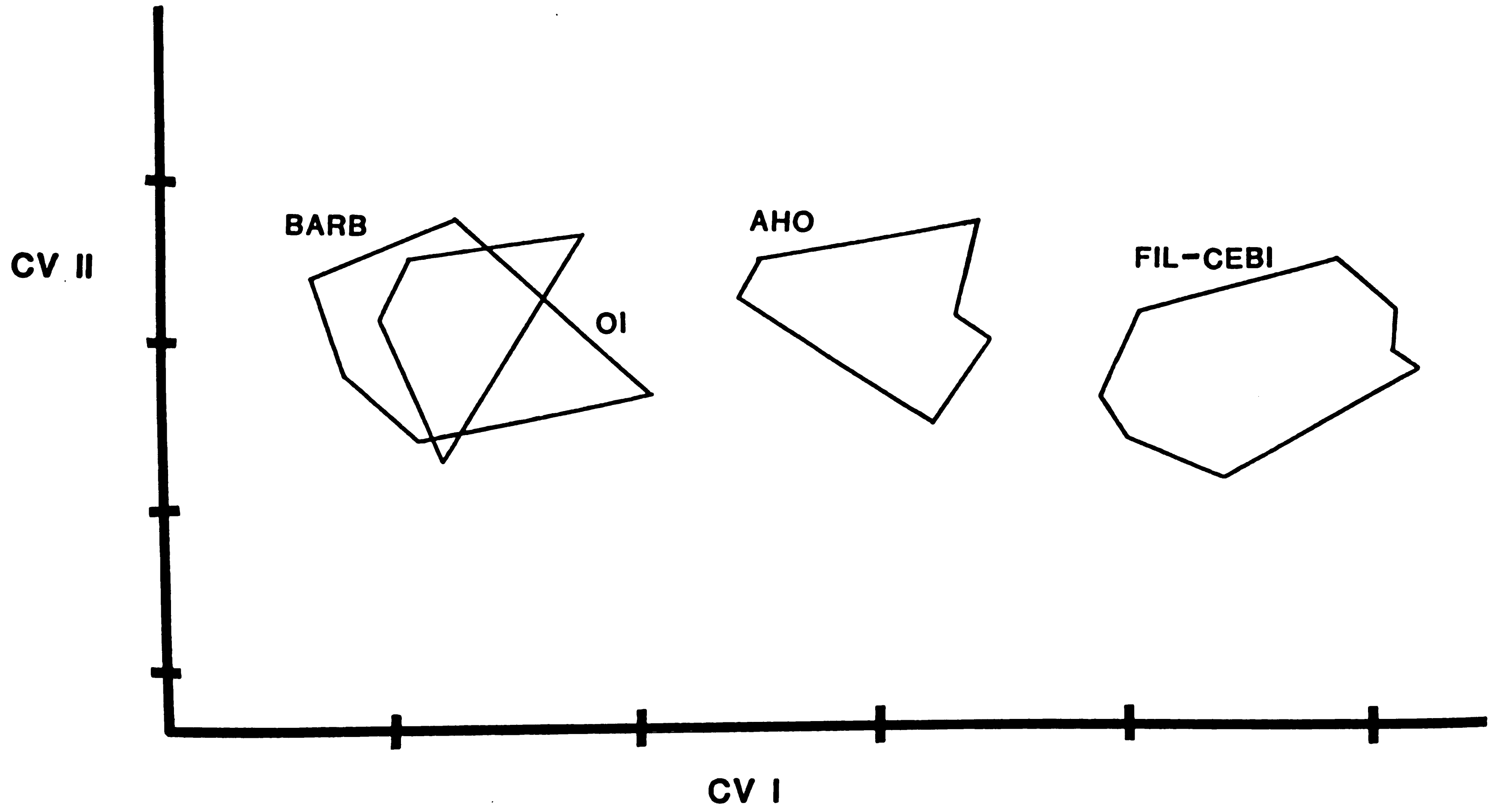


Figure 7

Canonical variates 1 and 2 plotted for all five OTUs.

differences which exist between taxa are overwhelmed in this analysis by the large size differences between taxa.

I compared the results of this analysis with a discriminant analysis performed by Groves. Although not specifically stated, I infer from accompanying tables that Groves' sample of adult males used for his analysis consisted of 39 *S. b. barbatus*, 15 *S. b. oi*, 8 *S. b. ahoenobarbus*, 12 *S. b. philippensis*, and 2 *S. b. cebifrons* (Groves 1981:Table 4). Sixteen measurements which depended on the presence of the right and left side of associated skull and mandible were taken. Measurement protocol in the anterior skull and tooth row was identical to the one I used. Measurements concerned with the posterior skull emphasized over-all skull dimensions which were not necessarily referenced to a homologous point. Analyses were performed on transformed variables, consisting of the original measurement divided by the basal length raised to the power of the allometry coefficient (Groves 1981:68).

A comparison of the results of this analysis with a discriminant analysis performed by Groves indicates that I obtained a clearer separation using this method (see Figure 8). I attribute these results to increased sample size, and landmark-based measurements. However, discriminant analysis attempts to create a composite variable which best separates the populations, and is not sensitive to complexes of variables which may discriminate between populations. To address questions of shape change I used principal component analysis and the shear procedure.

Principal Component Analysis

The results of discriminant analysis indicate that size differences between the OTUs separated the five groups into three. I performed conventional principal component analysis and the shear procedure to explore possible shape differences within and between the groups. Analyses were performed on all OTUs combined, as well as groups of OTUs combined by size.

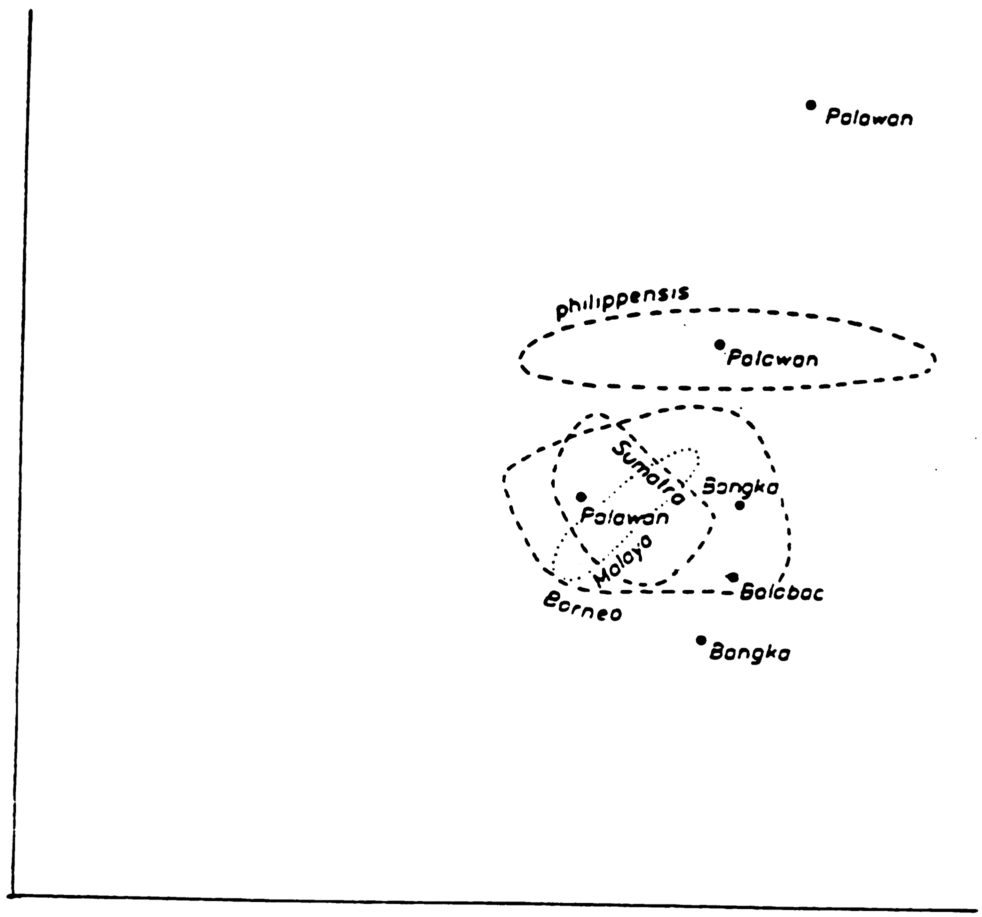


Figure 8

Discriminant Functions 1 and 2 to show the interrelations of the different samples of *Sus barbatus* (Groves 1981).

In adult populations, static allometry may be reflected in loadings on the first principal component (Jolicoer, 1963). Values greater than isometry (=1/n, where n= the square root of the number of variables used in the analysis) describe positive allometry with respect to size; values less than isometry indicate negative allometry with respect to size.

BARB males vs. BARB females

Sexual dimorphism, readily apparent in size and shape differences in the lower canine, and in pronounced saggital cresting in older males, may confound assessment of shape differences between OTUs. Therefore, I combined both sexes of the same OTU and performed principal component analysis to isolate cranial regions are influenced by sexual dimorphism between males and females. Unfortunately, BARB was the only OTU with an adequate sample size to permit comparison.

Mandibles. All loadings on the first principal component were positive and, with the exception of the premolar tooth row (M9), above 0.650 (see Table 5). I interpret this as a size axis. Premolar row and posterior length (M8) formed a contrast with ramus height (M6) in the second principal component. This component is a contrast of a vertical dimension with a horizontal one. The general pattern of negative and positive loadings suggest that length varies with respect to height of mandible, as vertical measurements of both posterior and anterior portions (M3, 4, 6) are negative, while horizontal measurements (M5, 8, 9) are positive. Horizontal measurements in proportion to the vertical measurements are greater in males than in females. Premolar tooth row forms a part of the contrast in all three components.

Lateral. All loadings on the first principal component are large and positive, with the exception of posterior nasal length (M5) (see Table 6). The second component is a contrast of posterior nasal length (M5) with three anterior nasal measurements (M2, 25, 27). All share a common landmark in the nasal-premaxilla-maxilla suture (C). The anterior nasal measurements are in a portion of the skull which contain the dimorphic canine. The third

Table 5

Principal Components I, II, and III for mandibles of BARB males vs. females (isometry=.353).

Variable	PC I	PC II	PC III
M2	.902	−.028	−.223
M3	.962	−.059	−.043
M4	.899	−.098	.112
M5	.794	.454	−.054
M6	.712	−.584	.247
M7	.900	.127	−.053
M8	.686	.533	−.308
M9	.476	.515	.675
% variance	64.86	78.94	87.45

principal component is a contrast between a measure of frontal length (M11) and anterior nasal height (M29).

Dorsal. The first component accounted for only 25% of the variance, and contained both positive and negative loadings (see Table 7). This indicates that there is shape as well as size information in this component. It constitutes a contrast between nasal length (M4) and frontal length (M8). The second component is a contrast of nasal width (M7) with oblique nasal length (M6). All four measurements share a common landmark in the nasal-frontal suture (D). The third component did not include any strong contrasts between measurements. The third component may be a residual size axis, as no clear patterns identifying contrasting portions of the skull were isolated.

Ventral. The first component of analysis of the ventral data subset also accounted for a relatively small amount of variance, 29% (see Table 8). This component included both negative and positive numbers, and constituted a contrast between premolar row (M23) and posterior width (M37) with two measurements of anterior length (M32, 33) which share a common landmark, the premaxilla-maxilla suture (P). Note that all

Table 6

Principal Components I, II, and III for lateral view of BARB males vs. females (isometry=.26).

Variable	PC I	PC II	PC III
M2	.796	−.393	.148
M5	.215	.939	.228
M11	.600	−.274	−.480
M16	.840	.164	−.129
M17	.837	.217	−.068
M18	.577	−.150	−.078
M19	.744	.139	−.033
M21	.767	−.003	−.237
M22	.690	.317	.388
M24	.633	.365	.213
M25	.696	−.571	.222
M26	.767	.171	−.211
M27	.587	−.352	.662
M28	.829	.191	−.302
M29	.647	.092	−.568
% variance	49	62	72

measurements pertaining to length at midline (M30, 33, 36, 39) exhibit negative loadings. The second component contained almost all positive numbers and may be a residual size axis. Pre-molar row (M23) and oblique palate width (M34) exhibit negative loadings. They share a landmark in the anterior PM^2. The third component is a contrast between three posterior measurements (M34, 36, and 37) bearing a common landmark, the maxilla-palatine suture (Q).

Discussion. Shape differences between sexes are localized in the region of the dimorphic canine. This is exhibited most clearly by analysis of the lateral data, where major shape differences involve the relative placement of the nasal-premaxilla-maxilla suture. This was anticipated, as the region provides structural support for the large canine in males.

Table 7

Principal Components I, II, and III for dorsal view of BARB males vs. females (isometry=.27).

