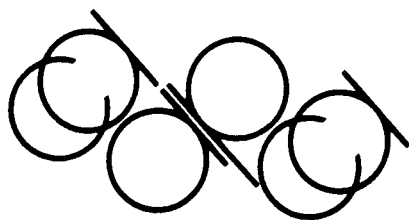


Canadian Journal of Anthropology Revue Canadienne d'Anthropologie

Volume 4, No. 2, Spring 1985



Canadian Association for Physical Anthropology
Association pour l'Anthropologie Physique au Canada

Canadian Review of Physical Anthropology
Revue Canadienne d'Anthropologie Physique

Volume 4, Numbers 1-2

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The CJA/RCA will award an annual prize in memory of Professor Richard Frucht for an essay of the general topic of historical materialism. While no strict limitations will be placed on the specific area, preference will be given to essays which cover aspects of the following topics which were central to Professor Frucht's scholarly interests: political economy of the nation-state; rural masses and political movements; post slave society in the New World; historical materialism in anthropological theory.

The value of the prize will be \$100 for students or \$50 for non-students and the winning essay will be published in the CJA/RCA.

Essays should be no more than 5,000 words long and must reach the Editor by the 1st of January. They should conform to the style outlined in the "Notes to Contributors."

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Manuscripts should be prepared according to the stylistic rules of the AJPA with the following additions:

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Canadian Journal of Anthropology

Revue Canadien d'Anthropologie

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CAPA/AAPC EDITORIAL

The *Canadian Review of Physical Anthropology/Revue Canadienne d'Anthropologie Physique* has become, for this volume and at least the next, a component of the *Canadian Journal of Anthropology/Revue Canadienne d'Anthropologie*. At the time this arrangement was being negotiated, it was the intention of both sides that it would become a long term liason. However, with the forthcoming changes in the status of the CJA/RCA, that may not be the case. The question of whether or not the CRPA/RCAP remains with the successor publication at the University of Alberta, or becomes, once more, an independent entity, is a matter which will be decided at the annual meeting of CAPA/AAPC in Thunder Bay.

This issue is made up of articles originally scheduled to appear in Volume 4 of the CRPA/RCAP under the editorship of Dr. William Wade of the University of Manitoba, plus submissions received and reviewed in 1984/85. Dr. Wade was forced to withdraw Volume 4 from the printer's production for good and sufficient reasons, and turned it over to me along with the directions of the association membership regarding the future of the journal. It has been a very busy time since then, but I hope that all subscribers will regard the results as a worthwhile effort.

The first eight articles were reviewed under Dr. Wade, and editorial assistance was provided by Louis Allaire of the University of Manitoba who was also responsible for the preparation of French abstracts for that set. The remaining articles were reviewed under my direction, and I wish to acknowledge the assistance of my three secretaries, Renate Hull, Myrna Haglund and May Ives, all of whom were forced into learning to handle the Honeywell Multics System at the University of Calgary in order to input the text. Patricia Miller-Schroeder and Michael Hull were responsible for the initial copy editing and proofing of the text files. All of them were indispensable. The editorial staff of the CJA/RCA, Drs. Regna Darnell and David Lubell, along with their assistants Jean Strong and Roslyn Madrid, must be thanked for the onerous task of keeping a neophyte editor on the straight and wobbly path towards publication. They were also responsible for taking care of missing keywords, setting up a number of tables which my staff could not provide in finished form, and arranging with Larry Fedigan to use his considerable expertise in preparing French translations of the remaining abstracts.

Some exciting developments are on line for our next issue (Volume 5, Number 2) which will focus upon the prehistoric populations of Ontario. At this point in time I am planning the succeeding issue and already have a few papers in hand for the proposed theme of "New Methodologies in Physical Anthropology". In order to keep the journal alive and active in any form, I once again urge you to keep those papers coming.

James D. Patterson, Editor/Rédacteur
Canadian Association for Physical Anthropology/
Association pour l'Anthropologie Physique au Canada.

CJA/RCA EDITORIAL

This issue of the *Canadian Journal of Anthropology/Revue Canadien d'Anthropology* marks the beginning of the end. Over the past year it has become clear to us that the CJA/RCA is not a viable entity. The Department of Anthropology can no longer afford to subsidize the journal to the extent that it has been doing up til now. We therefore announce, with regret, that the CJA/RCA will cease publication with Volume 5, No. 2. It will be replaced by an occasional publication series, intended for the publication of theme volumes (e.g. conference proceedings) and monographs. Although a name has yet to be decided, we lean towards something along the lines of *Anthropological Papers of the University of Alberta*. The first number of this new series will also be the last number of the CJA/RCA, and will be a volume on Ontario physical anthropology edited by Susan Pfeiffer. This issue also marks the beginning, and the end, of what we had hoped would be a long and interesting association with the *Canadian Review of Physical Anthropology*. That, however, is not to be. We regret this, especially in view of the very high quality and wide scope of the articles in this issue. A significant element in our decision was the cessation of new support for learned journals by the Social Sciences and Humanities Research Council of Canada.

David Lubell



PATRICK COOPER HARTNEY

1939 - 1980

Pat Hartney died on November 12, 1980, at the age of 41. After a brief illness he succumbed to acute pericarditis while on sabbatical leave in Paris. He is survived by his wife, Caroline, and his two children, Patrick, 10, and Laura, 13, all of whom were with him in Paris. He was an Assistant Professor in the Department of Anthropology and Archaeology, University of Saskatchewan, at the time of his death.

Pat was born on October 14, 1939, in the city of New York. He became interested in anthropology in the early Sixties while he was an undergraduate at the University of the South, Swannee, Tennessee. He applied for graduate work at the University of Chicago and was accepted in 1962. While at Chicago, he studied under several professors, including Sol Tax, Russell Tuttle, and Ronald Singer. Under Singer's guidance, he wrote his MA Thesis on Middle Stone Age Skeletons of South Africa.

In 1964 he was accepted for graduate work at the State University of New York at Buffalo. He immediately became involved with the excavation of the Fort Erie Site, Ontario, an Iroquoian ossuary excavated by the late Marion White. He suspended graduate studies to work full-time on the reconstruction and analysis of the Fort Erie skeletons under the direction of James Anderson. With the encouragement of White and Anderson, Pat became an "Iroquoianist", a passion which he pursued until his death. At Buffalo he worked with many graduate students, with some of whom he eventually achieved professional status, including Marie Clabeaux, Jerry Cybulski, Jerry Melbye, Joyce Sirianni, and Audrey Sublett. The focus of the "clan" was James Anderson. When Anderson returned to the University of Toronto in 1966, Pat accompanied him and they began excavating the Milton Ossuary that summer.

Pat's years at Toronto (1966-70) shifted from part-time lecturer, to demonstrator, to graduate student. He studied with Professors James Anderson, Norman Emerson, David Hughes, Howard Savage and Bin Yamaguchi. He was Associate Field Director on the Christian Island Site in Georgian Bay. He worked as the Field Director at the Glen Williams Ossuary, a site on which he was still working at the time of his death. During his residency at Toronto he worked with the Ontario Archaeological Society, and lectured frequently to classes and service groups. He generated enthusiasm among many undergraduates by working with them in the laboratory on human skeletons. A few of his fellow graduate students at Toronto who went on to get their degrees include: Steve Gabow, Geoff Gaherty, Sunny Jerkic, Chris Meiklejohn, Lindsey Neimann, Jim Paterson, Mike Pietrusewsky, Bob Sundick, Ed Way, Jim Webb, and Larry Williams. Some outstanding undergraduates whom he encouraged to go on in anthropology include Joan Johnson, Irene Knutson, and Elizabeth Salter.

In 1970 he accepted a full-time teaching post in the Department of Anthropology and Archaeology at the University of Saskatchewan. At Saskatoon he became involved with several departments (Anatomy, Dentistry, Pathology, Radiology, and Physical Education) in the promotion of physical anthropology. Again, his laboratory was humming with undergraduates, and he was lecturing to many service clubs and professional organizations. He continued his work on the Glen Williams Ossuary in his new laboratory, and began work on several projects in Saskatchewan. Outside of skeletal biology he worked on dermatoglyphics, comparative anatomy, and forensic anthropology with municipal police and the R.C.M.P. As a final tribute to Pat's influence on undergraduates, one of his students from Saskatoon, Ernie Walker, went on to get his Ph.D. and returned to fill the position left vacant by Pat's untimely death.

Pat's influence on physical anthropology in Canada was brief but significant. His Ph.D. thesis stands as the single, most comprehensive study of Ontario Iroquois palaeopathology ever written. Collectively, we are shocked by the death of a colleague who was so young and had so much promise. We are nonetheless happy to have known him and to have worked with him. His friends and his students will carry on the work he began with a new vigour. Thank you, Pat.

Jerry Melbye
John Reid

PUBLICATIONS OF PATRICK C. HARTNEY

- 1965 A Survey of the Cultural and Human Skeletal Remains Belonging to the Middle Stone Age of South Africa: including First Intermediate, Middle Stone Age Proper and Second Intermediate Period. M.A. Thesis, University of Chicago.
- 1972 Evidence of Severe Head Injuries Sustained by an Early Historic Canadian Indian From Ontario. (Abstract) *American Journal of Physical Anthropology*, 37:440.
- 1972 Report: Montgrand Missing Person. M.S. Royal Canadian Mounted Police, Prince Albert, Saskatchewan.
- 1974 Report: Prince Albert Burial M.S. Prince Albert Police Department, Prince Albert, Saskatchewan (In preparation for publication).
- 1974 (with E. Walker) Report: Greenwater Lake Burial M.S. Royal Canadian Mounted Police, Hudson Bay, Saskatchewan (In preparation for publication).
- 1975 Blood Group Phenotypes and Dermatoglyphic Analysis of Saskatchewan Children. Proceedings of the Second Canadian Symposium on Child Growth and Development, *Napao* 5:39-47.
- 1975 Report: Hudson Bay Missing Person. M.S. Royal Canadian Mounted Police, Hudson Bay, Saskatchewan.
- 1975 (with M. Anderson) Notes on the Battleford Industrial School Cemetery Burials. Unpublished M.S. Department of Anthropology, University of Saskatchewan, Saskatoon.
- 1975 (with D. Mandeville) "The Craigeleith Skull." A set of photographs produced by David Mandeville, of the Division of Audio-Visual Services, in cooperation with Professor Pat Hartney of the Department of Anthropology and Archaeology. Merit Award, Royal Photographic Society Medical Group, London, England. Display by British Medical Association, London.
- 1976 (with C. Garrad and H. Savage) The Craigeleith Skull: A Palaeopathological Specimen. *Napao* 6:1-4.
- 1978 Palaeopathology of Archaeological Aboriginal Populations from Southern Ontario and Adjacent Region. Ph.D. Thesis., University of Toronto.
- 1978 Tuberculous Lesion in a Prehistoric Population Sample from Southern Ontario. (Abstract) *American Journal of Physical Anthropology* 48:403-404. Invited paper presented at the 47th Annual Meetings of the Association, Special Symposium: Prehistoric Tuberculosis in the Americas (to be published in revised form by Northwestern University).
- 1978 Review of: Forensic Anthropology by M.J. El-Najjar and K.R. McWilliams. Springfield: Charles C. Thomas for the Journal of the Canadian Society of Forensic Science (to be published).
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- 1980 Hypodontia and Double Teeth. *Napao* 10:39-40.
- 1981 Paleo-odontologic research on an Iroquoian population from Ontario (Canada). *Bull. et Mém. de la Soc. d'Anthrop. de Paris.*, t. 8, série XIII: 43-61.

PALAEOPATHOLOGY OF ARCHAIC PEOPLES OF THE GREAT LAKES¹

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Abstract: Nine archaeological samples dating from ca. 4700 to 2875 B.P. are discussed. Traumatic injury is the most common cause of pathological bone alteration. Seventy to eighty percent of all pathological conditions identified are traumatic in origin. Among some local populations traumatic injury is distributed on the body such that it indicates an occupational hazard (adze usage) or warfare. Lesions indicate that in warfare males and females are affected equally. Palaeopathological examination does little to elucidate causes of death among populations from this time period. Although life expectancy was not high, measures of relative health indicate a robust population with adequate nutrition. Sporadic famine and climatic extremes may have affected mortality.

Résumé: Neuf échantillons archéologiques datant d'environ 4700 à 2875 avant le présent, ont été analysés. Les blessures traumatiques sont la cause la plus commune d'altérations osseuses pathologiques. Soixante-dix à quatre-vingt pour cent de toutes les conditions pathologiques identifiées ont une origine traumatique. Chez certaines populations locales, les blessures traumatiques sont distribuées sur le corps de façon à indiquer des dangers occupationnels (l'utilisation de l'herminette) ou la guerre. Les lésions indiquent que dans la guerre, hommes et femmes sont affectés de façon égale. L'étude paléopathologique contribue peu à éclaircir les causes de la mort dans les populations de cette période. Malgré une espérance de vie peu élevée, les indices de santé relative indiquent une population robuste ayant une alimentation adéquate. Les famines sporadiques et les extrêmes climatiques ont pu avoir un effet sur la mortalité.

Key Words: Palaeopathology, Archaic, Great Lakes.

Insofar as palaeopathology may be the study of the history of disease, the Archaic peoples of the Great Lakes are of little interest. Evidence of infectious disease, thought to have been an influential selective factor prehistorically, is rare. However, if we view palaeopathology as the study of the relative health status of prehistoric peoples, the Archaic peoples of the Great Lakes are of considerable interest. Their remains furnish evidence of a subsistence mode in which health (the relative absence of chronic disease or infirmity) was relatively good, yet life expectancy was low and traumatic injury was far more common than infectious disease.

The Archaic stage in this part of North America (considered here as ca. 7000-3000 B.P. after Wright, 1972) is a period of low population density. Seasonal exploitation of a wide range of biotic resources precluded permanent habitation. These factors, few people and frequent movement, have a negative effect on archaeological evidence. We know very little about the peoples' daily encampments or their normal tool kits. Burials from this time period are especially important, then, for the information that they provide cannot be verified from other archaeological sources.

The material being discussed here is derived from nine Archaic burial sites, with dates ranging from ca. 4500 to 2900 B.P. (Fig. 1). They include the following site samples, with number of pathological cases and total sample size in brackets:

From Quebec: Morrison's Island and Allumette Island (2 of 33);

From Ontario: the Hind sites (1 of 26);

From New York State: Cole (3 of 16) and Frontenac Island (20 of 100);

From Michigan and Wisconsin: Oconto (7 of 48), Osceola (0 of 12), Reigh (3 of 45), and Riverside (2 of 40).

These samples include the remains of at least 320 individuals, though many of the site samples are very small and fragmentary. There has been biased collection at some sites. From Frontenac Island, for example, a sample of 100 partial individuals includes over 40 crania, only 20 humeri, and almost no very young material. A further complication of analysis is cremation. Up to one half of all the deceased were cremated at some Archaic sites.

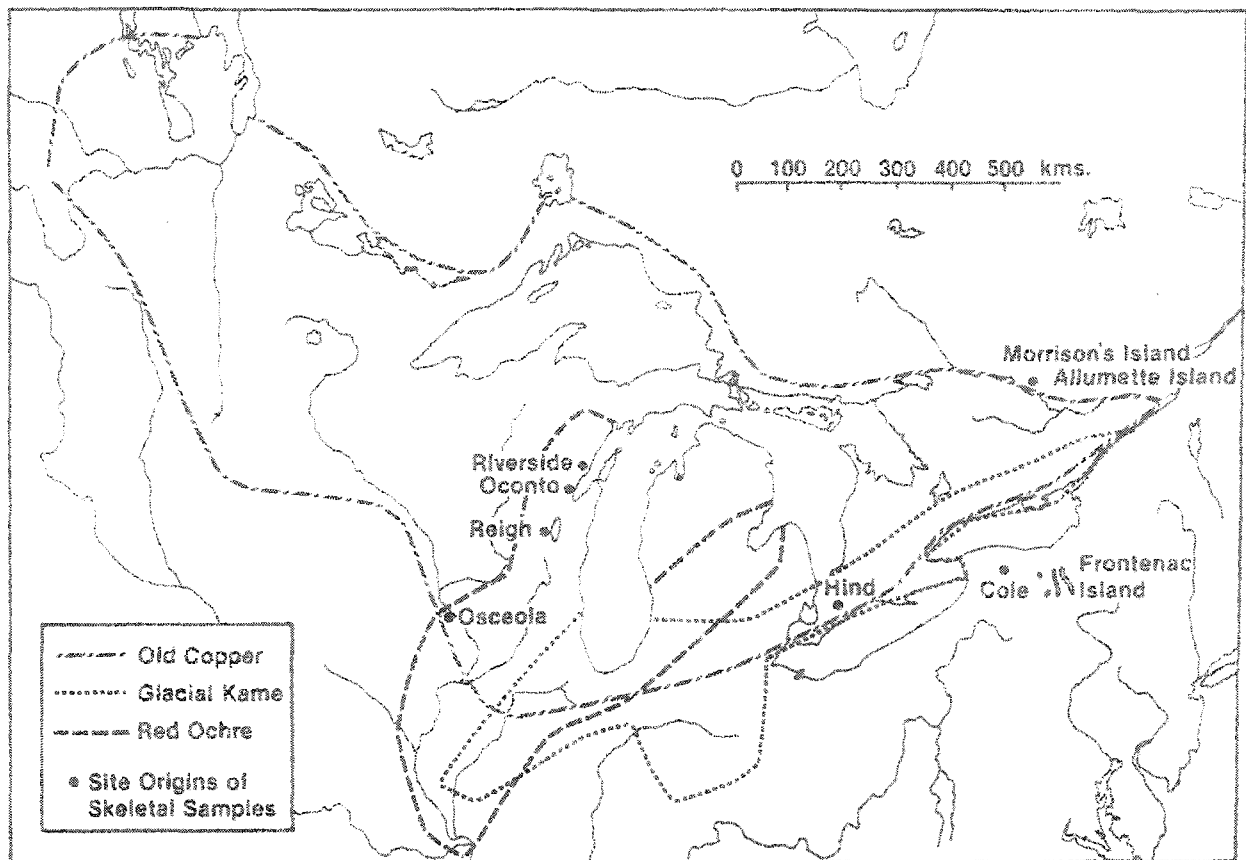


Fig. 1 Map of the Great Lakes region indicating locations of samples used in this study.

This discussion will be limited to skeletal features that were debilitating to the individual. Skeletal anomalies are not included. The reader is referred to Pfeiffer (1974) for individual case descriptions. Results are expressed in percentage terms, but even this simple statistic may be misleading due to the fragmentary nature of many samples.

These 320 individuals include 38 cases of pathology (11.9%), and all are from adults. This is explained at least in part by the biased demographic composition of the remains. The majority of the cases noted appear to have been traumatic in origin. At least 28, and possibly as many as 32, of the cases appear to be linked to trauma; an incidence of approximately eighty per cent. Those cases that cannot be linked to trauma include one congenital disability (dwarfism), two of nutritional origin (cribra orbitalia and related traits), one possible soft tissue tumor, one possible metastasized carcinoma (Ritchie and Warren, 1932), and one gummatous infection (Figure 2).

Various regions of the body are affected by trauma, but in certain samples patterns of location and appearance are apparent. In the Oconto sample the characteristic pattern is inflammation of the anterior tibiae. In the Frontenac Island sample, the most commonly affected area is the cranium.

Oconto

Four of the seven pathological cases from the Oconto sample involve trauma to the anterior tibia. Two specimens are from young males and two specimens are from adults of undetermined sex. Most frequently the injury is limited to the distal half of the shaft. It is tentatively suggested that these injuries may be related to the use of wood-working tools, especially the adze. No adzes are reported from the Oconto site (Ritzenthaler and Wittry, 1952, 1957), but it is thought that the Old Copper and Boreal Archaic cultures possessed the adze in their tool kit (Quimby, 1960). The location of the injuries could be thus explained. If an adze were to slip during use, it could produce just such a blow.

Frontenac Island

Seven of the pathological cases here involve trauma to the cranium. No other Archaic site yielded any cases of cranial trauma. Of the seven affected individuals, four are female, two are male, and one is of undetermined sex. Location of the wounds is characteristically on the frontal or parietal. The right and left sides are affected with equal frequency. Only one individual sustained damage to the occipital region.



Fig. 2 Cranium of a young male showing gummatous osteitis of the frontal and the inferior border of the left orbit. None of the extant intracranial material shows any sign of abnormality. Hence, it is unlikely to be a treponemal condition like syphilis.

W.R. Ritchie published the original site report in 1945. In that report he summarized the skeletal pathology as follows:

While traces of disease on the skeletons from Frontenac Island were fewer than might be anticipated considering the amount of material, the incidence of traumatism seems abnormally high. There are two classes of these lesions, fractures produced, in the main, probably by accident; and wounds, some consisting of skull-fractures, seemingly for the most part received in combat. Only skeletons of male individuals exhibit wounds, while fractures are about equally distributed between the sexes. Taken as a whole, the data indicate an active group involved in warfare (1945:12).

Upon a second analysis of the skeletal material (my own), it appears that this argument should be slightly modified. It does not appear that only males suffered cranial wounds. Based on my own independent assessment of sex, over half of the "victims" are female. It is interesting that the sex assessments differ so frequently here. Taking the site as a whole, my assessments differed from Ritchie's very rarely. One of the affected crania was complete enough to include in a statistical sexing exercise, using discriminant function analysis. The probability of its being female is quite high. Of course the possibility of both sexes being equally affected by cranial trauma does not rule out the possibility of warfare.