Variable	PC I	PC II	PC III
M1	.228	.241	.417
M3	.154	.206	.643
M4	.988	−.127	−.038
M6	.483	.753	−.025
M7	.020	−.805	.458
M8	−.803	.195	.538
M9	.381	.516	.635
M10	.680	.085	.528
M11	−.237	.644	.394
M12	.139	.233	.781
M13	.502	.166	.551
M14	.647	.223	.594
M15	−.199	.219	.415
% variance	25	42	69

Shape differences between sexes are also apparent in relative length of skull, which is illustrated by analysis of dorsal, mandible, and ventral data. There is a relative lengthening in males, in comparison to mandible height, or skull width. This analysis indicates that there is a significant degree of sexual dimorphism present in this subspecies. The presence of a dimorphic canine and saggital cresting in males for all subspecies suggests that this is a general characteristic. Therefore, sexes are analyzed separately, to avoid confusing sexual dimorphism with intra-specific morphological variation.

BARB males vs.OI males

BARB and OI constitute one of the three groups isolated by discriminant analysis. I performed principal component analysis on males of these OTUs alone to explore possible shape differences. In general, the amount of variance explained by each component of

Table 8

Principal Components I,II, and III for ventral view of BARB males vs. females (isometry=.27)

Variable	PC I	PC II	PC III
M19	.059	.695	.226
M23	.991	−.091	.066
M26	.270	.774	−.059
M28	.276	.862	.176
M30	−.206	.563	−.282
M31	.521	.638	.384
M32	−.562	.730	.107
M33	−.662	.482	.425
M34	.587	−.161	.657
M36	−.370	.695	−.523
M37	.869	.163	−.415
M38	.465	.529	.072
M39	−.324	.020	−.005
% variance	29	61	71

each data set was low, and comparable in magnitude to variance associated with principal component analysis performed on each OTU separately.

Mandible. All loadings for the first component were greater than isometry (=.357) (see Table 9) and accounted for less than half the total variance. The second component is a contrast between ramus height (M6) and posterior length (M8), which share a landmark. Note, too, that anterior horizontal measurements M2 and M5 form a contrast to ramus height. This differs from the mandible analysis of BARB males versus females, where all these measurements shared the same sign. The third component was a contrast between anterior and posterior mandible length (M2, 5), accounting for 4% of the variance. They share a landmark in the mental prominance (U).

Lateral. All loadings on the first component were greater than isometry, but accounted for 28% of the total variance (see Table 10). The second component is a contrast between distal nasal length (M5) and nasal height (M25). Both share the nasal-

Table 9

Principal Components I, II, and III for mandibles of BARB vs. OI males and BARB vs. FIL females (isometry=.353).

Variable	PC I	PC II	PC III
BARB males vs. OI males			
M2	.574	−.420	.649
M3	.907	.023	.228
M4	.881	−.002	−.269
M5	.713	−.398	−.521
M6	.602	.758	.083
M7	.881	.078	−.110
M8	.589	−.542	−.325
M9	.611	.115	−.395
% variance	53.68	68.98	72.70
FIL females vs. BARB females			
M2	.980	.036	−.064
M3	.956	−.043	.066
M4	.975	−.085	−.002
M5	.981	.115	−.094
M6	.965	−.247	.059
M7	.995	.008	−.038
M8	.974	.158	−.129
M9	.906	.246	.342
% variance	93.44	95.57	97.51

premaxilla-maxilla suture point (C) as a landmark. The third component is a contrast between two measures of anterior nasal width (M27, 29), accounting for 7.5% of the variance.

Dorsal. The first component accounted for only 15% of the total variance, and contained both positive and negative numbers (see Table 11). It is a contrast between nasal length (M6) and nasal width (M7), sharing a landmark in the nasal-frontal suture (D). Loadings for the second component were all positive and generally greater than isometry (=.27). This may suggest that the second component is a measure of size differences. The third component is a contrast between two measures of nasal length (M3,M5), sharing a common landmark (C).

Ventral. Again, the loadings on the first component are both positive and negative numbers (see Table 12). It is a contrast between premolar row (M23), and palate length and width (M33, 34). The second component is a weak contrast of a cluster of unassociated measurements in unrelated areas of the cranium (M23, premolar row; M34, oblique palate width; M39, distal cranium length) with premolar to incisor length (M26), incisor row (M28), and distal length (M36). It may be tentatively considered a size factor, because of the preponderance of positive loadings. The third component is a contrast between a measure of anterior width (M31) and posterior length (M36). It accounts for 11.3% of the variance.

Discussion. The relatively small amount of variance which is accounted for by the analyses of the data sets of BARB and OI OTU males suggest that consistent size and shape differences between these OTUs are minimal. Similarly weak patterns of contrast and low percentages of explained variance would be found in a principal component analysis of a single population, and may be accounted for by normal intra-populational variability.

Within this combined sample of BARB and OI males, patterns of variance magnitude indicates that these shape differences are more important than size differences in data

Table 10

Principal components I, II, and III for lateral view of BARB vs. OI males and BARB vs. FIL females.

Variable	PC I	PC II	PC III
BARB male vs. OI male			
M2	.610	−.487	−.125
M5	.304	.937	−.098
M11	.327	−.353	.562
M16	.663	.199	.321
M17	.416	.200	−.064
M18	.509	−.255	.011
M19	.604	−.006	−.047
M21	.500	.072	.322
M22	.647	.297	−.347
M24	.434	.526	−.129
M25	.602	−.581	−.240
M26	.577	.080	.502
M27	.668	−.251	−.470
M28	.466	.167	.586
M29	.396	−.086	.684
% variance	27.86	42.50	56.0
FIL females vs. BARB females			
M2	.923	−.277	.212
M5	.931	−.167	−.316
M11	.823	−.249	.248
M16	.925	−.275	.111
M17	.938	−.220	.062
M18	.796	.603	.013
M19	.921	.374	−.011
M21	.642	.754	.076
M22	.957	−.228	.010
M24	.855	−.315	.019
M25	.863	−.275	.345
M26	.938	−.248	−.023
M27	.920	−.268	.233
M28	.935	−.293	.009
M29	.940	−.261	.011
% variance	79.36	91.86	94.55

Table 11

Principal Components I,II, and III for dorsal view of BARB vs.OI males and BARB vs. FIL females (isometry=.27).

Variable	PC I	PC II	PC III
BARB males vs. OI males			
M1	−.055	.539	.372
M3	.083	.243	.649
M4	−.279	.609	.269
M5	.453	.664	−.571
M6	−.534	.716	−.440
M7	.980	.153	−.090
M8	.578	.536	.441
M9	−.222	.644	.619
M10	.028	.629	.535
M11	−.399	.293	.586
M12	.205	.547	.521
M13	.145	.571	.274
M14	−.021	.777	.334
M15	.155	.306	.139
% variance	15.49	45.52	65.83
FIL females vs. BARB females			
M1	.944	.013	.037
M3	.968	−.041	.142
M4	.948	.199	.105
M5	.944	.154	−.263
M6	.395	.893	−.045
M7	.947	−.272	−.100
M8	.978	−.074	.093
M9	.928	.105	.305
M10	.756	.051	.442
M11	.855	.121	.372
M12	.972	.033	.096
M13	.893	.008	.016
M14	.430	−.062	.347
M15	.839	−.025	−.018
% variance	74.41	81.38	86.24

pertaining to horizontal measurements (dorsal and ventral subsets). Conversely, size differences were more appareant in analyses of vertical plane subsets (lateral, mandible).

Analyses of the horizontal subsets delineate aspects of shape differences which are underlying factors of principal component analyses. Differences were restricted to the anterior portions of the skull, and delineate aspects of change in palate and nasal width with respect to length. Position of the premolar row (M23) in relation to the mid-line of the skull is also thought to be an underlying factor.

BARB females vs. FIL females

Principal component analysis of the smallest and largest OTUs was performed to further examine patterns of shape and size differences. Females of BARB and FIL OTUs were used, as these had the largest sample sizes.

Mandible. The first component was clearly a size axis as all loadings were above 0.900 (see Table 9). The second and third component combined accounted for less than 5% of the variance, and the contrasts were weak. The second component contrasted ramus height (M6) and premolar (M9). The third component contrasted premolar row with ramus width (M8).

Lateral. The first component was also a size axis, accounting for 80% of the variance. The second component isolated three posterior measurements (M18, 19, 21) sharing the distal end of the M3 (K) as a landmark. All other loadings were negative and ranged from −0.315 to −0.167 (see Table 10). The third component is a contrast of two anterior measurements (M5 and 25) sharing the nasal-premaxilla suture (C).

Dorsal. All loadings on the first component were well above isometry (see Table 11). The second component of the dorsal subset is a contrast between posterior nasal width (M7) and nasal length (M6). The third component isolated three measurements with negative loadings which formed a triangle in the posterior nasal region (M5, 6, 7). Except

Table 12

Principal Components I,II, and III for ventral view of BARB vs. OI males and BARB vs. OI females

Variable	PC I	PC II	PC III
BARB males vs. OI males			
M19	.000	.440	.476
M23	.996	−.025	.003
M26	.136	.696	.002
M28	.191	.777	−.193
M30	−.298	.432	.417
M31	.517	.495	−.601
M32	−.704	.556	−.375
M33	−.749	.411	−.244
M34	.681	−.008	.114
M36	−.505	.663	.333
M37	.894	.184	−.082
M38	.451	.543	.587
M39	−.323	−.097	−.066
% variance	32.95	55.80	67.15
FIL females vs. BARB females			
M19	.888	.415	−.176
M23	.886	−.210	.079
M26	.958	−.186	.040
M28	.954	−.240	.018
M30	.946	−.217	.105
M31	.710	−.231	−.126
M32	.862	−.340	−.002
M33	.958	−.141	−.189
M34	.914	−.108	−.317
M36	.949	−.131	.251
M37	.681	.616	.367
M38	.980	.081	−.104
M39	.834	−.220	.055
% variance	79.36	87.10	90.27

for distal length (M15), the rest of the loadings were positive. The largest was 0.442, oblique cranial width (M10).

Ventral. Again, the first component is a size axis. Positive loadings from the second component isolated two measurements of the posterior portion of the cranium (M19, 37). The remainder of the loadings were negative, ranging from −0.108 to −0.340 (see Table 12). The third component contrasted a measure of posterior and anterior width (M34, 37). They share a common landmark in the maxilla-palatine suture (Q).

Discussion. The results of the principal component analysis suggests that, overall, size is the best discriminator between these OTUs. The second and third components combined account for less than 16% of the variance in all the analyses. Contrasts within the second component pertain to the posterior region of the skull. Results of analyses of all the subsets concur, and many of the contrasts shared landmarks between the subsets. The position of the posterior margin of the third molar figures prominantly in these contrasts, and suggest that the position of the molar row may be an underlying factor.

All OTUs[1]

Principal component analysis of all subsets segregated by sex were performed to examine differences among all populations. Factor loadings from principal component analyses from more than two samples are problematic to interpret, as it is difficult to isolate the OTUs which are contributing most significantly to total variance. However, plots of these components can contribute much information for assessment of general morphological divergence.

In analyses of data from males and females performed separately, the first component describes a size vector in which all factor loadings have the same sign and similar values. Plots of PC I vs. PC II and PC I vs. PC III for all data subsets separated each OTU along PC I, indicating that size was the best descriminator for each OTU.

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[1] Because of small sample size CEBI is excluded from this analysis

These results supported the results from discriminant analysis. BARB and OI consistantly grouped together (see Figure 9 and 10 for representative plots). AHO and FIL maintained a separate status in plots from all analyses.

To isolate and remove the effects of size, the data were subjected to the shear procedure. Results indicate that shape differences occurred primarily in the horizontal planes of the skull (dorsal and ventral views). Plotting Sheared component II against size resulted in clear separation of OTUs into three groups for both sexes (see Figure 11 for representative plot). Results of standard principal component analysis and the shear procedure are discussed below.

Mandible. For each sex the first component of a standard principal component analysis accounted for a high percentage of the total variance, and contained only positive numbers (see Table 13). For females, the second component is a contrast between ramus height (M6) and premolar row (M9). The third component is a contrast between posterior length (M8) and premolar row.

For males the second component is a contrast between ramus height (M6) and posterior length (M8). This same contrast occurred in analysis of BARB vs. OI males (see Table 9). The third component is a contrast between anterior length (M2) and ramus height (M6).

Mandible data were not subjected to the shear procedure, as the loadings from the first and second component were not correlated (females $= -0.4524$, males $= -0.3505$ ($p < .05$)), indicating that shape differences detected on axes II and III are independent of size differences among OTUs. However, these shape differences explain very little total variation (5%) not explain by size (92%).

Lateral. The first component of standard principal component analysis for each sex describes a size vector (see Table 14). All loadings are positive; the variance is 79% for females and 78% for males. The second principal component in the data for females isolated three measurements sharing the same landmark, distal M^3 (K) in the posterior

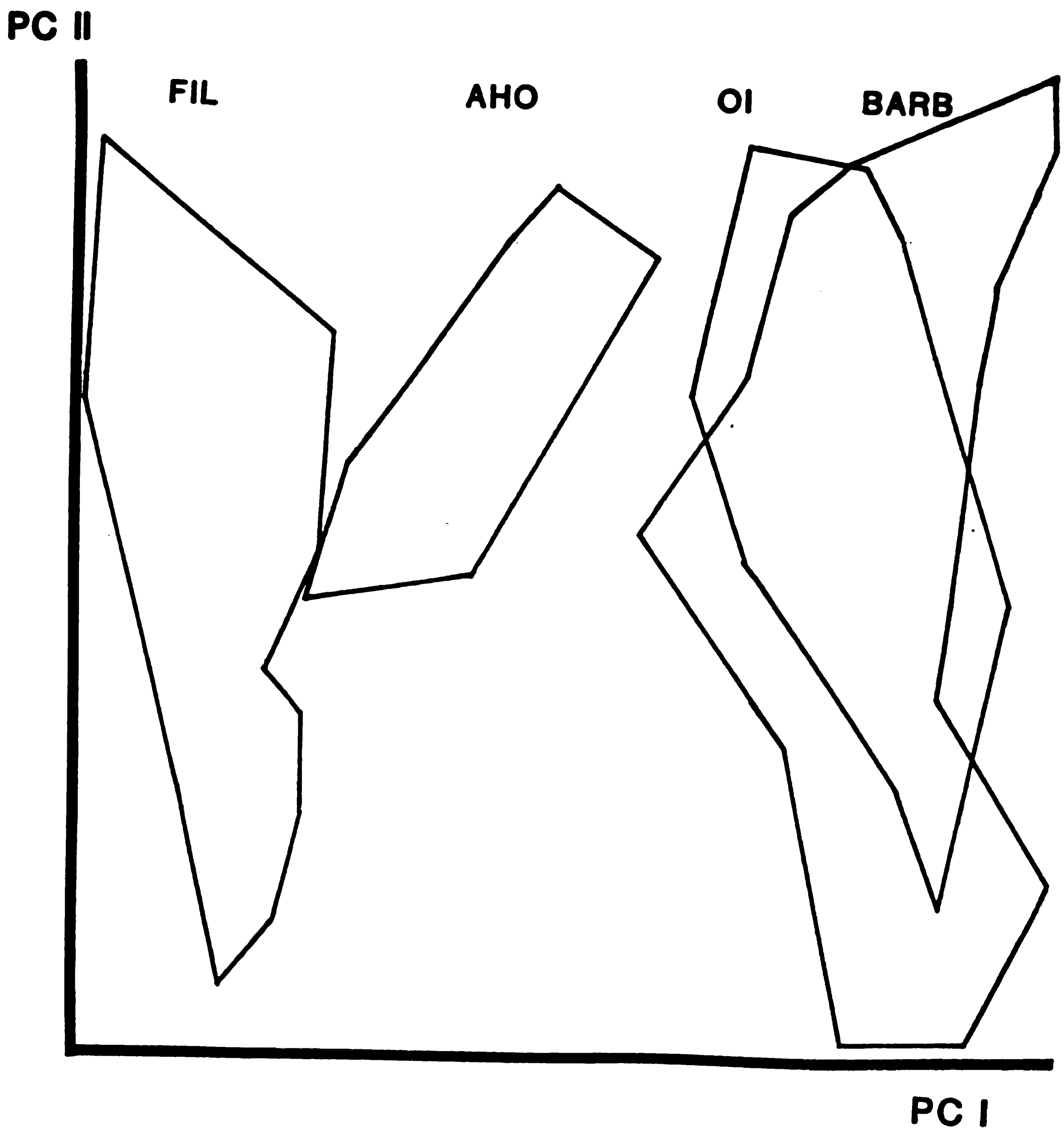

Figure 9

Plot of PC I vs. PC II for mandibles from males, all OTUs.

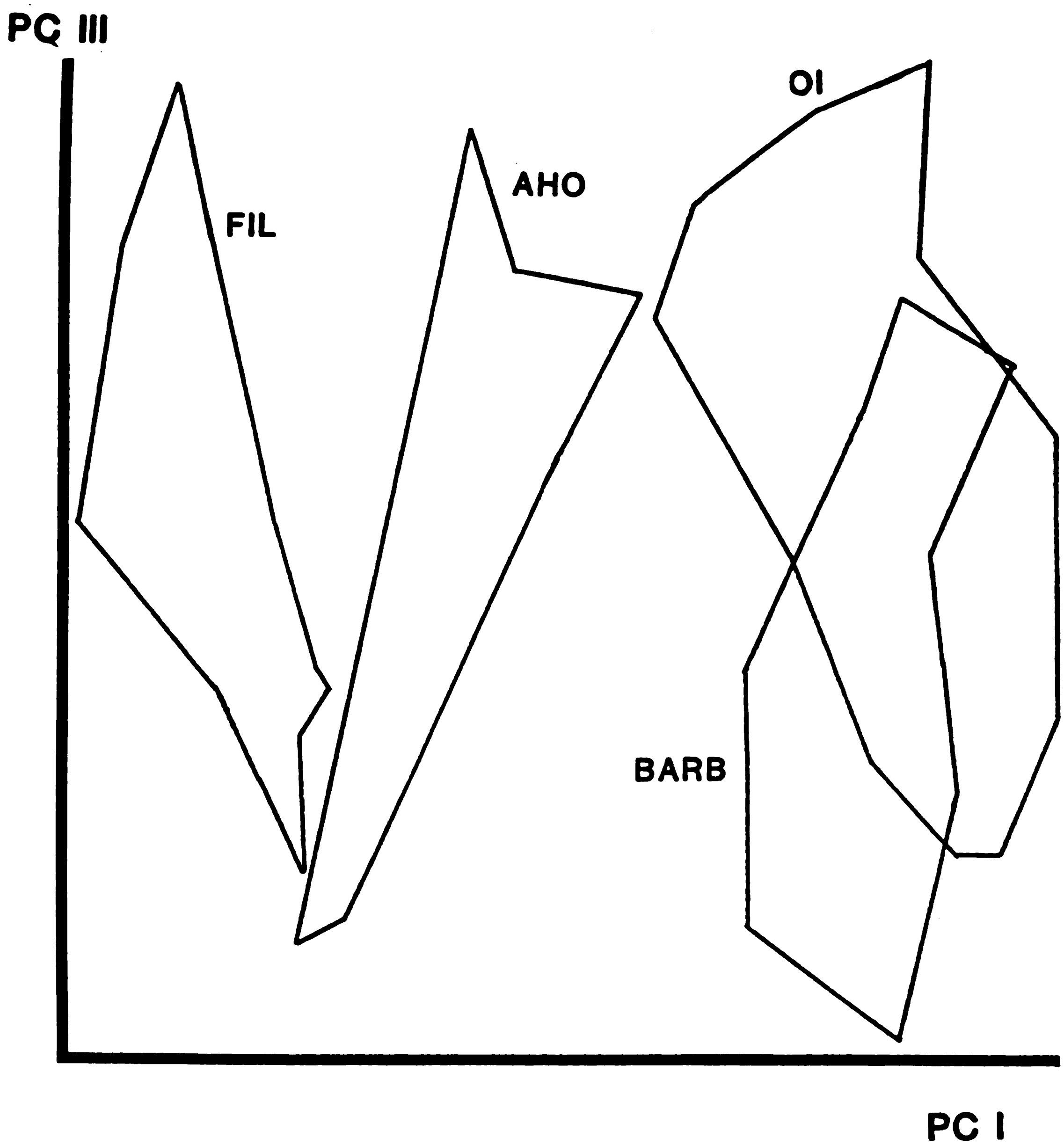

Figure 10

Plot of PC I vs. PC III for mandibles from males, all OTUs.

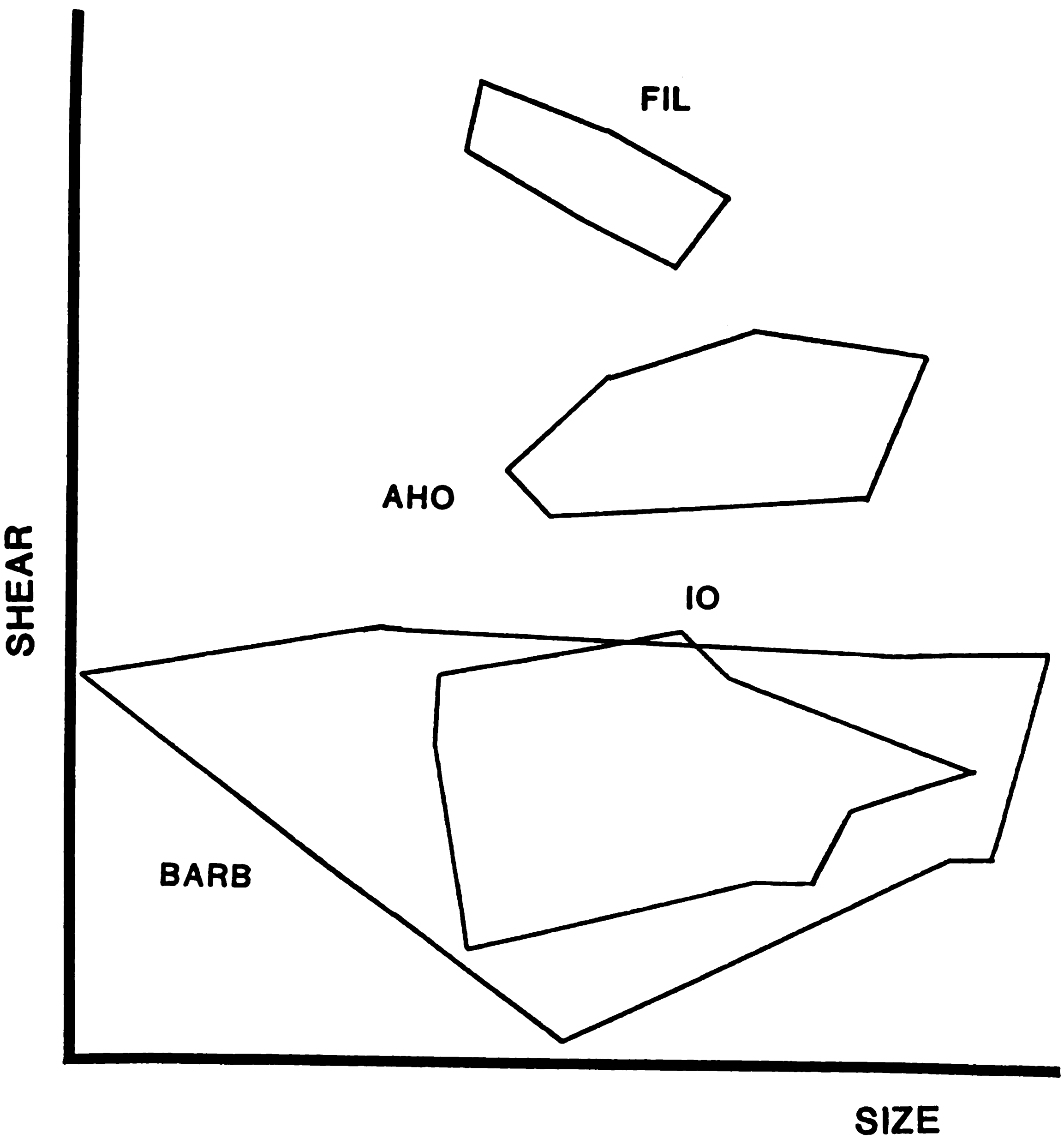

Figure 11

Plot of size vs. shear for dorsal view of males, all OTUs.

Table 13

Principal Components I, II, and III for mandibles, all OTUs. (isometry = .353)

Variable	PC I	PC II	PC III
Females			
M2	.422	.133	.170
M3	.283	−.266	−.222
M4	.305	−.166	.031
M5	.338	.266	.291
M6	.441	−.648	−.203
M7	.392	−.030	.153
M8	.335	.339	.371
M9	.267	.523	−.794
% variance	93.18	95.57	97.12
Males			
M2	.381	−.040	−.741
M3	.339	−.299	−.359
M4	.357	.019	.091
M5	.355	.424	.163
M6	.401	−.674	.401
M7	.370	.077	.167
M8	.345	.605	.031
M9	.258	.105	.309
%variance	91.25	94.10	96.86

region of the skull pertaining to skull height (M18, 19, 21). These measurements were a contrast with a measure of anterior height (M26). The third component contains a contrast between posterior nasal length (M5), and height (M25) sharing a landmark in the nasal-premaxilla-maxilla suture (C). As the first and second components were correlated ($r = -0.20$ ($p < .05$)), the shear procedure was not performed.

In males, these components were correlated ($r = -0.67$ ($p < .05$)); the shear procedure was performed. The pattern of factor loadings for the sheared second component for males was little different than that for PC II. Sheared component II for males is a contrast between posterior nasal length (M5) and nasal height (M25). The second component for analysis of BARB vs. OI male also contained the same contrast (see Table 10). Loadings on the sheared PC III for males were similar to those from the standard PC III. It is a contrast of a posterior height measurement (M18) with the canine region (M26). Although neither measurement encompasses the cheek teeth, premolar and molar teeth provide landmarks for both.