DISCUSSION

Indeed, it seems that the practice of warfare would help explain at least two factors: (1) the prevalence of blows to the head at Frontenac Island, where none are found at any of the other Archaic sites, and (2) the nature of certain wounds. In one case, the fractured region of the skull is a neat rectangle. In two other cases, fragments of stone remain embedded in the bone. At least these three wounds indicate the use of weapons (Figure 3). Several of the other cranial wounds might be classifiable as trephinations if there were some evidence of cutting, scraping or grinding on the outer surface. There is no such evidence.

A further observation concerning injury to Archaic peoples is that individuals occasionally survived multiple injuries. Two cases illustrate this especially well. A female from the Oconto site suffered from fractures of the clavicle and ribs, none of which healed cleanly. There is no indication that these factors contributed to her death. Similarly, an adult male from the Cole site sustained at least five broken bones plus the loss of his entire maxillary dentition (Figures 4,5,6). The breaks affect the left tibia, fibula, radius and at least two ribs. The fact that at least one of these breaks is a green-stick fracture indicates that injuries were sustained many years before death. This large, robust male survived to be the oldest individual interred at the Cole site.

Observations of pathological conditions contribute most to our understanding of human prehistory when they are examined in a context of general health status. Such an examination of these Archaic gatherer-hunters indicates several distinctive features.

Osteo-arthritis is mild in its expression and is less common than in some later horticultural groups. Total fre-

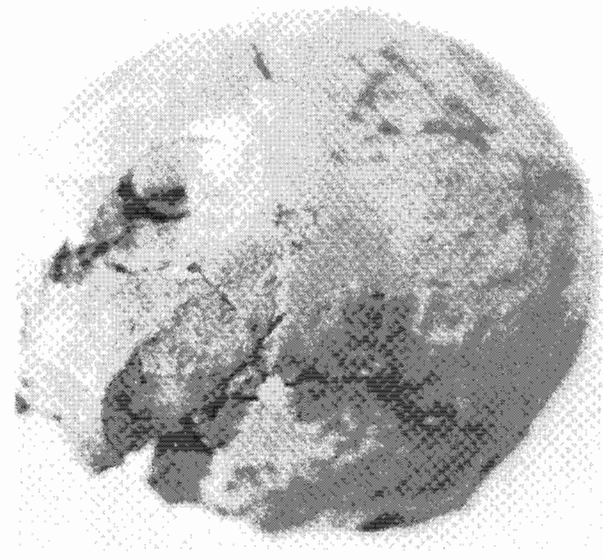


Fig. 3 Cranium of an adult male showing a depressed skull fracture on the left half of the frontal bone, apparently caused by a blow from a rectangular instrument. The inner table of the skull bends inward, but is intact.

quency of expression for Archaic right femoral condyles, for example, is 35-40%. The comparable figure for a proto-historic horticultural group (Kleinburg) is 56-61%. As with later populations, Archaic groups show more change to joint capsules on the right side of the body than on the left, and males show more arthritic involvement than females – perhaps because they lived longer. Arthritis of the temporomandibular joint, however, is 5% more common in females (20% vs. 15%) and this joint damage is severe one third of the time (no severe cases are seen among males).

Tooth wear is marked among most age groups. It is difficult to compare wear data across research studies because of the application of different quantification schemes. Using the 0-4 scheme of Broca, the Archaic deciduous dentitions can be compared with those of East Greenland Eskimo children (Davies and Pedersen, 1955). The six to eight year old Eskimos average around 1.8, while the Archaic group scores near three. Among adults one most commonly sees a heliocoidal occlusal plane and advanced cusp obliteration by early adulthood. There is no sex difference in attrition. At the Reigh and Frontenac Island sites, considerable pre-mortem enamel chipping may indicate nut cracking or some similar habitual activity. Caries are rare and are associated with wear-related abscessing.

Cortical bone remodeling has been explored with one Late Archaic sample. Femora of the six complete adults from Hind were thin-sectioned and aged using the Ahlqvist and Damsten technique of age determination (1969). Ages based on cortical remodeling correlated well with pubic symphysis-derived ages, though the remodeling ages tended to be older (Pfeiffer, 1980). The cortices of the femoral midshafts were thinner than Caucasians of

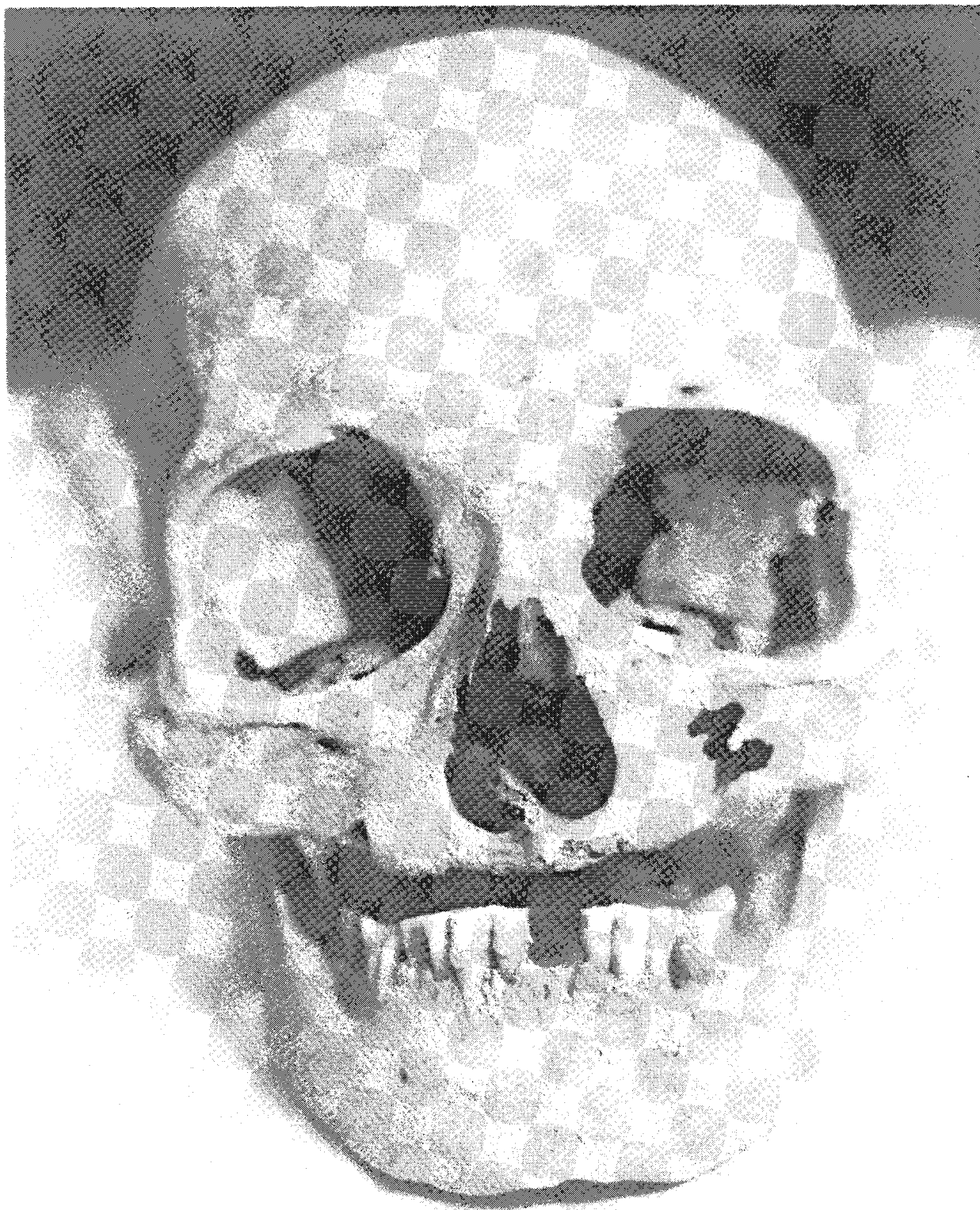


Fig. 4 Cranium and mandible of a male, aged 45-50 years demonstrating an edentulous maxilla and almost complete mandibular dentition. (This mandible was articulated *in situ*.) Wear on the mandibular teeth is even and pronounced. Five intracranial healed fractures are also present.

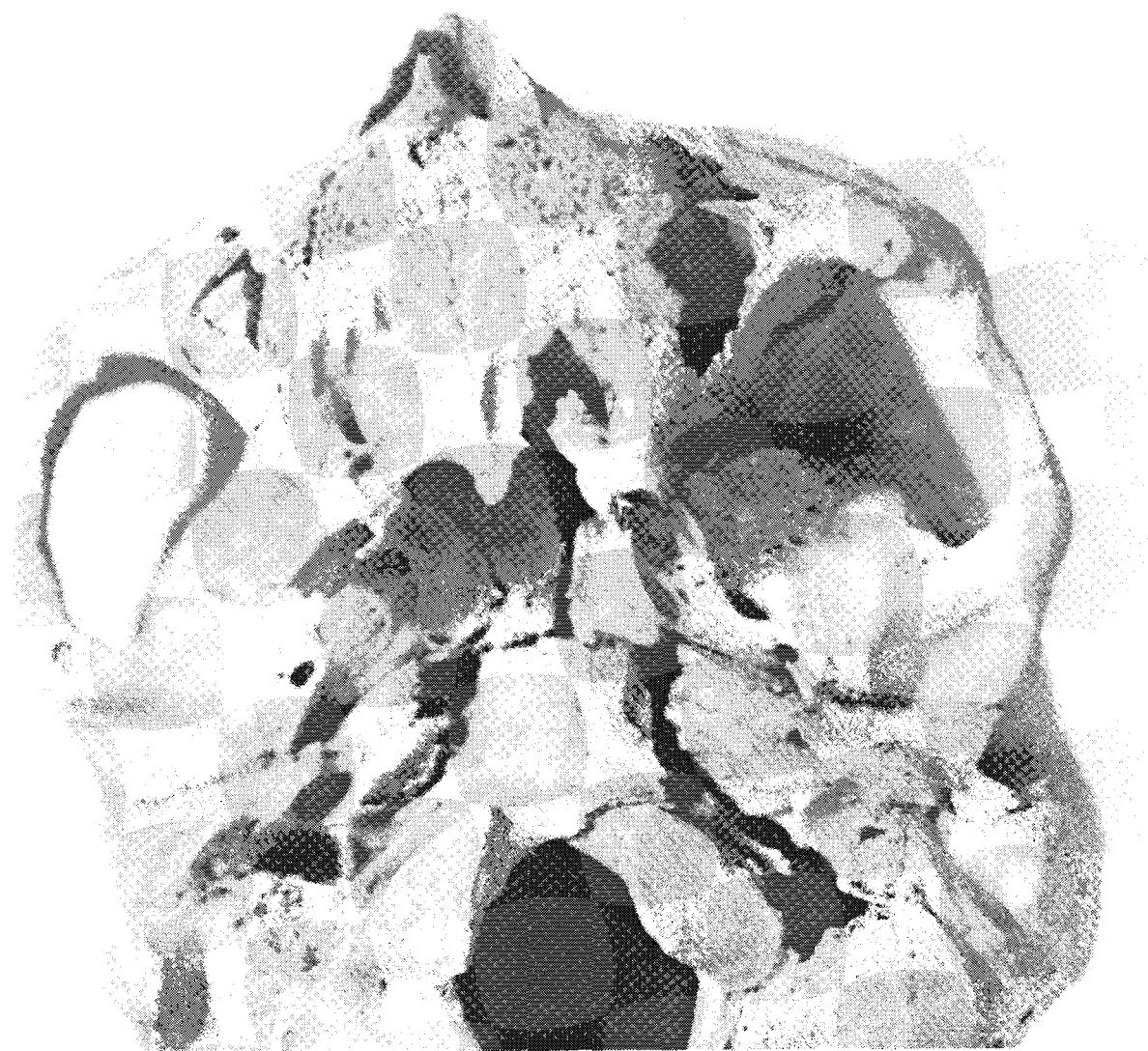


Fig. 5 Inferior view of the maxilla from the male of Fig. 4. Note the flatness and absence of evidence for recent alveolar resorption.

comparable age, some to a marked degree. Two of the six adults, all under 50 years, fall into an "osteoporotic" category using Barnett and Nordin's femoral index (1960). This may be a racial difference, or the over-ageing and the cortical thinning taken together may be the result of some chronic nutritional or activity factor.

To generalize rather broadly, I propose that analysis of remains from these nine Archaic burial sites adds cre-

dence to certain apparent temporal trends in health status. As we approach the earliest inhabitants of the Great Lakes region, the frequency of infectious disease decreases, arthritis decreases in incidence and severity, evidence of muscular robusticity increases (though not necessarily bone density), and dental wear increases with a concomitant decrease in caries.

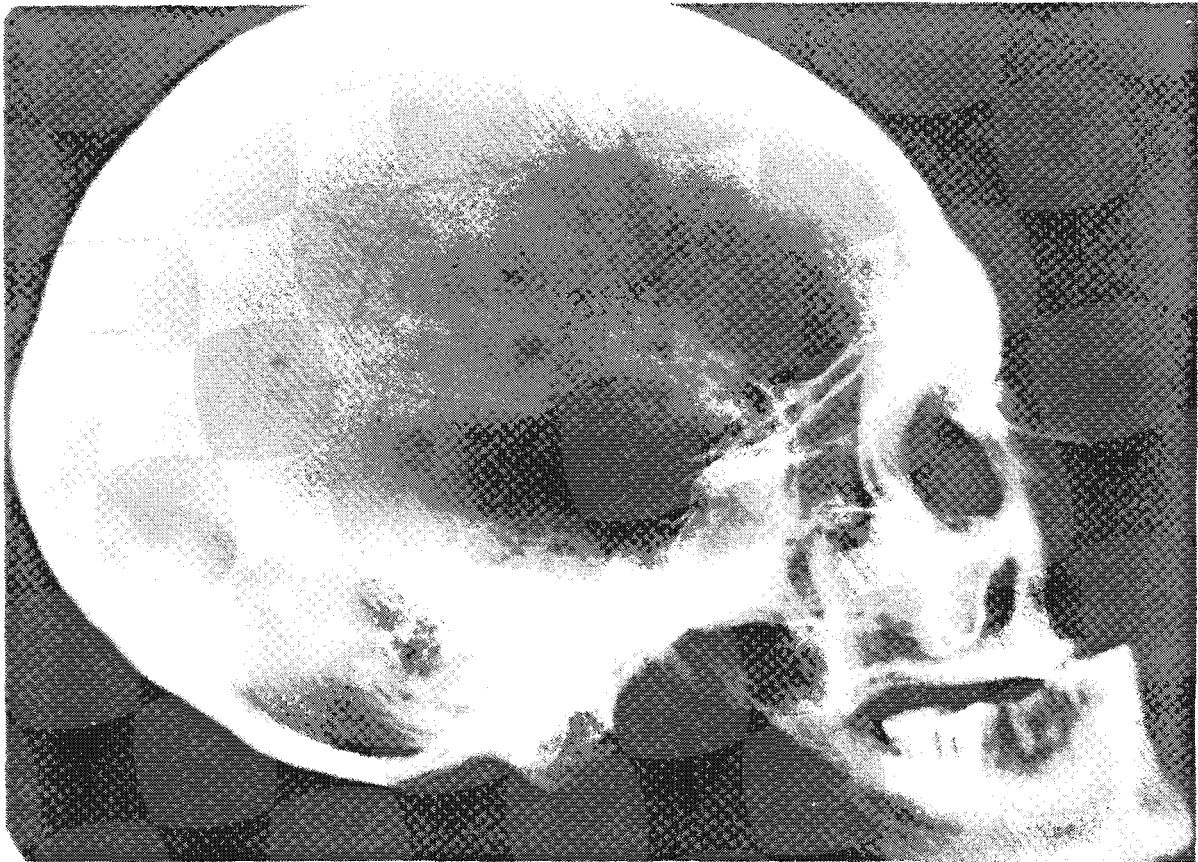


Fig. 6 Lateral radiograph of the cranium and mandible of Fig. 4. There is no evidence of maxillary dental material. Regions of mid-parietal bone thinning, not apparent on gross examination, may be indicative of some systemic disorder.

NOTES

1. A version of this paper was presented at the 147th annual meeting of the American Association for the Advancement of Science, Toronto, Ontario, 1981.

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PALAEOPATHOLOGY OF THE ONTARIO IROQUOIS¹

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Abstract: Most categories of pathology occur in relatively high frequency in skeletons of the horticultural Iroquois of prehistoric Ontario. The "burden limit" theory is invoked to account for this phenomenon.

Résumé: La plupart des catégories pathologiques apparaissent en fréquences relativement élevées parmi les squelettes des Iroquois horticulteurs de l'Ontario préhistorique. La théorie du "fardeau limite" semble pouvoir expliquer ce phénomène.

Key Words: Palaeopathology, Archaic, Iroquois, Burden Limit Theory.

Horticulture is a relatively rare phenomenon in Canada in prehistoric times. While this appears to be a patently obvious observation because of the climate, there are some further implications. Domesticated plants and technology had to achieve a certain level of sophistication before horticulture could be introduced. That level was clearly achieved by A.D. 900. Admittedly, it was introduced at an incipient level slightly earlier, but by A.D. 900 we have horticultural villages established which are increasingly dependent upon domesticated plants. This period has been named the Ontario Iroquois Tradition, and has a continuous development until about A.D. 1650. The Ontario Iroquois, therefore, are of particular interest to us because they represent the most northern occurrence of horticulture in prehistoric North America.

In general, their adaptation included rather large villages of about 1000 people. These villages were semi-permanent in the sense that they had to be relocated about every ten years as the soil and local resources became exhausted. Villages were prone to fusion and fission along internal, familial lines which cross-cut the village structure. As the population became denser, there is evidence that warfare increased between villages. One can easily speculate that the ultimate cause was competition for preferred farming locations and local resources. Probably, the people had a nutritionally adequate diet. Katzenberg (1983) has suggested that the usual maize deficiencies were supplemented with meat, fish, squash, and beans. However, their carbohydrate intake was certainly higher than previous northern populations.

Sedentism has a significant effect on pathology. Almost every pathology has an increased probability of being sustained for a longer period of time. For example, any debilitating pathology can last longer and be more serious without terminating the affected individuals. Society can afford a larger burden of non-productive members who have to be cared for. All societies (including our own) have a "burden limit" at which point affected persons are allowed to terminate. There are many instances of recognition of this on a specific level. For example, Anderson (1967) first noted the significance of the ab-

sence of healed fractures of the lower limb amongst hunting and gathering groups. A society whose subsistence demands constant movement cannot afford the burden of individuals who are unable to move with the group. The burden limit theory would arrange these societies in a continuous hierarchy based upon their capacity to sustain healed fractures. Note that this is an entirely different phenomenon from a society's propensity to receive fractures in the first place. If various forms of pathology are at a constant rate (and, of course, they rarely are), then we will expect a regular increase in the "burden limit" as food production and technology become more complex. The net result in the above example will be that the advanced society will appear to have more fractures because most of our frequencies are based on counts of healed fractures; however, it may be experiencing relatively fewer fractures than the hunting and gathering society.

Also, infections will appear to occur more frequently and more severely, because infections are sustained for longer periods of time by the advanced society. Degenerative diseases will appear to increase; though, in fact, we simply have more old people living longer. Tumors, congenital disturbances, or other possible disfigurements could more readily be accepted in a diverse society than in a simple, hunting society.

In other words, the burden limit theory suggests that all forms of pathology have a better opportunity of being represented in terms of number of cases and in terms of severity. The quantification of the burden limit for a society is not within the scope of this paper. Indeed, it may not be possible to quantify on the basis of our present knowledge. As a working hypothesis, however, it points to a major source of error in comparing populations. We are probably more justified in making comparisons among the Maritime Archaic, the Laurentian Archaic, and the Central Plains Archaic because they probably have fairly similar burden limits on their societies. The west coast of Canada has long been recognized as unique. The lush environment provided one of the most advanced cultures that a hunting and gathering economy has ever produced.

Indeed, many similarities to the Ontario Iroquois can be observed such as village size, long houses, permanence, clans, and warfare. It is difficult to weight these against an entirely different food base, climatic variation, and a completely different technological base. I would speculate that the burden limit is fairly similar between the West Coast and the Ontario Iroquois peoples. Perhaps a better judgment will emerge. The following generalizations about pathology amongst the Ontario Iroquois will, perhaps, place them in a new perspective:

Congenital Disturbances

Defects of inadequate or excessive bone production are relatively rare in all populations whether historic or pre-historic. However, it is clear that there are more defects, quantitatively and qualitatively, than any population presented in this symposium. Cases of congenital absence, bifid ribs, congenital fusions, vertebral body defects, numerical variation in vertebrae, spina bifida and spondylolysis are not common. We even have rare cases of cleft palate and epiphyseal dysplasia. Now, how can we explain this? Are the Ontario Iroquois genetic misfits? Obviously not. Is it simply sheer quantity of bones that increases the possibility of finding such defects? I think not. If you measure just one Ontario Iroquois ossuary (Kleinburg) against all the Archaic populations in Canada, the Iroquois still have more defects. The simplest explanation is that the burden limit for congenital defects is significantly higher for the Ontario horticulturalists than any of the previous populations.