<u>Dorsal</u>. The first component of an analysis of data from females is a size vector, containing positive numbers ranging from 0.070 to 0.558 (see Table 15). I then performed the shear procedure, because the first two components of the principal component analysis were significantly correlated ($r = -0.67$ ($p < .05$)). The sheared second component showed no contrasts, as all loadings were positive and with one exception, less than 0.1. The sheared second component demonstrated that there was no residual shape information present, once the information in PC II correlated with size had been removed. Interpretations concerning the second component of the standard principal component analysis would have been erroneous if I had not performed the shear procedure on this data. Shape information is contained in the third shear component. Contrasts in the sheared third component consist of distal nasal length and width (M6, 7) sharing a landmark (D) in the nasal-frontal suture, and two measures of distal width (M10, 14).

Table 14

Principal Components I, II, and III for lateral view, all OTUs (isometry = .26)

Variable	PC I	PC II	PC III	SPC II[1]	SPC III[2]
		Females			
M2	.225	.164	.260		
M5	.436	.182	−.749		
M11	.164	.117	.195		
M16	.189	.136	.122		
M17	.170	.097	.094		
M18	.323	−.552	.049		
M19	.403	−.362	−.031		
M21	.195	−.533	.115		
M22	.281	.162	.017		
M24	.176	.151	.038		
M25	.173	.137	.485		
M26	.337	.217	.001		
M27	.252	.181	.352		
M28	.227	.164	−.034		
% variance	79.05	92.07	95.81		

Table 14 (Continued)

Variable	PC I	PC II	PC III	SPC II[1]	SPC III[2]
Males					
M2	.242	.309	.060	.254	.139
M5	.482	−.711	.179	−.776	.329
M11	.167	.195	−.207	.158	−.119
M16	.194	.060	−.077	.022	.002
M17	.184	.038	.226	.003	.262
M18	.231	.234	.424	.185	.452
M19	.341	.083	.161	.018	.262
M21	.143	.042	−.014	.014	.039
M22	.313	.020	.280	−.037	.356
M24	.200	−.072	−.021	−.106	.053
M25	.173	.423	.164	.378	.204
M26	.354	−.035	−.646	−.098	−.434
M27	.262	.320	−.241	.262	−.115
M28	.234	−.036	−.274	−.078	−.154
% variance	78.32	86.34	89.34		

[1] For females: ?alpha? = .854, ?beta?$_1$ = −.525, ?beta?$_2$ = .851
For males: ?alpha? = .179, ?beta?$_1$ = 1.015, ?beta?$_2$ = .181

[2] For females:?alpha? = .035, ?beta?$_1$ = −1.2818, ?beta?$_2$ = −.343
For males: ?alpha? = −.378, ?beta?$_1$ = .951, ?beta?$_2$ = −.343

In males, the first component is also a size vector. A shear of the second component ($r = -0.64$ ($p < .05$)) also appears to have removed the underlying size factor, leaving very little size-independent shape information. The sheared third component contrasts posterior nasal length (M6) and width (M7).

Ventral. The first component of a standard principal component analysis of data from female responds to a size vector (see Table 16). The second component is a contrast of two posterior measurements (M19, 37) sharing a landmark in the M^3 (K), and an anterior measurement (M32). The third component contrasts two posterior length measurements (M19, 36).

For males, the first component also reflects static allometry. The second is a contrast of premolar row (M23) and anterior width (M32). They share the proximal PM^2 as a landmark. The third component is a contrast of proximal (M31,32) and distal (M38) width.

Principal components I and II were not significantly correlated in either males or females (females; $r = -.15$, males; $r = .13$ ($p < .05$)). Therefore, the shear procedure was not performed, as it would not add new insight to the analysis.

Discussion. Standard principal component analysis performed on mandible and ventral data sets for each sex, and the lateral data from females did not yield first and second components which were significantly correlated (see Table 17). Therefore, I concluded that the first components contained size information and the second contained shape information. Correlation of the first and second components produced by standard principal component analysis of lateral data sets for males, and dorsal data for both sexes prompted the use of the shear procedure. The sheared second component of dorsal data for females contained only one loading above 0.1, indicating that the second component from the standard principal component analysis was also a size vector. Information concerning shape differences were found in the third component of the shear procedure. In all procedures, the patterns of contrast produced were unique to each sex. However, within

Table 15

Principal Components I, II, and III for dorsal view, all OTUs (isometry = .27)

Variable	PC I	PC II	PC III	SPC II[1]	SPC III[2]
Females					
M1	.348	.042	−.045	.078	−.050
M3	.283	−.005	.125	.061	.120
M4	.246	.186	.002	.062	−.002
M6	.086	.834	−.405	.057	−.406
M7	.558	−.439	−.426	.102	−.435
M8	.399	−.025	.144	.086	.137
M9	.253	.151	.323	.062	.319
M10	.202	.138	.445	.050	.442
M11	.198	.151	.268	.050	.265
M12	.236	.067	.031	.054	.027
M13	.128	.035	−.062	.029	−.064
M14	.070	.034	.383	.016	.382
M15	.189	.024	−.295	.042	−.298
% variance	79.85	89.02	92.47		

Table 15 (continued)

Variable	PC I	PC II	PC III	SPC II[1]	SPC III[2]
Males					
M1	.274	.170	.127	.202	.127
M3	.235	.179	.033	.187	.033
M4	.617	−.645	−.101	.048	−.099
M6	.213	−.023	.638	.096	.638
M7	.425	.280	−.651	.321	−.649
M8	.153	.558	.057	.296	.057
M9	.204	.109	.191	.144	.191
M10	.247	−.045	.133	.104	.133
M11	.126	.199	.217	.141	.217
M12	.205	.166	.063	.167	.063
M13	.145	.042	.049	.054	.049
M14	.154	−.038	.163	.061	.163
M15	.176	.216	.038	.172	.038
% variance	66.86	79.69	86.22		

[1] For females: ?alpha? = .978, $?beta?_1$ = −.223, $?beta?_2$ = .975
For males: ?alpha? = −.779, $?beta?_1$ = .633, $?beta?_2$ = −.774

[2] For females: ?alpha? = −.035, $?beta?_1$ = −.464, $?beta?_2$ = .031
For males: ?alpha? = −.002, $?beta?_1$ = .1.224, $?beta?_2$ = .019

Table 16

Principal Components I, II, and III for ventral view, all OTUs (isometry = .27)

Variable	PC I	PC II	PC III
Females			
M19	.368	−.508	−.464
M23	.164	.073	.147
M26	.326	.202	.050
M28	.222	.180	.031
M30	.266	.161	.178
M31	.148	.186	−.131
M32	.263	.328	.012
M33	.237	.137	−.202
M34	.219	.092	−.309
M36	.394	.054	.588
M37	.182	−.665	.414
M38	.461	−.110	−.229
M39	.114	.088	.042
% variance	83.54	90.69	94.06

Table 16 (continued)

Variable	PC I	PC II	PC III
		Males	
19	.321	.078	.198
23	.230	−.712	.004
26	.336	.058	−.252
28	.228	.033	−.155
30	.270	.151	.127
31	.153	−.142	−.586
32	.214	.314	−.454
33	.183	.243	−.186
34	.189	−.134	.106
36	.417	.271	.136
37	.238	−.417	−.209
38	.473	−.040	.446
39	.099	.112	.027
% variance	64.46	86.30	90.69

each sex differences between the OTUs were more pronounced in horizontal movement of landmarks (dorsal, ventral), than in vertical displacement (lateral, mandible).

For males, contrasts within dorsal and lateral subsets both involve relative movement of two landmarks in the nasal portion of the skull-the nasal-maxilla-premaxilla suture, and the nasal-maxilla suture. Another landmark, the anterior PM^2, integrates contrasts in lateral and ventral data subsets. However, mandibular data emphasizes contrasts between ramus height and length, utilizing landmarks which do not include the PM^2.

For females, the patterns of contrasts between data subsets are not as well-integrated as for males. Contrasts from analyses of dorsal and lateral subsets emphasize contrasts between the nasal and the frontal areas of the skull. However, several of the same landmarks are shared between the subsets- the nasal-premaxilla-maxilla suture and the frontal-parietal suture. Lateral and ventral data sets shared landmarks in the tooth row in measures of contrast, and delineate shifts in relative placement of the tooth row. Contrasts of mandibular data supports this interpretation, as the premolar row forms a contrast to ramus height.

FIL age series

Wild pigs in the Philippines are distinct from the other subspecies in that they are the only group found on oceanic islands, and they have the smallest body size among the subspecies. I performed principal component analysis on a static cross-section of the age classes to explore aspects of growth. This type of data is not as useful as longitudinal data, as it does not yield information on individual variation in growth rates (Cock 1966;136–137). However, static cross-sectional data can yield information on the static growth rates of the entire population, which I thought adequate for the purposes of this study. Unfortunately, the utility of this data was decreased by other aspects of the sample. Not all age classes are equally represented (Age Class 4: N=1, AC5: N=5, AC: N6=24, AC7: N=4, AC8: N=1, AC10: N=2, AC11: N=3). In addition, information concerning

Table 17

Varience and correlations from principal component analysis of all OTUs.

View	Females				Males			
	PC I	PC II	Corr.	Shear	PC I	PC II	Corr.	Shear
Mandible	93.18	2.39	.-45	No	91.25	2.85	−.35	No
Lateral	79.05	13.02	−.20	No	78.32	8.02	−.67	Yes
Dorsal	79.85	9.17	−.67	Yes	66.86	12.83	−.64	Yes
Ventral	83.54	7.15	−.15	No	64.46	21.84	.13	No

the sex of immmature individuals was not available. No shear procedures were necessary, as the first and second components in all analyses were significantly correlated.

Mandible. The second component is a contrast of ramus width (M8) and height (M6) (see Table 17). The first measurement exhibits positive allometry on the first component, the second is isometric. This suggests that the ramus grows vertically compared to horizontally. The third component is a contrast of anterior length (M2) and ramus height (M6).

Lateral. The second component is a contrast of nasal length (M5) with nasal height (M25) (see Table 19). The third component is a contrast of skull height (M22) and the portion of the tooth row which includes the canine (M26).

Dorsal. The second component is a contrast between anterior nasal length (M4) and posterior width (M10) (see Table 20). The third is a contrast between anterior (M4) and posterior (M15) length.

Ventral. In this data set the second component is a contrast between anterior length and width (M26, 32) and posterior width (M34) (see Table 21). All three share a landmark in the anterior PM^4. The third component is a contrast of posterior (M36) and anterior length (M30), with anterior width (M31).

Table 18

Principal components I, II, III for age series of OTU FIL, mandibles (isometry=.353).

Variable	PC I	PC II	PC III
M2	.485	.178	−.727
M3	.327	.249	−.243
M4	.094	.143	.135
M5	.256	−.326	.193
M6	.371	.658	.501
M7	.459	−.183	.266
M8	.482	−.538	.123
M9	.012	.144	.139
%variance	94.0	96.4	97.8

Table 19

Principal components I, II, III for age series of OTU FIL, lateral view

Variable	PC I	PC II	PC III
M2	.392	.155	.095
M5	.360	−.897	.085
M11	.179	.207	−.225
M16	.326	.087	−.017
M17	.289	.045	−.072
M22	.244	−.022	.323
M24	.073	.033	.113
M25	.308	.277	.472
M26	.347	.045	−.737
M27	.323	.165	.176
M28	.327	.095	−.106
%variance	83.4	91.0	93.9

Table 20

Principal components I, II, III for age series of OTU FIL, dorsal view (isometry=.27).

Variable	PC I	PC II	PC III
Dorsal (isometry=.27)			
M1	.326	−.021	.051
M3	.384	−.079	.083
M4	.374	−.748	−.413
M6	.380	.118	.028
M7	.205	.153	.411
M8	.258	.203	−.084
M9	.269	.246	−.228
M10	.262	.364	−.121
M11	.196	.080	−.149
M12	.238	.014	.118
M13	.170	−.086	.326
M14	.274	.201	.011
M15	.103	−.326	.656
%variance	81.1	85.7	89.5

Table 21

Principal components I, II, III for age series of OTU FIL, ventral view

Variable	PC I	PC II	PC III
M23	.026	.022	.108
M26	.346	−.534	−.081
M28	.326	.010	−.214
M30	.202	−.087	−.488
M31	.427	.143	.550
M32	.426	−.475	.239
M33	.405	.245	.043
M34	.345	.612	.011
M36	.270	.135	−.567
M39	.100	−.072	−.107
%variance	87.8	91.7	93.8

Discussion. Principal component analysis performed on lateral data sets (lateral view, mandible) produced contrasts in the second component similar to thise of all other analyses containing male individuals. Ramus height contrasts with ramus width for all analyses. It must be noted that the second component of the ager series accounted for a small percentage of the total variance (2.4 and 7.6%). Analysis of the dorsal data produced contrasts involving the canine region and palate width. This suggests that sexual dimorphism is the underlying factor influencing the results of this analysis.

Results of analysis of the age series of FIL is difficult to interpret, possibly for methodological reasons. A static-cross section data set may have had an effect on results; a longitudinal data set is preferred. Sample size may have influenced the results, as several age classes were under-represented, and the age classes were of unequal time length. Results of adult BARB males and females indicate that sexual dimorphism is present in the taxa. This may have obscured growth trajectories present in the results, as juveniles were unsexed, and both male and female adults were included in the analysis.

DISCUSSION

Results of these analyses indicate that shape and size differences separate the five subspecies into three groups. Within each group, males and females exhibit unique patterns of contrast as a result of sexual dimorphism. An assessment of these patterns and examination of sources for variation follow below.

Size

Both discriminant analysis and principal component analysis isolated three size groups. From largest to smallest they are BARB-OI, AHO, and FIL-CEBI. Both males and females could be placed in the appropriate size group with a high degree of confidence. Previous studies suggest that the body size of island dwellers may influenced by the size of the island where they live (Marshall and Corrucini 1978).

Foster's study (1964) suggests that artiodactyls on islands should become smaller through time. He compared the average body size of 11 artiodactyl species to average body size in ancestral mainland populations. All were either the same size (12%) or smaller (88%) than mainland representatives. This hypothesis suggests that *S. barbatus* found on islands should be smaller than mainland populations. It further suggests that, if body size is only influenced by island size, *ahoenobarbus* should be smaller than *philippensis* as Palawan is smaller than Luzon. In addition, the hypothesis indicates that there should be a reduction in size through time in the fossil record for the smaller subspecies.

The results of discriminant analysis indicates that the populations on small islands are smaller than samples from either the largest islands or the mainland. However, if island size is the only influence on body size, AHO populations should be smaller than FIL, as Palawan is smaller than Luzon. The average body size of AHO is larger than FIL, suggesting that other factors, such as length of time of genetic isolation, are also pertinent.

Extensive fossil material for *S. barbatus* from small islands for study of size reduction through time has not been recovered. Middle Pleistocene material has been recovered from the Cagayan Valley in Luzon, Philippines, but has not been identified to species (Dr. J. Peralta, personal communication). No fossil material, to date, has been recovered from Palawan.

Shape

Sexual dimorphism

Sexual dimorphism was readily apparent in all subspecies. Male individuals had massive upper and lower canines in comparison to females, and older males exhibited saggital cresting. One goal of this analysis was to assess the effect of this dimorphism on over-all skull dimensions.

All analyses of data from a vertical plane (lateral view, mandible) resulted in only two patterns of contrast. One pattern was characteristic of data composed of females only (Figure 12,13:c,d). Data sets containing only males, or males and females exhibited another pattern (Figure 12,13:a,b,e,f).

For females, analyses of mandible data produced contrasts between ramus height and premolar row. In the skull, measurements in the rear centering on the posterior M^3 form contrasts with measurements centered on the anterior PM^2.

Mandibular contrasts consisted of anterior ramus height and width for all data sets containing measurements from males. Lateral data sets from males alone and males and females combined produced a contrast of nasal length and nasal height.

Patterns of contrast in the horizontal planes of the skull, dorsal and ventral data, cannot be explained by reference to sexual dimorphism, and will be discussed below.

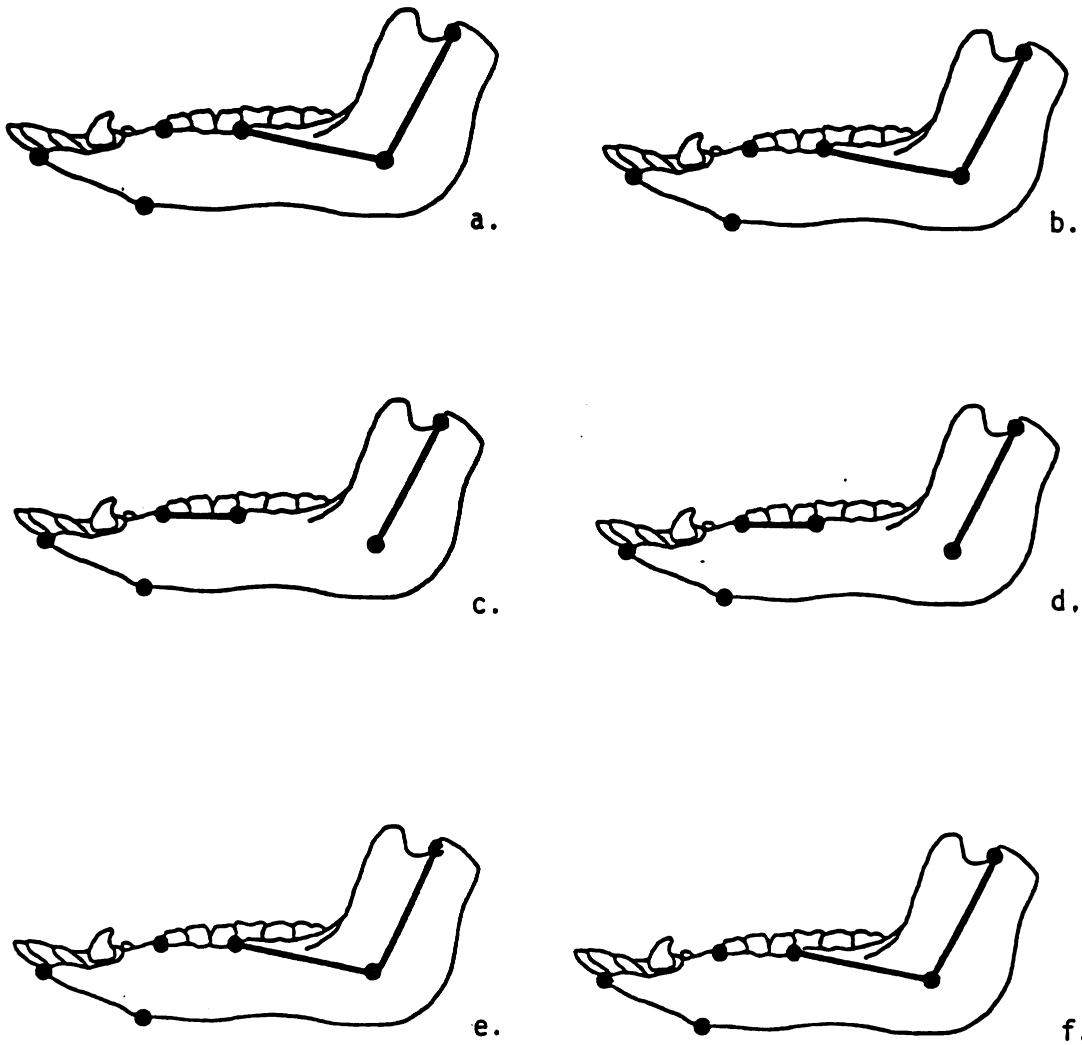

Figure 12. Patterns of contrasts from principal component analysis, mandibles.

a.) BARB males vs. females (PC II) b.) BARB vs. OI males (PC II)
c.) FIL vs. BARB, females (PC II) d.) all OTUs, female (PC II)
e.) all OTUs, male (PC II) f.) FIL age series (PC II)

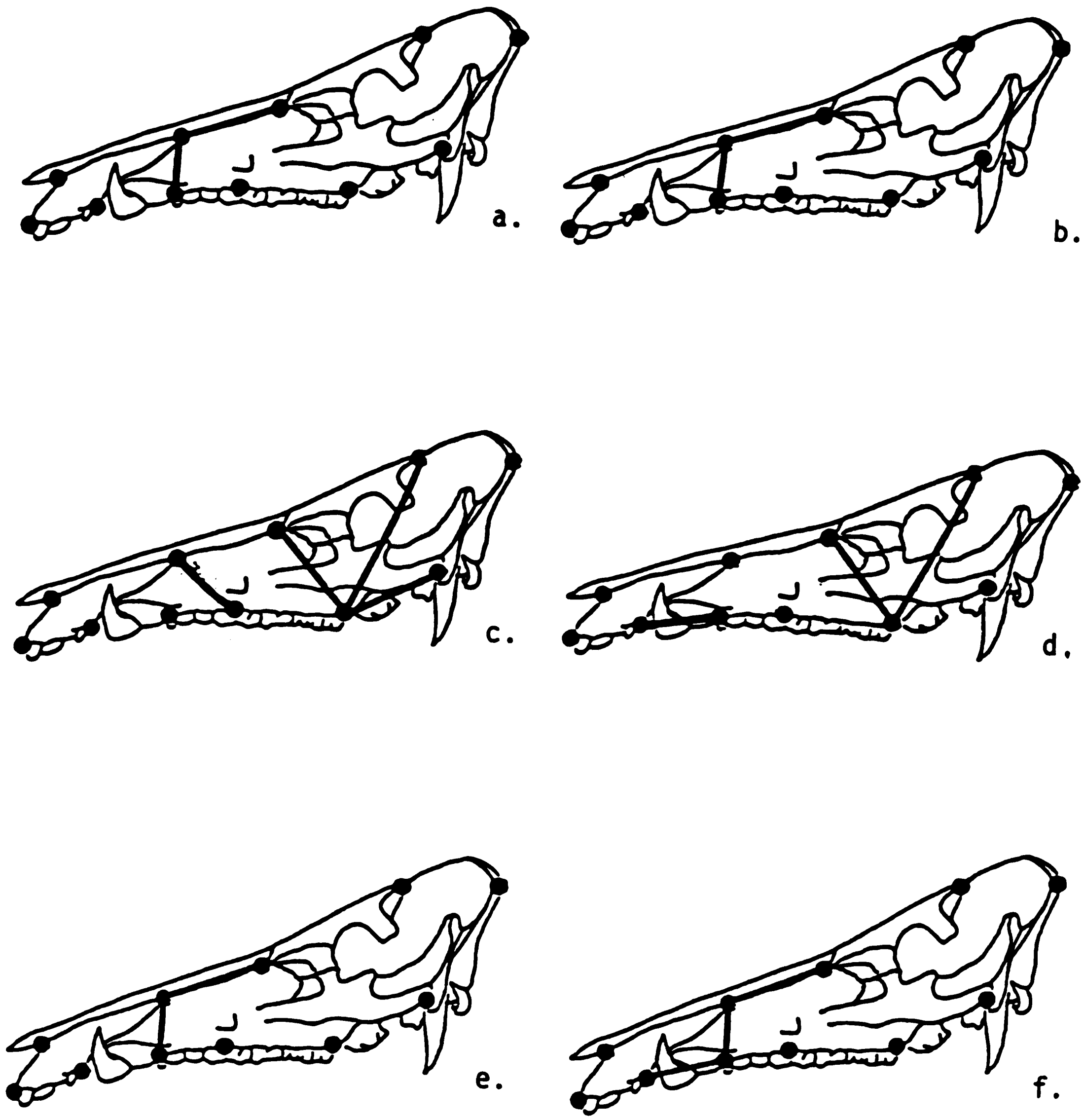

Figure 13. Patterns of contrast from principal component analyses, lateral view

a.) BARB males vs. females (PC II)
b.) BARB vs OI males (PC II)
c.) FIL vs. BARB, females (PC II)
d.) all OTUs, female (PC II)
e.) all OTUs, male (SPC II)
f.) FIL age series (PC II)

Inter-populational variability

Although size was the best indicater of differences between OTUs I conducted further analyses to explore the nature of shape differences. Shape differences between OTUs were most pronounced in the data from the horizontal planes of the skull (i.e. dorsal and ventral views) (see Figures 14, 15).

The shear procedure identified three clusters of OTUs which were congruent with those identified by discriminant analysis- BARB-OI, AHO, and FIL-CEBI. Similarity in size and shape between these clusters may be function of genetic relationships. Patterns of genetic relationships between the taxa are predicated on the historical geography of insular Southeast Asia.

The genus *Sus* probably evolved on the Asian mainland; representatives first appear in the Swialik beds of the Indian Pliocene. The genus appears next appears in Middle Pleistocene contexts in Java (Badoux, 1959). During the Middle Pleistocene sea levels were an estimated 160 to 180 meters lower than currently, exposing most of the Sunda Shelf and uniting the Malaysian Peninsula, Sumatra, Java, and Borneo into one land mass. The island chain of Palawan was a peninsula of Borneo during this time. During the Late Pleistocene it was separated from Borneo by a channel.

It seems unlikely, judging from faunal distributions and geological reconstructions, that the Philippine archepelago was ever part of this land mass. Heaney (1984) compared the number of species and composition of current faunal assemblages from the Philippines to those from islands on the Sunda Shelf and concluded that the assemblages from the Philippine archipelago were depauperate in the number of species that the land masses could support. This is typical for oceanic islands which, by definition, were never part of a larger land mass.