Trauma

Again, there is a great deal of evidence of traumatic disturbances. Trauma attributable to violence such as foreign bodies embedded, wounds, and parry fractures is common. Trauma attributable to accidental mishaps such as a wide variety of fractures, dislocations, and secondary reactions are equally common. We even have some trauma attributable to surgical intervention such as amputation (questionable) and trephination. Cosmetic trauma such as cranial deformation or dental alterations are absent. This latter feature is a significant distinction from the West Coast populations. However, the higher incidence of trauma – especially healed trauma – is undoubtedly due to a much higher burden limit for the Ontario Iroquois. It is interesting that trauma is still quite common in Archaic populations. This may infer that people in Archaic populations were receiving relatively more trauma even though the actual frequencies are lower.

Infection

Non-specific infections seem to be common in all populations from Archaic to horticultural. Obviously, the burden limit theory would account for a somewhat higher observed frequency in the more advanced societies. Two specific infections appear for the first time in the horticultural villages – syphilis and tuberculosis.

Degeneration

Osteoarthritis and osteophytosis in one sense are not pathological because they are the result of natural wear through aging. However, they are pathological in the sense that they are debilitating conditions whose onset is largely dependent upon the daily rigours of the society. Recent studies have suggested that hunters and gatherers have more leisure time than horticulturalists. The current state of the art of palaeopathology is not prepared to add information to this area. Until we can very accurately age adults, studies of degeneration will tell us little more than that degenerative disease is more common in old people than in young people. A fine analysis of aging and demography is being conducted by Norman Sullivan (1983) at the University of Toronto.

Endocrine and Metabolic Disturbances

These are so rare that I cannot make any generalizations. Among the Ontario Iroquois there is some slight evidence of rickets (vitamin D deficiency) and slightly more evidence of iron deficiency. Studies of palaeonutrition through trace element analysis by Katzenberg (1983) and through carbon and nitrogen isotopic analysis by Schwarcz *et al.* (1983) are quite promising.

Tumors

These are very rare. A few primary and secondary tumors are present, some of which must have disfigured the persons greatly. This, along with the cleft palate, suggests to me that the burden limit for physical disfigurement must have been outstanding among the Ontario Iroquois.

Dental Pathology

This is perhaps the only area where the proposed burden limit theory does not apply. Though one could argue that advanced societies could sustain morbid dental conditions longer, I am unwilling to push the theory that far.

Diet is the main cause of pathological variations in Ontario Iroquois teeth. The high carbohydrate intake is indirectly responsible for the high caries and high periodontal rates.

Attrition is slighter – probably due to softer foods with less grit. An analysis of dental pathology has been completed by Patterson (1982).

CONCLUSION

That is the general picture of pathology among the Ontario Iroquois. There is a great deal to be learned from their skeletal remains. The studies currently underway are but the beginning of a bright future for Ontario palaeopathology. I hope to encourage these studies to fill the gaps in current knowledge of how humans adjust to new problems as their culture progresses. Comparisons, however, should be tempered by consideration of comparable pathology burden limits imposed by the technological advancement of a given society.

NOTES

1. A version of this paper was presented at the 147th annual meeting of the American Association for the Advancement of Science, Toronto, Ontario, 1981.

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COMPARISON OF ADULT AGE ESTIMATION TECHNIQUES, USING AN OSSUARY SAMPLE

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Abstract: Three techniques of adult age estimation were applied to a skeletal population from the Kleinburg Ossuary (southern Ontario, ca. A.D. 1600, N=561). Age at death was estimated by assessment of pubic symphysis remodeling (N=89), and by assessment of femoral cortex remodeling following the techniques of Ahlqvist and Damsten (1969) (N=112) and Thompson (1978) (N=82). Results from the three techniques are not compatible. Differences between the three age distributions are all statistically significant. Pubic symphysis age estimates are youngest, femoral ages derived from the Thompson technique are oldest. It is argued that none of the techniques is clearly superior for a sample of this type. Poor slide quality may have had a substantial effect on the histological results. More research is needed to explain variability in the underlying mechanisms of remodeling.

Résumé: Trois méthodes pour évaluer l'âge adulte ont été appliquées à la population de l'ossuaire de Kleinburg (sud de l'Ontario, environ 1600 après J.-C., N=561). On a pu évaluer l'âge de la mort en se basant sur le remodelage de la symphise pubienne (N=89) et sur le remodelage du cortex fémoral d'après les méthodes d'Ahlqvist et Damsten (1969) (N=112) et de Thompson (1978) (N=82). Les résultats des trois méthodes ne sont pas compatibles. Les différences entre les trois distributions d'âges sont statistiquement significatives. Les évaluations basées sur la symphise pubienne sont les plus jeunes, les âges basées sur le fémur, d'après la méthode de Thompson, sont les plus anciens. Il est permis de penser qu'aucune de ces méthodes n'est nettement supérieure pour un échantillon de ce genre. La pauvre qualité des lamelles a pu avoir un effet important sur les résultats histologiques. De plus amples recherches sont nécessaires afin d'expliquer la variabilité dans les mécanismes responsables du remodelage.

Key Words: Age Estimation, Osteon Ossuary, Pubic, Symphysis.

Application of an accurate and reliable age estimation technique is very important to any analysis of skeletal material. Because of the cumulative nature of functional variability, adulthood poses greater problems of age estimation than does childhood. Assessment of the pubic symphysis is the most commonly used technique of adult age estimation, but newer techniques of cortical remodeling assessment appear attractive (Kerley, 1965; Ahlqvist and Damsten, 1969; Singh and Gunberg, 1970; Thompson, 1978). They are based on the principle that bone tissue is continuously turned over at a regular rate during the life span. Because they require samples of long bone cortex instead of delicate pubes, sample sizes can be larger and elderly (osteoporotic) individuals are more likely to be represented (Ubelaker, 1974). Sex and par-tuition are not of concern, as they are with pubic symphysis assessment. The cortical assessment techniques are, however, more expensive and require specific technical skills. Their relative analytical value needs to be quantified before they will be more broadly applied.

This study compared the results of three estimation techniques applied to one ossuary population. From this comparison, none of the techniques can be recommended unequivocally.

MATERIALS AND METHODS

The material examined is from the Kleinburg Ossuary sample. The Kleinburg Ossuary, (AlGv-1) Kleinburg, Ontario, was excavated in 1970 by F.J. Melbye and D. Knight. It is an Iroquoian ossuary dating from approximately A.D. 1600 based on analysis of trade goods (Melbye, personal communication). Its specific cultural affiliation remains undetermined. A minimum of 561 individuals is represented: 157 subadults and 404 adults.

An initial demographic study of the Kleinburg people was reported in 1974 (Pfeiffer, 1974; Saunders, 1974). At the time model life tables were constructed, using juvenile age estimates based on dental emergence and adult age estimates based on pubic symphysis remodeling. Saunders used the techniques of McKern and Stewart (1957) for evaluating male pubes and Gilbert and McKern (1973) for evaluating female pubes. Total sample size for individuals over twenty years of age is 89. The present study again uses Saunders' pubic symphysis-derived adult ages, and compares them with ages derived from more recent assessments of femoral cortical remodeling.

The Ahlqvist and Damsten (1969) and the Thompson (1978) techniques of age determination were used to eval-

uate undecalcified thin sections derived from left femora. Approximately three hundred left femora were complete enough to be sampled. After a C-shaped bone specimen was removed, it was de-greased for twenty-four hours in trichloroethylene, sonicated, oven dried and embedded in an ultra-low viscosity epoxy-type embedding medium. Although embedding is sometimes an optional step, it can be very important for many samples, such as this one.

The final age determination relies on assessment of sample sites along the periosteal surface. This surface will flake off these specimens at any and all stages of slide preparation if the specimens are not embedded. After embedding, the sample was glued onto a glass slide for mounting on the vacuum chuck of an Ingram thin-sectioning saw. The cut surface of the cube was ground and polished, the specimen was again cleaned and dried, and the prepared surface of the cube mounted on a large glass slide. The mounted cube was then cut on the thin sectioning saw to a thickness of 800 - 100 μ . The cut surface was ground and polished and the specimen cleaned and dried again. The completed slides have a final thickness of 50 - 80 μ . This process takes approximately two hours per slide.

One apparently unique problem with the Kleinburg bone is the presence of intrusive iron. Probably absorbed from deteriorating iron ax heads, this iron frequently leaves a gold-colored residue along the periosteal and endosteal surfaces. Besides obscuring histological structures, the iron has the deleterious effect of creating areas of differential hardness. The iron problem, plus initial problems with the embedding medium, reduced our sample size from a potential 300 to 112.

The prepared slide is examined under polarized light at a magnification of 100x. For the Ahlqvist and Damsten technique (1969) a 100-square grid is superimposed on the field such that it covers an area of one square millimeter of the bone surface. One side of the grid is laid along the periosteal surface. The researcher then counts how many squares are more than half filled with remodeled bone. This procedure is repeated at three more sites equally spaced around the perimeter. A percentage remodeled figure is then calculated. This percentage is entered into a regression formula to estimate age at death. Reassessments of the same bone section (not exactly the same fields) by the same researcher show a correlation of $r = .80$ ($N = 10$).

For the Thompson technique (1978, 1979), only the anterior portion of the slide is observed. Four contiguous fields are assessed, using the same grid, but a point-

counting technique. Values for relative secondary osteon area and Haversian canal area are used in a regression formula to estimate age at death. The same undecalcified thin sections were evaluated, using these two techniques. Because the most anterior portion of the cross-section was not always suitable for quantification, the sample size applied to the Thompson technique is reduced from 112 to 82. Reassessments of the same bone section (not exactly the same fields) by the same researcher show a correlation coefficient of $r = 0.75$ ($N = 8$).

RESULTS

The three distributions of adult ages at death are indicated in Table 1. These figures have been used to construct the survivorship profiles shown in Figure 1. The three age profiles are clearly different from one another. The two cortical assessment techniques yield older ages. The oldest individuals from each of the three techniques are "36+" (pubic symphysis), 54 ± 6.71 years (Ahlqvist and Damsten), and 75 ± 8.64 years (Thompson).

The relative distribution of individuals from ages 20 to 45 years (ages represented by all three techniques) was tested using log-likelihood tests of independence (Sokal and Rohlf, 1969). The pubic symphysis age distribution ($N = 89$) is not significantly different from the Ahlqvist and Damsten age distribution ($N = 91$, $G = 3.7$, $df = 4$). When the older individuals from the Ahlqvist and Damsten estimates are added to the uppermost category, making it 40+ years, the two distributions do differ significantly ($G = 20.3$, $p \sim .005$). The pubic symphysis age distribution is significantly different from the Thompson distribution ($N = 44$ for ages 20 to 45 years; $G = 17.7$, $p \sim .005$).