Water gaps between the eastern edge of Borneo and Mindanao were no more than 15 miles, and could have been traversed by swimming animals. Pigs can and do swim (Wallace 1881;69), but their endurance is not known. Unless introduced by man (Heaney

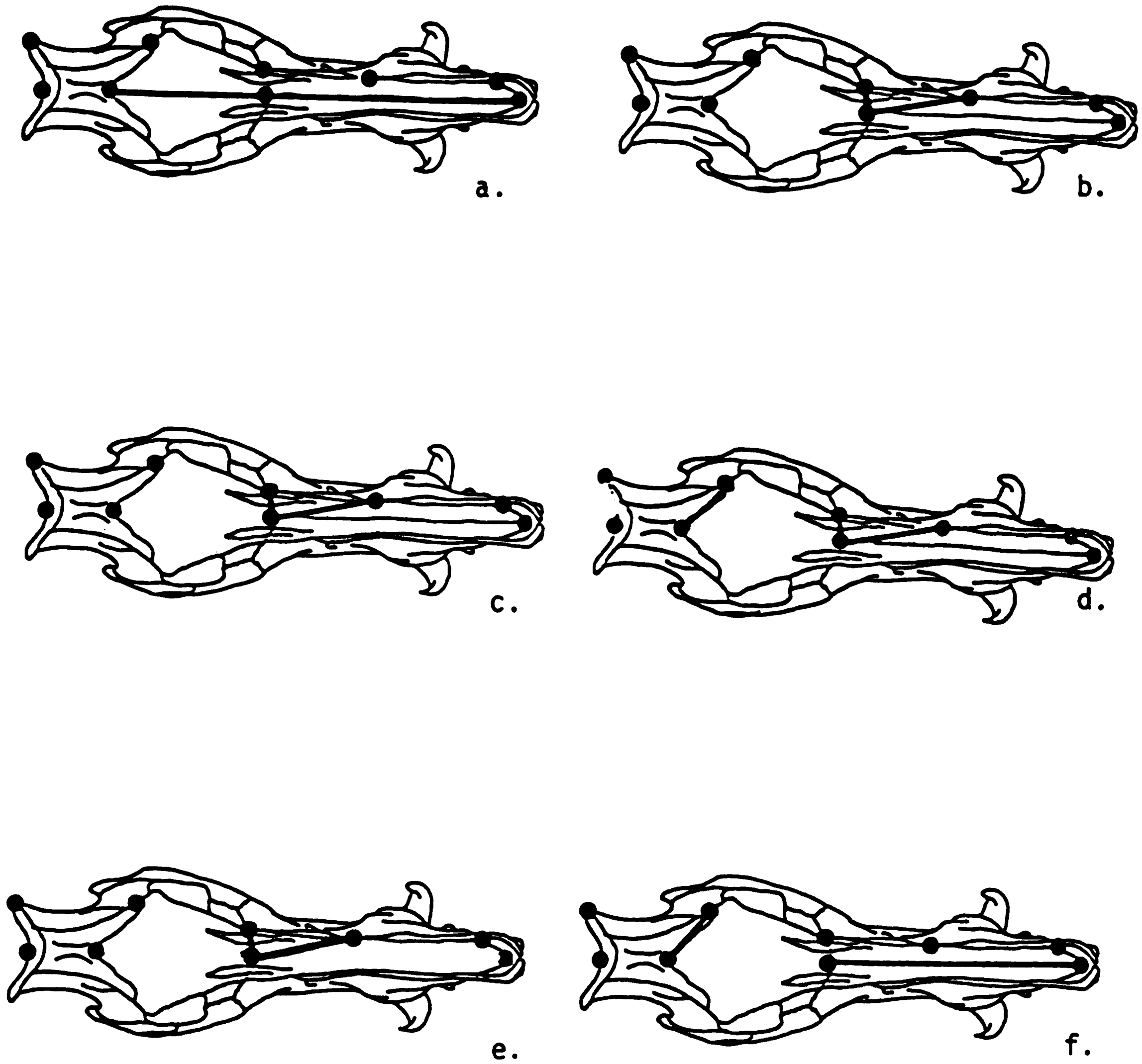

Figure 14. Patterns of contrast from principal component analyses, dorsal view.

a.) BARB males vs. females (PC I)
b.) BARB vs. OI males (PC I)
c.) FIL vs. BARB, females (PC II)
d.) all OTUs, female (SPC III)
e.) all OTUs, male (SPC III)
f.) FIL age series (PC II)

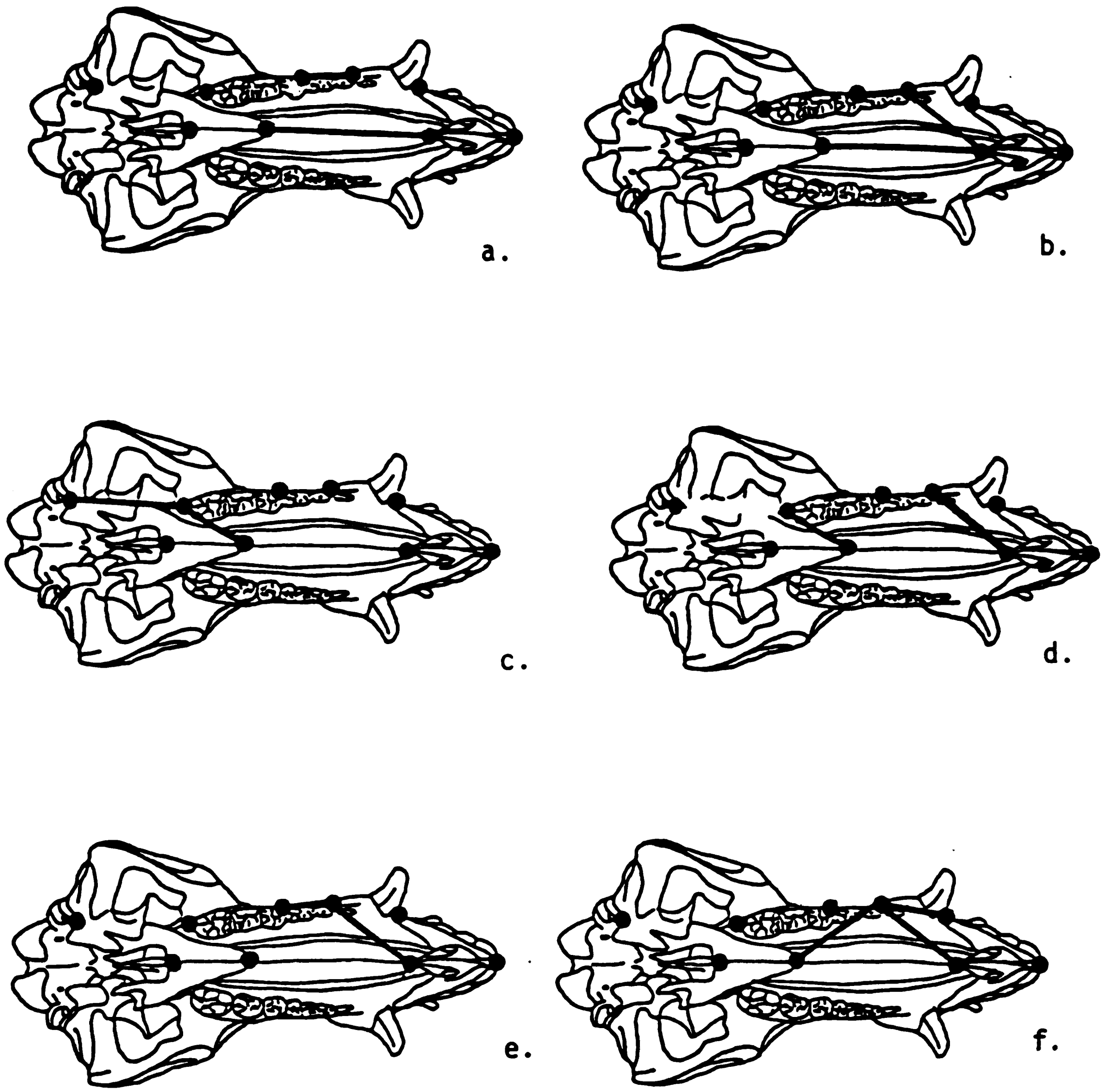

Figure 15. Patterns of contrast from principal component analyses, ventral view.

a.) BARB males vs. females (PC I)
b.) BARB vs. OI males (PC I)
c.) FIL vs. BARB, females (PC II)
d.) all OTUs, female (PC II)
e.) all OTUs, male (PC II)
f.) FIL age series (PC II)

1985), the bearded pig probably entered the Philippine archipelago by swimming water gaps between the Sulu archepelago and Mindanao. An alternate route of entry is through the Palawan chain to Mindoro or Panay, but it involves a larger water gap and therefore is considered less likely a route. Once across this boundary, pigs could have easily spread throughout the archepelago. At this time, the Philippines consisted of three islands, Negros-Cebu-Panay-Masbate, Luzon, and Mindanao.

Rising of the sea level by 40 meters during the Late Pleistocene did not appreciably change the configuration of the land mass of the Sunda Shelf, but separated Palawan from Borneo.

If this reconstruction is correct, we would expect to see *ahoenobarbus* resemble *barbatus* more closely than it does *cebifrons* and *philippensis*, as Palawan was connected to Borneo and not to the Philippines. We would also expect to see the subspecies in the oceanic islands resemble each other, and the species in the continental islands resemble each other. Middle Pleistocene material assigned to *Sus barbatus* has been recovered from Java (Badoux, 1959) although this species is not found there presently. Late Pleistocene fossil material identified as *Sus barbatus* has been recovered from Niah Cave (Medway 1977,1979).

Historical reconstruction of migration routes suggest that AHO has remained in genetic contact with BARB longer than with FIL-CEBI. Therefore, shape characteristics of AHO should more closely resemble BARB than FIL-CEBI. The shear precedure, while isolating AHO as a distinct group, produced ambivalent results for assignment of closer genetic relationships, although discriminant analysis indicates that, based on size, AHO most closely related to FIL-CEBI. A larger sample of *ahoenobarbus* would permit a more detailed comparison with both the oceanic groups and the continental groups, and perhaps assessment of degree of morphological similarity.

Principal component analysis was performed on BARB and FIL females to explore the nature of shape differences between the largest and the smallest OTU. This was the only analysis of dorsal data to produce contrasts in the reat portion of the skull, and not pertaining to the palate. However, one landmark on the tooth row, the M^3, was included. Analysis of ventral data contrasts posterior nasal length and width, also including landmarks on the tooth row. This indicates that FIL is not a scaled-down version of BARB, but that shape parameters also differentiate the two OTUs.

This conclusion is also supported by analysis of the FIL age series.The patterns of contrast demonstrated through this analysis resemble those of males in the mandible and lateral view, but are unique in the dorsal and ventral view (see Figure 11–14:f). Results of analysis of this data set indicate that the nasal region of the skull exhibits positive allometry in relation to the back of the skull. Overall, the morphometric contrasts among age classes do not parallel either contrasts among BARB males and females, or contrasts among BARB and FIL. This suggests that the growth patterns of FIL do not parallel morphometric differences between BARB and FIL. Lack of congruence in these patterns of contrast may indicate that FIL exhibits an independent developmental tragectory. That is, FIL, the smallest OTU, is not a neotenic form of BARB, the largest.

In all analysis comparing dorsal views of OTUs contrasts include posterior nasal length and width. This region contains the tooth-bearing portion of the skull. Analysis of ventral data all produced unique contrasts. Analyses of data from both males and females emphasize the placement of the tooth row in relation to the longitudinal axis of the skull.

Shape differences betweeen OTUs were particularly pronounced in the regions of the skull pertaining to the tooth row. Groves (1981;51) notes that the molar row forms a smaller proportion of the maxillary tooth row in *S. b. oi* than in *S. b. barbatus*. He interprets this as an example of character displacement, as *oi* occurs sympatrically with wild *S. scrofa*. Unfortunately, principal component analysis of *oi* vs. *barbatus* excluded the molar row, because of high correlation coefficients, so this potential discriminator was not closely examined. However, analysis of the ventral data set produced contrasts between palate length and width and premolar row (Figure 14:b).

The diversity of loading patterns of the ventral view of the skull, a data subset which contains measurements referring to the feeding apparatus, suggests that the influences on shape configuration are not uniform. Each population may be adapting to specific ecological parameters within their respective environments, presumably relating to food resources. Testing this would involve establishing evidence of a relationship between patterns of morphological diversity and some aspects of the environment. While I am not suggesting that there will be a close relationship between morphology and feeding ecology, these results suggest that separation between populations may be accomplished through reliance on measurements of tooth row alignment. At this time, the ecological data is not available to evaluate the influence of local environment on cranial morphology.

This study established by quantitative means the existance of shape and size differences between three of five subspecies of the bearded pig. There is no evidence to indicate that the current taxonomy of the bearded pig includes any inappropriate groups. *S. b. philippensis* should not be given specific status, as Groves suggests (1981). However, this study indicates that several of the subspecies are not valid. Lack of separation between *S. b. barbatus* and *S. b. oi* on the basis of size or shape indicates that the two subspecies are actually geographically separate populations of the same subspecies. These should be combined under the older name of *S. b. barbatus*. Although my sample size was inadequate for analysis of shape, discriminant analysis of size suggests that *S. b. philippensis* and *S. b. cebifrons* should also be combined under the older name of *S. b. philippensis*.

Size differences between the subspecies are only partially accounted for by reference to size of land mass on which they are found. The largest subspecies are found on the largest islands and the mainland, while the smallest are found on the smallest islands. However, *ahoenobarbus* is larger than predicted by this hypothesis.

Geological reconstruction of dispersal of bearded pigs suggest that *ahoenobarbus* remained in genetic contact with *barbatus* longer than with *philippensis* populations. The larger than expected body size may be a function of a closer genetic relationship with a larger-bodied subspecies. However, it was not possible to assign a closer genetic relationship to either *barbatus* or *philippinenesis* on the basis of shape analysis with the sample available.

Results of this study indicate that ventral portions of the skull pertaining to tooth row are undergoing morphological divergence. This may be in response to specific ecological conditions within their geographical ranges. The nature of the factors influencing this diversity cannot be examined until further ecological studies are conducted.

Comments on methodology

The results and interpretations of this analysis are not independent of the analytical techniques employed. The limitations of the truss as a way of examining individual specimens, and the assumptions of the statistical procedures will be reflected in the results. Here I wish to discuss the shortcomings of this particular analysis.

The truss network represents a distinct advantage over conventional measurement protocols. The use of homologous landmarks contributed to a clearer separation of the OTUs and facilitated biologically meaningful interpretations of the results. However, the particular truss scheme which I utilized had several deficiencies which hampered the effefctiveness of this method. Mandibles and skulls were not measured as complementary units, and thus could not be interpreted as such. Few measurements were chosen which accomodated the articulation of skull with mandible. Measurements of the ventral skull included medial-lateral distance from the midline of the palate, while mandibular measurements were taken exclusively in a lateral plane. Alteration of the truss network to include measurements of this nature may facilitate explanation of differences between OTUs.

A second deficiency is that potentially useful measurements, particularly those in the tooth row, were eliminated to render the co-variance matrix mre amenable to statistical manipulation. The truss network should be tailored to accomodate the problem examined.

Principal component analysis has been used as an analytical tool in separation of hybrid fishes from parental groups (Neff and Smith 1979), separation of species of fish (Humphries et al. 1981), and separation of subspecies of elk (Schonewald-Cox et al. 1985), among other studies. These studies all indicate that this technique is sensitive to differences within data sets. However, the protocols for deciding whether these results are biologically significant are not well established. Neff and Smith discuss their assumptions:

> An implicit assumption frequently made is that the important biological phenomena will be represented most clearly by the components in the directions of the greatest variance, permitting generalized inferences to be drawn from the first few components, especially when they explain a very large percentage of the total variation.. The validity of these (assumptions) was not examined in this study, but instead remains an assumption when generalizations are made from principal components analysis results since only the first few components were examined in detail. If there is known or hypothesized to be more than one group in the data it is often assumed that the direction of greatest variance is approximately the same for all groups (1979;192).

I also assume that the most important biological phenomena will be represented by the components which explain the largest proportion of the total variance. In the majority of analyses in this study, and in the studies enumerated above, the largest proportion of total variance is accounted for by the first component. The underlying biological factor is assumed to be size differences between the groups examined.

Interpretation of the second component of a multi-group principal component is also problematic. If the first component generally represents size, and accounts for the majority of the variance, how much variance must the second component account for to be biologically meaningful? The total amount of variance accounted for by PC I and PC II in the study by Humphries et al. was not recorded; Neff and Smith recorded 41% for PC I and 29% for PC II for the principal component analysis of *Lepomis* species and 96% for PC I and 3% for PC II for principal component analysis of *Notropis* species. Schonewald-Cox et al. record percentages of explained variance which range from 10–70% for components I and II. All studies suggest that these were biologically significant differences. In this study, the majority of analyses produced a first principal component which accounted for a high percentage of the total variance, while the second was gnerally low, accounting for less than 10% of the variance. The shear procedure acted on this low variance and, when plotted, separated the OTUs into non-overlapping groups. Whether these shape discriminators are significant in a biological sense is a matter of interpretation.

An additional problem in interpretation of multi-group principal component analysis is assigning significance to contrasting loadings on the second component. Neff and Smith (1979;192) note that the results can be patterned in an extreme manner by the presence of a single meristic character. Humphries et al. employed principal component analysis in a comfirmatory way rather than an exploratory way, and were able to assign species to positions of positive or negative contributions to loadings on the basis of prior biological knowledge. Schonewald-Cox et al. referred to univariate statistics to interpret loadings on the second component of analysis of four OTUs of elk. In this study the problem was addressed by performing analysis of pairs of OTUs and comparing the resulting patterns, but the problem of assigning relative positions still remains.

CONCLUSION

The influence of environment and genetic background on skeletal morphology is a significant problem in evolutionary biology. This study has examined cranial variability among 5 closely related populations of one species of pig. This taxa is distributed both on oceanic and continental islands, and on the Southeast Asian mainland. The purpose of this study is to identify sources of morphological variation through examination of cranial skeletal morphology in these populations.

To identify sources of variation I examined differences between the sexes, among all the subspecies combined, and between subsets of the total sample, separated by sex. I also examined an age series of *S. b. philippensis* in an effort to characterize growth patterns in one subspecies.

Examination of male and female *S. b. barbatus* revealed that differences in cranial morphology were not isolated to areas containing the dimorphic canine. Patterns of contrast isolated general length and height dimensions, rather than local regions.

Results of discriminant analysis, a precedure sensitive to size differences between populations, combined the five subspecies into three groups. These were *barbatus-oi*, both from land masses on the Sunda Shelf, *ahoenobarbus* from Palawan, and *philippensis-cebifrons*, both from the Philippine islands. Results of principal component analysis confirmed these groupings, and supplied additional information on the nature of the shape differences between groups.

My findings indicate that head size of bearded pigs is largest on land masses on the Sunda Shelf, and smallest on the oceanic Philippines islands. They are also the smallest islands supporting populations of bearded pigs. Shape differences group the samples in an congruent manner. Hypothese drawn from historical and island biogeography are presented but are not conclusively tested. The small sample size of *ahoenobarbus* do not allow for fine discrimination between hypotheses. However, the findings do suggest that, on the basis of size, *ahoenobarbus* is genetically closer to *barbatus* than *philippensis*, and should resemble this group more closely in shape as well. Fossil specimens are also necessary to explore the implications of these hypotheses. Analysis of cranial morphology of other endemic suid species in island Southeast Asia may reveal shed further light on this bio-geographical problem.

Principal component analysis performed on the data subsets indicate that significant patterns of contrast were consistantly isolated in the ventral portion of the skull. All contrasts emphasized some aspect of the tooth row to the palate midline. The variation in results suggests that divergence is occurring in the masticatory morphology of these subspecies. The source for this variation may lie in habitat characteristics specific to each subspecies. Baseline ecological studies are necessary to test this proposition.

This study established by quantitative means the existance of shape and size differences between three of the five subspecies of the bearded pig. These groups are *S. b. barbatus-S. b. oi*, *S. b. philippensis-S. b. cebifrons* and *S. b. ahoenobarbus*. There is no evidence to suggest that any taxa is mis-identified or should be given separate status. This study also suggests that several of the sub-specific classifications are not valid. Lack of separation between *S. b. arbatus* and *S.b. oi* on the basis of size or shape indicates that the two subspecies are actually geographically separate populations of the same subspecies. These should be subsumed under the older name of *S. b. barbatus*. Although my sample size was inadequate for a shape analysis, analysis of size suggests that *S. b. philippensis* and *S. b. cebifrons* should also be combined under one name, *S. b. philippensis*.

This study has demonstrated that the basic stock of bearded pigs have diverged morphologically through time. Change in shape and size as well as, possibly local extinction, has occurred concomitantly with geographic isolation. Understanding the factors which have influenced this divergence and the dynamics of this process can increase our understanding of general evolutionary processes.

BIBLIOGRAPHY

BIBLIOGRAPHY

Badoux, D. M.

1959. Fossil mammals from two fissure deposits at Punang (Java), with some remarks on migration and evolution of mammals during the Quaternary in Southeast Asia. Utrecht: Proefschr.

Cock, A.G.

1966. Genetical Aspects of Metrical Growth. Quarterly Review of Biology Vol. 41:131–190.

Cranbrook, E.

1979. A review of domestic pig remains from archaeological sites in Sarawak. Sarawak Museum Journal. Vol. 27.

Dixon, W.J. et al.

1985. BMDP Statistical Software. University of California Press, Berkeley

Foster, J.B.

1964. Evolution of mammals on islands. Nature Vol. 202:234–235.

Fox, D.J. and K.E. Guire

1976. Documentation for MIDAS,Third Edition Statistical Research Laboratory, University of Michigan.

Groves, C.

1981. Ancestors for the Pigs: Taxonomy and Phylogeny of the Genus Sus. Technical Bulletin No.3. Australian National University.

Heaney, L.H.

1984. Mammalian species richness on islands on the Sunda Shelf, Southeast Asia. Oecologia Vol.61:11–17

1985. Zoogeographical evidence for Middle and Late Pleistocene land bridges to the Philippine Islands. Modern Quaternary Research in Southeast Asia Vol.9:127–144

Jolicoeur,P.

1963. The multivariate generalization of the allometry equation. Biometrics, Vol. 19:497–499.

Humphries, J.M., F.L. Bookstein, B. Chernoff, G.R. Smith, R.E. Elder, and S.G. Poss.

1981. Multivariate Discrimination by shape in relation to size. Systematic Zoology, Vol. 30:291–308.

Marshall, L.G. and R.S. Corruccini

1978. Variability, evolutionary rates, and allometry in dwarfing lineages. Paleobiology, Vol.4:101–118.

Matsche, G.H.

1967. Aging European hogs by dentition. Journal of Wildlife Management, Vol.31:109–113.

Medway, L.

1977. Wild pig remains from the mouth of Niah Cave. Sarawak Museum Journal Vol. 25:21–33.

Neff, N.A. and G. R. Smith

1979. Multivariate analysis of hybrid fishes. Systematic Zoology, Vol. 28:176–196.

Nie, N., C. Hull, J. Jenkins, K. Steinbrenner, D. Bent

1975. Statistical Package for the Social Sciences. Second edition. McGraw-Hill Book Co., New York.

Sanborn, C.C.

1952. Philippine Zoological Expedition. Fieldiana: Zoology Vol.33:89–158.

Schonewald-Cox, C., J. Bayliss, and J. Schonewald

1985. Cranial morphology of Pacific coast elk (Cervus elaphus)) Journal of Mammalogy Vol. 66:63–74.

Strauss, R.E. and F.L. Bookstein

1982. The truss: Body form reconstructions in morphometrics. Systematic Zoology, Vol.31:113–135.

Wallace, A.

1881. Island Life. Harper and Brothers, New York.

APPENDIXES

APPENDIX A

List of specimens examined

The collecting localities are grouped below according to subspecies. Specific localities are grouped by country within land mass. Acronyms are: FNMH, Field Museum of Natural History, Chicago, Illinois; NMP, National Museum of the Philippines, Manila; ZRC, Zoological Research Collections, National University, Singapore; JM, Jabatan Muzium, Kuching, Sarawak; MS, Muzium Sabah, Kota Kinabalu, Sabah; MZB, Muzeum Zoologici Bogoriense, Bogor, Indonesia; BM, British Museum, London England; CZB, Cambridge Zoology Museum, Cambridge, England, USNM, U.S. Natural History Museum, Washington D.C.; UMMZ, University of Michigan, Museum of Zoology, Ann Arbor, Michigan; BG, personal collecation of Dr. Bion Griffin (these specimens will be donated to UMMZ).

Sus barbatus ahoenobarbus

PHILIPPINES
Culion Is.: skull, 1 male (USNM 152244).
Palawan Is.: skull and mandible, 1 male (BM 94688); mandibles, 2 males (NMP, non catalogued, but inscribed with locality and date of capture).
Iwahig: skull and mandible, 1 male, 3 females (NMP, none catalogued, but inscribed with locality and date of capture).
Binuan: skull and mandible, 1 male (FMNH 62830).
Lapulapu: mandible, 1 male (FMNH 62825).
Balabec Is.: skull and mandible, 3 females (BM 94687,94689,946810).

Sus barbatus barbatus

MALAYSIA
Sabah: Sandakan District: skull and mandible, 1 male (FMNH 68756).
Gomantong Forest Reserve: skull and mandible, 1 male (FMNH 468758).
8 miles west of Sandakan: mandible, 2 females (FMNH 33553–4).
Kinabatongan District: Little Kretam R., skull, 1 male 68757); mandible, 1 male (FMNH 68755).

Tawau District, Kalabakan, Sungei Tibas Camp: mandible,
1 female (FMNH 85916).