The mean age for Ahlqvist and Damsten estimates is 33.4 years ($\sigma = 10.97$). The mean age for Thompson estimates is 41.9 years ($\sigma = 13.1$). Thompson age estimates are higher in 74% of the 82 pairs. The two femoral assessment techniques were compared with one another using linear regression. They show a statistically significant correlation of $r = 0.45$ ($df = 1.80$). However, only a very small percentage of the variance is explained by this correlation ($r = 20.65$). Examination of slope and intercept values indicate that there is slightly greater agreement between the techniques when ages are estimated at under fifty years than when ages are estimated at over fifty years. The paired age estimates fell within eight years of one another (roughly one standard error) in only 36 cases out of 82.

TABLE 1
Results of Age estimation techniques applied to the Kleinburg sample.

Age Estimation Technique	Age Categories											N	
	15-20	20-25	25-30	30-35	35-40	40-45	45-50	50-55	55-60	60-65	65-70		70-75
Public Symphysis*		5	27	38	8								89
Ahlqvist & Damsten		19	20	36	8	8	13	8					112
Thompson	5	3	7	9	13	12	11	11	2	5	2	2	82

*McKern and Stewart (1957) for males, Gilbert and McKern (1973) for females.

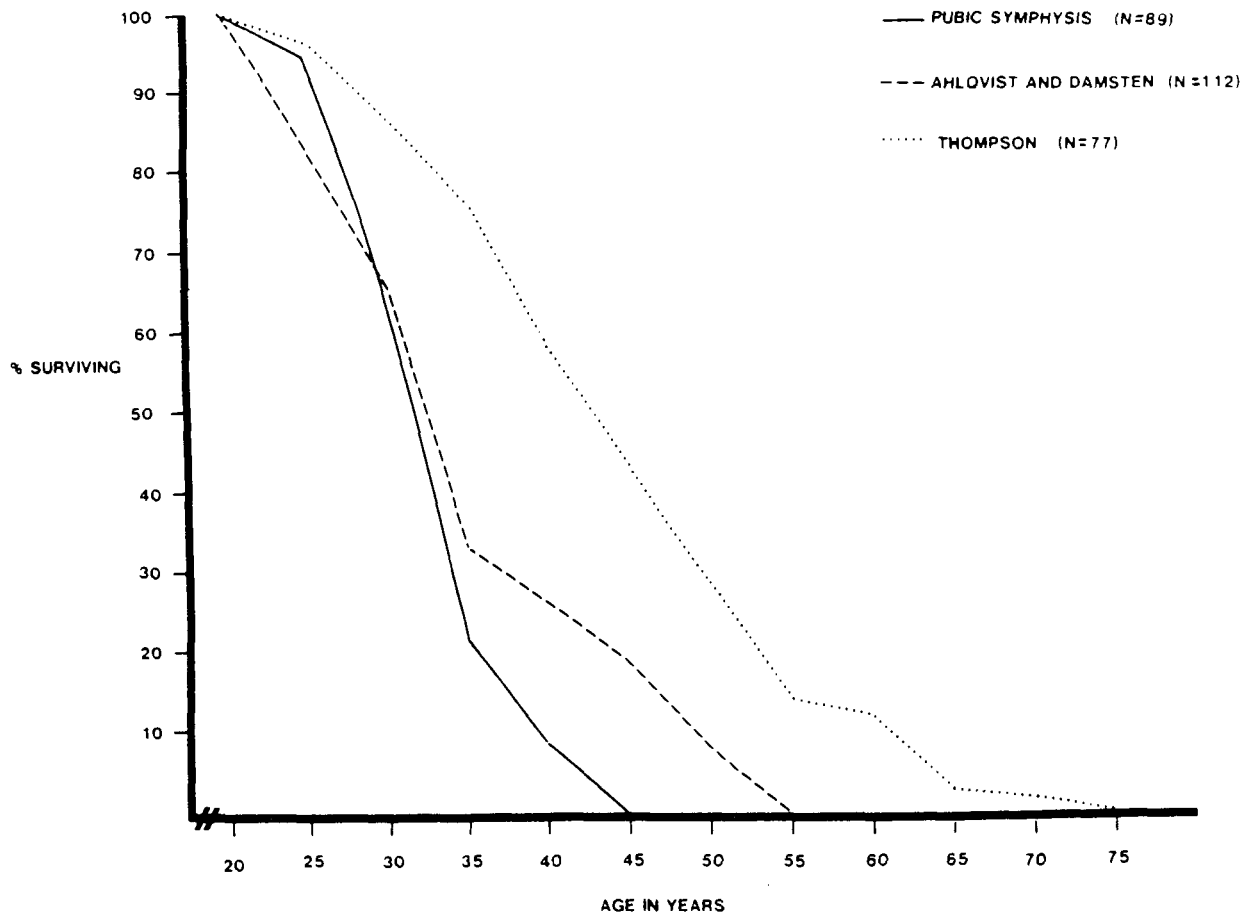


Fig. 1 Survivorship profiles for adults from the Kleinburg Ossuary. The three lines reflect the results from three different techniques of adult age determination.

DISCUSSION

Two conclusions of this study are that not all skeletal samples are physically suited to histological research, and that there is much to be learned about the accuracy of age determination techniques when they are applied to prehistoric samples.

The presence of intrusive iron in the Kleinburg sample added time and expense to the slide preparation procedure. It had a negative influence on the final slide quality, which in turn may have affected the age estimates. The presence of such elements should be added to the list of factors which negatively affect histological research on archaeological bone (cf. Stout, 1978; Stout and Simmons, 1979; Buikstra and Cook, 1980).

The pubic symphysis-derived ages yield a very short survivorship curve. Everyone is dead by age fifty years. Such a demographic profile, though commonly presented in the ossuary literature, is hard to believe. Such a society would include very few grandparents and many orphans.

It has been recognized that cortical remodeling age estimation techniques will yield higher age values than examination of pubic symphyses, ostensibly because the older more osteoporotic pubic symphyses are not preserved (Ubelaker, 1974). This interpretation would be compatible with the present study, insofar as the Ahlqvist and Damsten age distribution is not significantly different from that of the pubic symphyses up to age 45 years. There is then a tail of 21 more femoral samples over age 45 years.

The cortical remodeling techniques may also yield more older ages because of inherent shortcomings in the pubic symphysis technique. The pubic symphysis reference populations tended to be young, and so there was little differentiation of "aged" pubic symphyses. For example, the upper age category for the McKern and Stewart technique is "36+". Suchey (1979) has noted the inaccuracy inherent in application of the Gilbert and McKern (1973) method. Her results demonstrate random

rather than systematic error, however. These factors are probably not sufficient to explain the magnitude of difference seen in the Kleinburg estimates. They also do not explain the disparities between the two techniques based on cortical remodeling.

When compared for precision and accuracy, the Ahlqvist and Damsten technique did not compare favourably to the Kerley technique (Bouvier and Ubelaker, 1977). Unfortunately, the Kerley technique requires a very high quality slide of a section that includes the *linea aspera* region, so we could not apply it to the Kleinburg sample. The Ahlqvist and Damsten technique was compared to pubic symphysis ages on a small Archaic sample with results that were marginally satisfactory (Pfeiffer, 1980; Martin, Goodman and Armelagos, 1981; Pfeiffer, 1981). It is the opinion of the author and of technicians working on this project that the Ahlqvist and Damsten technique has a large subjective element regarding what constitutes a grid square more than half filled with remodeled bone. This factor probably has a deleterious effect on replicability.

The Thompson technique, while no more replicable in this study, seems less subjective and is faster to use. It appears to be functioning well in forensic cases. It did, however, yield older age estimates than gross morphological methods when applied to various Eskimo samples (Thompson and Gunness-Hey, 1981; Thompson, Salter and Laughlin, 1981) just as it did in the present study. Thompson has argued that population-specific norms must be established. It remains to be seen whether Amerindian remains will be amenable to Eskimo norms, or whether they, too, will show a unique pattern of remodeling. The Thompson technique does not include osteon fragments in the assessment of percent remodeled bone. The poor slide quality sometimes made osteon reversal lines difficult to distinguish. This may have caused inclusion of fragments and contributed to older age estimates.

This study of adult age at death estimates in the Kleinburg sample concludes with three survivorship profiles, none of which can be accepted as true. It would, perhaps, be helpful to have more studies comparing age estimation techniques on samples of known age. However, unless these samples share some genetic or environmental similarities with prospective anthropological samples, this approach will be of limited usefulness.

Evidence has been accumulating that lifestyles factors and genotype may influence not only cortical thickness, but also adult remodeling of cortical bone (cf. Richman, Ortner and Schuller-Ellis, 1976; Perzigian, 1973; Garn, 1970; Ortner, 1970). Perhaps the most fruitful approach to choosing an accurate adult age estimation technique will be to learn more about the response of bone as a tissue in epigenetic interaction, and then proceed accordingly.

ACKNOWLEDGEMENTS

I wish to thank Dr F.J. Melbye of Erindale College, University of Toronto, for access to the Kleinburg sample. Preparation of the thin sections benefitted from the efforts of Dr. Portia Lynn and Ms. Patricia King. This research was funded by a grant from the Social Sciences and Humanities Research Council of Canada.

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PRINCIPAL COMPONENTS ANALYSIS: ITS USE IN MULTIPLE INFORMATION REDUCTION ¹

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Abstract: Sometimes in the study of phenomena that take the form of multiple repetitive risks, it is rather difficult to synthesize the whole phenomenon in a single dimension. Principal components analysis can help us overcome that difficulty. We applied it to two tests in order to draw one or two dimensions from the results. The first component corresponded to a general ability dimension of manual performance, and the second represented a dimension of bilateral asymmetry. We subsequently tested these two dimensions by other analyses in terms of sex and hand preference. We found differences in terms of the sex and of the preferred hand on one or the other dimension.

Résumé: La multiplicité des informations obtenues d'un test donné peut poser un problème tant dans l'analyse que dans l'interprétation des résultats. L'analyse en composantes principales nous permet de pallier à cette difficulté. Nous avons appliqué cette technique à deux tests dans le but d'obtenir une ou deux dimensions. La première composante correspond à une dimension d'habileté générale des performances manuelles et la seconde est indicative d'une dimension d'asymétrie bilatérale quant aux performances entre main gauche et main droite. Par la suite, l'analyse de ces dimensions a été faite en fonction du sexe et de la main prévalente. Il semble y avoir des différences entre les sexes et en fonction de la main prévalente.