INDONESIA

Kalimantan: Pasir R.: skull, 1 male (USNM 154376).
Pamukang Bay: skull and mandible, 2 females (USNM 151851,154380).
Mahakam R., Longiram: skull and mandible, 1 female (USNM 176197).
Kalei R., Toembit: skull and mandible, 1 female (USNM 196832).
Segah R., south bank: skull, 1 male (USNM 196834).
Sandaren Baagoe: skull and mandible, 1 female (USNM 197667).
Sungai Karangan: skull and mandible, 1 female (USNM 198302).
Sungai Djambajan: skull, 1 male (USNM 198850).
Labuan Pendjang: skull, 1 male (USNM 197669).
Sempang R.: skull and mandible, 2 females (USNM 145293,151845); skull, 1 male (USNM 145292).
Sempang Kampong: skull, 1 male (USNM 145299).
Klumpang Bay: skull, 1 female (USNM 151843).
Landak R.: skull, 2 males, 1 female (USNM 142350, 142351,142354).
Pulo Pelapis: skull, 2 males (USNM 145288–89).
Pulo Panebangan: skull, 2 males (USNM 145290–91).
Sejok: skull, 1 male (USNM 145298).
Matan R.: skull, 1 male (USNM 145297).
Semandang R.: skull, 1 male (USNM 145295).
Tjangtung: skull and mandible, 1 female (USNM 151846).
Sempanahan R.: skull and mandible, 1 female (USNM 151852).
Pangkallahan R.: skull, 1 male (USNM 151849).
Balikpapan Bay: skull and mandible, 1 female (USNM 154377).
Pulo Bauwal: skull and mandible, 1 female (USNM 153785).
Samarinda: skull and mandible, 1 female (MZB 8366), skull, 1 male (MZB 8367).
Buntok: skull and mandible, 1 male (BM 1045158).
Pontianak: skull and mandible, 1 male (ZRC4.1940)

W. Kalimantan: skull and mandible, 1 male (MZB 8381).

BRUNEI

(no other locality information) skull and mandible, 1 male (ZRC4.1939).

MALAYSIA

Sarawak: (no other locality information) skull and mandible, 10 males, 5 females (JM 2/2,5,8–11,13,16,17,19; BM 97621, 033011,033015–16,976251); skull, 1 female (JM 2/7); mandible, 2 males, 2 females (BM 97622; JM 2/4,14,18).
Mt. Dulit, 4000'el.: skull and mandible, 1 male (ZRC4.1938).

Borneo

(no other locality data): skull and mandible, 7 males, 1 female, 1 sex unknown (BM 951148; H.12.631–33,635–36,638; ZRC4.1965; MS, uncatalogued); skull, 4 males, 1 female (CZB H.12.634, BM uncatalogued (Medway 83); USNM 196840; MS, uncatalogued); mandible, 4 females (MS, uncatalogued).

Sus barbatus cebifrons

PHILIPPINES

Negros Is.: Inubungan: Santa Catalina: skull and mandible, 1 female (FMNH 66322); mandible, female (FMNH 68002).
Amio: skull and mandible, 1 male (FMNH 65454).
Kaigangan: skull and mandible, 1 female (FMNH 65455).

Negros Oriental: Lake Balinsasayao: mandible, 3 males, 3 females (UMMZ 130420,158002,3,5,158626,158851).

Sus barbatus oi

MALAYSIA

Malaysian Peninsula: skull and mandible, 1 male, 1 female (BM uncatalogued, (HRC 368,375)); skull, 2 males (BM uncatalogued (HCR 367,374)).
Perak: Ulu Bernam Estate: skull and mandible, 1 male, 1 female (ZRC4.1930–31).
Paheng: skull and mandible, 1 male (ZRC4.1932).
Pekan: skull and mandible, 1 female (BM uncatalogued, has 'pekan' on skull).

Rhio Archepelago: skull and mandible, 1 male (BM 941504).

INDONESIA

Sumatra: Palembang: Bajung Lencin: skull and mandible, 1 female (MZB 1713).
S. Sago R.: skull and mandible, 4 males, 1 female (MZB 8386–89,8392).
Medan: Kota Pinang: skull and mandible, 5 males (ZRC4.1925–28,1937); skull, 1 female (ZRC4.1929).
Rengat Indragiri: skull and mandible, 1 male (BM 32371).
Pulo Tebing: Tinggi: skull and mandible, 2 males, 1 female (USNM 144308,144310–11).
mouth of Kempar R.: skull and mandible, 1 male (USNM 144304).
Pulo Rangsam:skull and mandible, 1 female (USNM 144355).

Sus barbatus philippensis

PHILIPPINES

Luzon Is.: Cagayan Prov.: Blabeg Cr.: skull, 1 female (UMMZ 157696).
Cagayan Prov.: Bagio Stream Valley: skull and mandible, 7 males, 15 females, 13 sex unknown (BG 1,4,6,10,13, 15,18,21,22,24,26,27,36,63–65,68,72,74,75,78,81–83, 86–89,92,94,98,100,102; UMMZ 157907); skull, 4 males, 11 females, 5 sex unknown (BG 8,11,14,17,23,25,31,33, 67,69,71,76,77,91,93,97,107; UMMZ 157909,157921–22);

mandibles, l male, 5 females, 11 sex unknown (BG 3,5, 12,16,19,66,84,85,90,95,96,99,104,109,113,117).

Cagayan Prov.: Ilang R. Valley: skull and mandible, 1 female (UMMZ 157956); skull, 1 male, 1 female (UMMZ 157958,157961); mandible, 1 male (UMMZ 157957).

Isabella Prov.: Blos R. Valley: skull and mandible, 3 females (UMMZ 157923,158000–1); skull, 1 female (UMMZ 157965), mandible, 1 male (UMMZ 157966).

Isabella Prov.: Divilakan R. Valley: skull and mandible, 1 male, 4 females, 1 sex unknown (UMMZ 157894–6, 157903–5); mandible, 1 male, 10 unknown sex (UMMZ 157893,157897–907).

Isabella Prov.:Dimansalansan Pt.: skull and mandible, 1 male (UMMZ 157697).

Catanduanis Is.: skull, 1 female (NMP, uncatalogued, (inscribed with date and location of capture)).

Mindanao: Cotabato: Upi: Becrunghat: skull and mandible, 1 male (NMP, uncatalogued (FMNH 56479)).

Parang Bugason: skull and mandible, 1 female (NMP, uncatalogued (FMNH 56473)).

Buayan: skull and mandible, 1 female, (NMP, uncatalogued (FMNH 56471)).

Pikit: mandible, 1 male (NMP uncatalogued (FMNH 56478)).

Davao: Malita: Lacaron: skull and mandible, 1 female (NMP uncatalogued (FMNH 62064)).

Appendix B

A verbal description of the landmarks used.

The points that were used in this analysis are presented below (see also Fig. X and X). Toward the nose is designated as anterior, toward the tail is designated posterior, regardless of orientation to foramen magnum.

A.) Anterior tip of nasals.

B.) Anterior edge of nasal-premaxilla suture.

C.) Nasal-premaxilla-maxilla suture point.

D.) Nasal-frontal suture at midline. This point was easy to identify in all but the oldest males.

E.) Anterior edge of lacrimal-maxilla suture. This suture was partly fused in a significant portion of the sample, making it one of the less reliable landmarks.

F.) Midline frontal parietal suture. This point was often difficult to identify in large males, where heavy muscle attachments had deformed the parietals.

G.) Frontal parietal suture, where it is dissected by the parietal crest. This was the only landmark readily discernable in this region of the skull, but I suspect it to be variable.

H.) The most lateral expansion of the nuchal crest of the occipital. This is clearly an analagous point.

I.) Dorsal end of the occipital at midline. The point in question could be considered analgous rather than homologous, but some reference point on this part of the skull was necessary.

J.) External acoustic meatus.

K.) Distal end of third molars. I took tooth measurements at the alveolus.

L.) Distal end of PM4.

M.) Anterior end of PM2. I divided the tooth row into two units to make measurement compatible with juvenile tooth eruption patterns.

N.) Premaxilla-maxilla suture immediately anterior to the canine.

O.) Anterior premaxilla-premaxilla suture. This was not strictly a suture, as the two bones were sometimes separate. I took measurements from the midline.

P.) Premaxilla-maxilla suture, at midline.

Q.) Maxilla-palatine suture at midline, ventral surface.

R.) Posterior edge of palatine bone, at midline.

S.) Anterior end of mandible at symphasis. This is a homologous landmark, but a little impractical, as the presence of the incisors sometimes hindered accuracy. Whenever possible, I removed the teeth in question before taking the measurement.

T.) Anterior PM2.

U.) Mental prominance of the mandible.

V.) Distal end of PM4.

W.) Mandibular foramen, ventral-anterior margin. This landmark was rather unsatisfactory, as it was possible to introduce inaccuracy when transferring the location of this point from the lingual to the buccal side of the mandible. However, I judged it to be the most suitable landmark in a rather uniform area of the mandible.

X.) Anterior edge of the condyle. I made an effort to take measurements from the edge of the condyle pad.

APPENDIX C

A verbal description of the measured distances.

A verbal description of the landmarks used for each of the distances measured is presented here.

Cranium

1.) Anterior tip of nasals (A) to nasal-premaxilla suture (B).

2.) Nasal-premaxilla suture (B) to nasal-premaxilla-maxilla suture (C).

3.) Anterior tip of nasals (A) to nasal-premaxilla-maxilla suture (C).

4.) Anterior tip of nasals (A) to nasal-frontal suture(D).

5.) Nasal-premaxilla-maxilla suture point (C) to lacrimal-maxilla suture (E).

6.) Nasal-premaxilla-maxilla suture (C) to nasal-frontal suture (D).

7.) Nasal-frontal suture (D) to lacrimal-maxilla suture (E).

8.) Nasal-frontal suture (D) to frontal-parietal suture (F).

9.) Lacrimal-maxilla suture (E) to frontal-parietal suture (F).

10.) Frontal-parietal suture (F) to frontal-parietal suture dissected by parietal crest (G).

11.) Lacrimal-maxilla suture (E) to frontal-parietal suture dissected by parietal crest (G).

12.) Frontal-parietal suture dissected by parietal crest (G) to lateral nuchal crest (H).

13.) Frontal-parietal suture (F) to lateral nuchal crest (H).

14.) Lateral nuchal crest (H) to dorsal end of occipital at midline (I).

15.) Frontal parietal suture (F) to dorsal end of occipital at midline (I).

16.) Lateral nuchal crest (H) to external acoustic meatus (J).

17.) Frontal-parietal suture dissected by parietal crest (G) to external acoustic meatus (J).

18.) Frontal-parietal suture dissected by parietal crest (G) to distal M^3 (K).

19.) External acoustic meatus (J) to distal M^3 (K).

20.) Distal M^3 (K) to distal PM^4 (L).

21.) Lacrimal-maxilla suture (E) to distal M^3 (K).

22.) Lacrimal-maxilla suture (E) to PM^4 (L).

23.) Distal PM^4 (L) to anterior PM^2 (M).

24.) Nasal-premaxilla-maxilla suture (C) to distal PM^4 (L).

25.) Nasal-premaxilla-maxilla suture (C) to anterior PM^2 (M).

26.) Anterior PM^2 (M) to premaxilla-maxilla suture at C^1 (N).

27.) Nasal-premaxlla-maxilla suture (C) to premaixilla-maxilla suture at C^1 (N).

28.) Premaxilla-maxilla suture at C^1 (N) to anterior premaxilla-premaxilla suture (O).

29.) Nasal-premaxilla suture (B) to anterior premaxilla-premaxilla suture (O).

30.) Anterior premaxilla-premaxilla suture (O) to premaxilla-maxilla suture at midline (P).

31.) Premaxilla-maxilla suture at C^1 (N) to premaxilla-maxilla suture at midline (P).

32.) Premaxilla-maxilla suture at midline (P) to PM^2 (M).

33.) Premaxilla-maxilla suture at midline (P) to maxilla-palatine suture (Q).

34.) Anterior PM^2 (M) to maxilla-palatine suture (Q).

35.) Posterior PM^4 (L) to maxilla-palatine suture (Q).

36.) Maxilla-palatine suture (Q) to anterior edge of palatine (R).

37.) Distal M^3 (K) to maxilla-palatine suture (Q).

38.) Distal M^3 (K) to anterior edge of palatine (R).

39.) Distal edge of palatine (R) to external auditory meatus (J).

Mandible

1.) Anterior end of mandible (S) to PM_2 (T).

2.) Anterior end of mandible (S) to mental prominance (U).

3.) Anterior PM_2 (T) to mental prominance (U).

4.) Mental prominance (U) to PM_4 (V).

5.) Mental prominance (U) to mandibular foramen (W).

6.) Mandibular foramen (W) to anterior condyle (X).

7.) Distal PM_4 (V) to anterior condyle (X).

8.) Distal PM_4 (V) to mandibular foramen (W).

9.) Anterior PM_2 (T) to distal PM_4 (V).