INTRODUCTION

The application of multivariate statistical analysis is an attempt to reduce complex structures into simpler dimensions, susceptible to bear coherent meaning. In certain studies we are sometimes overwhelmed by the numerous data resulting from the chosen tests. It is subsequently quite difficult to underline common elements or to find specific structures. In seeking to circumvent this difficulty, we believe that principal components analysis offers interesting possibilities, being a statistical technique that reduces multiple and complex structures or relations into simpler components.

The problem then consists of interpreting the components obtained and attributing specific meaning to them which would explain the generality and particularity of the data. There remains a problem: these components, per se, cannot be tested. However, by computing a score or a composite value as a function of each component, these in turn can be tested. We analyzed these scores in terms of sex and hand preference.

The principal goal of this paper is to show the usefulness of principal components analysis where multiple information is encountered. Secondly, we are interested in identifying the configurations we have obtained for manual performance. Finally, we want to examine the possibility that there are differences in manual performance between the sexes and between left/right-handers and ambidextrous subjects.

MATERIALS AND METHODS

Principal components analysis is based on the existing relations between many variables, using either the covariance or the correlation matrices. In this paper we have chosen to deal with the correlation matrix (Overall and Klett, 1972).

This analysis extracts from the matrix as many components as there are variables in the matrix; each of these components in turn contains the same number of variables as the matrix. The relative importance of each component goes in decreasing order, the first having more than the second and so forth. Each component has a specific meaning which corresponds to a particular configuration or dimension. Consequently, we can give or compute a score for each individual. This possibility permits us to locate or classify an individual among others. This is widely used as a classificatory function to find taxonomic affinities in, for example, osteology (Jolicoeur, 1963), paleoanthropology (Andrews and Williams, 1973), or for biological, physiological or physio-pathological functions (Forest, 1975).

We have applied this statistical method to our two tests: a hand-tapping test and a written alphabet test (Provins and Cunliffe, 1972). The two tests are motor tasks and measure manual ability; both are constituted of many trials for the right and left hands. The procedure of these tests is quite simple. For the hand-tapping test, the subject must hit a key repetitively with one hand as quickly as

possible during a 30 second period. The strokes are registered continuously by a digital counter in ten-second units. This kind of activity seems infrequently performed by the subjects. The second test is the written alphabet test, in which the subject must write the alphabet from A to Z in detached letters as rapidly as possible. The test is repeated four times for each hand. The execution times are recorded by a chronometer, the resulting times at the end of each completed alphabet forming the original data. This is an activity which is widely performed on a daily basis by the preferred hand and much less by the non-preferred hand (Provins and Cunliffe, 1972). It is a more complex activity than the hand-tapping test and does not solely measure motor performance. It seems that for the written test, not only are motor performance and manual dexterity being measured, but memory of the alphabet and primary structure of the written language as well (Desjardins, 1980).

We analysed the data using statistical methods other than principal components analysis – the simple and multiple analysis of variance (Forest and Berthelette, 1980). Models pertaining to multiple analysis of variance have been discussed in a previous paper (Desjardins, 1980). It suffices to say that we tried to consider as many sources of variation as possible with a special interest in two criteria: sex and hand preference. The sample on which these analyses were made is composed of 144 undergraduate students in anthropology, with ages varying from 18 to 25. We assumed initially that the subjects were homogeneous with regard to their status, and did not expect them to differ much in terms of the measured functions.

RESULTS

The hand-tapping test (HT) is composed of a sequence of taps for each hand. The sequence is made up of three moments: 10, 20 and 30 seconds. The basic data have been transformed to a number of taps per second. As shown in Table 1, we have the mean (\bar{X}), the standard deviation (S_x) and the coefficient of relative variation (CV). For this test there are 117 observations. As Table 1 indicates, the means of the left hand are relatively lower on the whole than those of the right hand, which tends to point out the higher proportion of right-handers in our sample. It seems that for the majority of the subjects, the performances of the right hand are slightly faster than the ones of the left hand. We see that there is also a decrease in the number of taps in terms of the period. The mean

TABLE 1
Statistics of the moments of the hand-tapping test
(HT) (N=117)

Hand	\bar{X}	S_x	CV%
Left 10 sec.	6.32	0.91	14.36
Left 20 sec.	5.87	0.84	14.39
Left 30 sec.	5.55	0.80	14.32
Right 10 sec.	6.88	1.03	14.94
Right 20 sec.	6.57	0.90	13.74
Right 30 sec.	6.25	0.70	12.29

performance of the left hand for the first ten seconds is 6.3 and diminishes to 5.6 for the last ten seconds. The right hand has the same tendency, decreasing from 6.9 to 6.3. It seems that the mean performance of both hands tends to decrease similarly, but a simple calculation of differences between periods of one hand versus the other might indicate a larger decrease for the left hand. This may be explained in part by the proportion of right-handers and a greater endurance with the right hand than with the left. In terms of endurance, it seems that we tire less with the right hand than with the left, if we take into account the mean performances of both hands.

As we can see in Table 2, all the correlation coefficients are significantly different from zero. The correlations between homologues – that is, between the periods of one hand – are relatively higher than the correlations between hands. We also see that the correlations between homologues tend to decrease from 10 to 20 to 30 seconds. However, the coefficients between 20 and 30 seconds for both hands are slightly higher than the rest. This shows that we have a relative decreasing tendency between homologues and non-homologues.

We then proceeded with the calculation to obtain the components. We retained only the first and second components as shown in Table 3. They represent 85% of the information contained in the correlation matrix. These components are formed with as many coefficients as there are variables in the correlation matrix, as evidenced in Table 3. We organized these components in order of decreasing value.

The variance of the first component is 4.19, which represented 69.8% of the explained variation or information. This is a very large proportion of variation if we take into account the criterion of significance, which is usually $1/p \times 100$ of the total variance. The high percentage of the first component tends to show unity in the significance and the meaning of the obtained coefficients. As a matter of fact, they have the same polarity and the same amplitude. We can express them as follows:

$$1/\sqrt{6} (-1, -1, -1, -1, -1, -1)$$

in which the importance of each moment of HT (hand-tapping) is comparatively similar. In this sense, as other studies analyzing equivalent objects have shown, the first component reflects a tendency for all the variables to decrease (or increase) simultaneously (Jolicoeur, 1963). It is then assumed that the first component corresponds to a trend of size variation. In terms of motor activity, however, and considering the direction of the coefficients, it is a dimension of general ability expressed by the amplitude of the subjects' performances. Yet, we must add that it is also a dimension of tiredness where the level of performance is directly proportional to the level of physical endurance.

The variance of the second component in Table 3 is 1.03, which represents 17.1% of the information obtained from the residual matrix. It is a significant percentage of explanation of the variation if we consider the pertaining

TABLE 2
Correlation matrix of the moments of the hand-tapping test

Hand	L 10s	L 20s	L 30s	R 10s	R 20s	R 30s
Left 10s	1.0000	.8044	.7578	.6395	.5510	.5253
Left 20s	.8044	1.0000	.9285	.5162	.4887	.5584
Left 30s	.7578	.9285	1.0000	.4755	.4817	.5451
Right 10s	.6395	.5162	.4755	1.0000	.7808	.6719
Right 20s	.5510	.4887	.4817	.7808	1.0000	.8382
Right 30s	.5253	.5584	.5451	.6719	.8382	1.0000

level of significance, which is in that case 16.6%. The second component explains much less than the first in terms of significance. This second component can be expressed as the first component, giving the following vector:

$$1/\sqrt{6} (1, 1, 1, -1, -1, -1)$$

Unlike the first component, the coefficients of the second component are both negative and positive. They tend to reflect the increase of some variables while others decrease. The second component corresponds to a trend of shape variation, expressed by the amplitude of performance of one side versus the other (Jolicoeur, 1963). It does reflect a phenomenon of lateralization, the level of performance of the right being greater than the left or vice-versa. The bilateral asymmetry of performance indicates the departure from symmetrical performance.

TABLE 3

Components obtained from the correlation matrix of the moments of the hand-tapping test

First component		Second component	
Right 10s	-.3962	Left 30s	.4575
Right 20s	-.4014	Left 20s	.4482
Right 30s	-.4014	Left 10s	.2765
Left 30s	-.4104	Right 10s	-.3649
Left 10s	-.4187	Right 30s	-.3800
Left 20s	-.4207	Right 20s	-.4857
Variance	4.188		1.026
Variance %	69.801		17.070
Remaining variance: 0.786 (13.129%)			

The written alphabet test is composed of four trials per hand. The results are expressed in number of seconds for completion of an alphabet. Table 4 indicates the statistics of the moments of the written alphabet test.

As shown in Table 4, the mean performance times on the left are much longer than the ones on the right and differ relatively more. The previous explanation of the higher proportion of right-handers in our sample also applies for the written test. Like the hand-tapping test, we observe a decreasing tendency in terms of the trials. However, this decreasing trend does not have the same meaning. It is for this test an improvement of the mean performance times of both hands. On the left, the performance decreases from 26.5 seconds for the first trial to 22.3

seconds for the last trial; on the right, it goes from 15.4 to 13.1 seconds. The mean performance times of the right hand seem to decrease or improve as much as the ones of the left hand. Nevertheless, if we examine the differences between the trials of one hand, we see that it might be on the left that there is a greater improvement. The greater proportion of right-handers explains in part these discrepancies between hands. The right-handers represent more than 85% of all subjects in the written alphabet test. In terms of variation, the right hand tends to stay relatively stable throughout the four trials. The left hand, however, tends to vary relatively more.

The correlation matrix of the variables of WA (written alphabet), unlike that of HT, shows strong discrepancies. For HT, correlations were all significant and positive. As we can see in Table 5, it is otherwise, all correlations between non-homologues being practically nil. The correlations between homologues, however, are highly positive and significant. They follow more or less the same pattern or tendency as the correlations of HT, that of a decreasing tendency from one moment to the next.

TABLE 4

Statistics of the moments of the written alphabet test (WA) (N=65)

Hand	\bar{X}	Sx	CV%
Left 1	26.51	6.92	26.12
Left 2	24.43	6.16	25.43
Left 3	23.29	5.94	25.51
Left 4	22.29	5.69	25.51
Right 1	15.43	3.40	22.01
Right 2	13.68	3.12	22.80
Right 3	13.26	3.08	23.21
Right 4	13.12	2.92	22.24

In Table 6, we retained only the first two components which represent 90% of the total variation. The variance of the first component is 3.84, which is 47.5% of the explained or contained variation from the correlation matrix of WA. The relatively high percentage of variation tends to show a homogeneity in terms of significance. All the coefficients have the same direction, which can be expressed as:

$$1/\sqrt{8}(-1, -1, -1, -1, -1, -1, -1, -1)$$

TABLE 5
Correlation matrix of the moments of the written alphabet test

Hand	L 1	L 2	L 3	L 4	R 1	R 2	R 3	R 4
L1	1.0000	.9063	.9041	.8585	.0544	.0605	.0377	.0618
L2	.9063	1.0000	.9337	.9386	.0340	.0389	.0017	.0245
L3	.9041	.9337	1.0000	.9353	.0347	.0254	.0257	.0343
L4	.8585	.9386	.9353	1.0000	.0266	.0036	-.0098	.0204
R1	.0544	.0340	.0347	.0266	1.0000	.8693	.8410	.8760
R2	.0605	.0389	.0254	.0036	.8693	1.0000	.9384	.9025
R3	.0377	.0017	.0257	-.0098	.8410	.9384	1.0000	.9408
R4	.0618	.0245	.0343	.0204	.8760	.9025	.9408	1.0000

It corresponds, like the first component of HT, to a trend of size variation where all the moments of WA tend to decrease. This component corresponds to a dimension of ability, which is much less important than that of HT. The percentage of the second component tends to demonstrate this fact, being almost equal to the first. It stands, however, that it is a dimension of general ability, which represents an improvement of the performance times in terms of trial.

TABLE 6
Components obtained from the correlation matrix of the moments of the written alphabet test

First component		Second component	
Right 1	-.3087	Left 4	.3216
Right 3	-.3093	Left 2	.3180
Right 2	-.3160	Left 3	.3161
Right 4	-.3180	Left 1	.2960
Left 4	-.3826	Right 1	-.3750
Left 1	-.3906	Right 4	-.3919
Left 2	-.3929	Right 2	-.3921
Left 3	-.3934	Right 3	-.3998
Variance	3.836		3.590
Variance (%)	47.945		44.871
*Remaining variance: 0.574 (7.184%)			

The variance of the second component is 3.59 representing 44.9% of the associated variation from the residual matrix. As mentioned before, this component contains nearly as much information as the first one. Unlike HT, the meaning of the second component is as important as that of the first. We see in Table 6 that there is an opposition between the left and the right hand. The coefficient of the second component tends to reflect the increase of the right hand and the decrease of the left. It corresponds to a trend of shape variation which can be expressed as:

$$1/\sqrt{8}(1, 1, 1, 1, -1, -1, -1, -1).$$

We have a phenomenon of bilateral asymmetry or lateralization. Nonetheless, we have to keep in mind that the increase or decrease in performance is an artifact of the technique of principal components analysis. Yet it is indicative of a departure from symmetrical performance.

SUPPLEMENTARY ANALYSIS

We now have the general picture of these tests as extracted by principal components analysis. Still, we wonder if there may be differences in terms of sex and hand preference. We have used two statistical methods: the simple analysis of variance, and the analysis of variance by multiple regression (Forest and Berthelette, 1980). Before these analyses, we had calculated factorial or component scores. For some component scores, we have inverted the polarity of the coefficients for convenience. Empirically, the meaning of each test score is determined by the previous coefficients and the level of performance. For the first component of HT, the individuals who obtained a high and positive score will in turn have a performance superior to the sample mean. Those with a low or negative score will demonstrate an average or lower performance than the sample mean. As in HT, a high and negative score for WA will mean a weak performance, and a high and positive score will mean a performance superior to the sample mean and therefore a quicker performance time. For the second component score of HT, those who have a negative score will be more proficient with the left hand than with the right, and a positive score will indicate the reverse. The individuals with a score of zero represent equality in performance for both hands. The meaning of the second component score of WA is the same as HT where we have better performances in the left hand with a negative score, better in the right with a positive score.

Sex -

Table 7 shows us the results of the four component scores from both analyses by sex. The unadjusted results are from the simple analysis of variance, and the adjusted results are from the multiple analysis of variance. In a previous paper, we discussed many of the criteria used in conjunction with sex and with hand preference.

As shown in Table 7, there are significant differences between the sexes at the unadjusted level for the first score of HT and WA. We did not encounter differences for the second scores of HT and WA. When adjusted, there remains a significant difference between the sexes only for the first component score of HT. There is, however, a slight indication that there could be a difference

TABLE 7
Simple and multiple analysis of variance of the four components scores by sex

UNADJUSTED				
Variables	Female	Male	R ² %	P(1 - α)
1st cp HT	-0.56	0.68	9.17	0.999
2nd cp HT	-0.06	0.05	0.28	0.422
1st cp WA	0.72	-0.66	12.57	0.996
2nd cp WA	-0.12	0.11	0.37	0.364
ADJUSTED				
Variables	Female	Male	R ² %	P(1 - α)
1st cp HT	-0.61	0.62	5.44	0.995
2nd cp HT	0.03	-0.04	0.06	0.239
1st cp WA	0.01	-0.01	0.00	0.023
2nd cp WA	0.28	-0.28	0.67	0.808

for the second score of WA. In summary, for the first score of HT, we had a slower rate of tapping than the sample mean for females and a higher rate for males. This tendency remains after being adjusted by other circumstances. For the second score of HT, no tendency is noted. There is a definite difference for the first score of WA if one considers sex alone. Adjusted, however, that difference between the sexes disappears. It seems that the females in our sample had a better overall performance time than the males, if we consider sex as the only criterion in the analysis. We do not find a difference for the second component score of WA; rather, when adjusted, there is an indication that the females in our samples are more proficient with their right hand than with their left, the reverse being true for the males.

Hand preference

We also tested the four component scores to see if there were differences between left-handers, right-handers and the ambidextrous. Table 8 shows that there are signifi-

cant differences, unadjusted and adjusted, between hand preference categories only for the second component scores of HT and WA. This one criterion alone, hand preference, largely explains the variation of the dependent variables - more so than sex. If hand preference alone is considered in the analysis of the second score of HT, the left-handers are more proficient with the left hand and the other two groups show little difference between left and right. When adjusted to other circumstances, however, the left-handers remain proficient with the left hand but the other two groups are more proficient with the right hand than with the left. It seems that the ambidextrous do not have equal performance with both hands, but rather a right-hand proficiency. The second score of WA follows nearly the same patterns. Nevertheless, in the unadjusted analysis, the ambidextrous are closer to the left-handers than to the right-handers. Finally, analysis of both second component scores identifies only two groups of proficiency: left and right.

TABLE 8
Simple and multiple analysis of variance of the four component scores by hand preference

UNADJUSTED					
Variables	Left-h	Ambid	Right-h	R ² %	P(1 - α)
1st cp HT	0.10	0.02	-0.01	0.02	0.012
2nd cp HT	-1.69	-0.04	0.16	26.68	0.999
1st cp WA	-0.12	1.23	-0.10	3.36	0.652
2nd cp WA	-5.87	-0.45	0.46	65.66	0.999
ADJUSTED					
Variables	Left-h	Ambid	Right-h	R ² %	P(1 - α)
1st cp HT	-0.20	0.15	0.06	0.10	0.079
2nd cp HT	-1.26	0.57	0.67	20.61	0.999
1st cp WA	-1.36	1.40	-0.04	3.04	0.762
2nd cp WA	-3.06	1.17	1.90	28.74	0.999

DISCUSSION

It would seem, after analysis, that in both our tests the performances of the left hand vary relatively more than those of the right hand. This tendency could be explained, we think, by related phenomena. First, the sample structure is directly responsible for the level of the performance, and also for the variation of both hands, due to the higher proportion of right-handers (85% of the total sample) than the left-handers and ambidextrous (10 to 12% of the total sample). Our sample does reflect, in a sense, the general population structure (Annett, 1972). We think, therefore, that our results are normal, the performance of the left hand being lower than the sample mean and varying much more in amplitude than that of the right hand. Secondly, a greater use of the right hand tends to minimize variation and, conversely, less use of the right hand tends to amplify differences between subjects.

We arrived at known components, which are size and shape. There is, however, a limiting prescription in arriving at these results: if one uses different sets of data or, to be more precise, different types of objects, one may obtain different results. The results we arrived at are significant of a unique phenomenon in humans, motor performance. Through these results, we can therefore characterize motor performance as being primarily a phenomenon of a capacity with which every human is endowed, and a residual dimension which, in our study, is bilateral asymmetry.

Both tests are quite different as we have seen through the simple statistics. Moreover, they differ in their complexities, as principal components analysis has shown. It would seem that the hand-tapping test is simpler than the written alphabet test. This statement is confirmed by the relative importance of the first components, the variance of the hand-tapping test being greater than that of the written alphabet test. We must add that the ratio between the first and second components of each test is indicative of a different complexity of bilateral asymmetry. When the difficulty of the tasks increase, the asymmetries of manual tasks as well as their amplitudes increase (Vanden-Abeele, 1980). Thus, it is evident that the hand-tapping test is a simpler test where we find slight asymmetries. However, as our results indicate, the written alphabet test is very complex if we refer to the almost equal variance between the first and second components. This test is more than a measure of motor performance; it involves memory and the verbal (alphabet) structure (Ajuriaguere *et al.*, 1971; Desjardins, 1980). Moreover, it involves finer motor control than the hand-tapping test (Desjardins, 1980, 1981). We found differences between the sexes in terms of general manual performance for the hand-tapping only. Males, it seems, show better overall performance in both hands for an unspecialized task than do females. For those kinds of tasks, males show better performances (Maccoby and Jacklin, 1974; McGuiness, 1976). Males generally surpass females in speed and coordination of gross bodily movements at all ages (Garai and Scheinfeld, 1968).

For the written alphabet test, no significant tendencies were encountered at the adjusted level. Instead, if we take sex as the sole source of variation, it seems that the females in our sample have better performance times than the males. Yet, this tendency does not hold up at the adjusted level. In the literature it is mentioned that females have better performance times than males for this kind of activity (Garai and Scheinfeld, 1968). Judging from the results obtained by multivariate statistical analysis of our sample, however, it would seem that there is no difference between the sexes for this kind of manual activity. Yet there is a tendency in terms of different proficiency levels from one hand to the other, whereby females are more proficient with their right hand and the reverse for males. This tendency is not statistically significant, however.

It would seem, as our results and the results of others have shown, that there is a significant difference between the sexes in regard to gross bodily movements. The tasks involved are simple and more or less specialized. For more specialized tasks, we cannot suggest from our results that there are significant differences, although other studies have shown a slight superiority in females (Garai and Scheinfeld, 1968).

In regard to hand preference, we found differences for the second components of both tests. It is, we think, indicative of the phenomenon of lateralization, which is the hemispheric organization of brain activities and functions. It seems from our results that there is a crossed control. Nevertheless, it is suggested that this operating model is not a true image of the mechanisms involved (Vanden-Abeele, 1980). The operating model would be contra-lateral for the right-handers, and ipsi-lateral for the left-handers in terms of motor performance and verbal structure (Buffery and Gray, 1972). We, on the other hand, observe a significant asymmetry for the written alphabet which shows that the left-handers are as much lateralized as the right-handers, and the ambidextrous are less lateralized compared to the other groups. We suggest, from our results, that we face a crossed-control model. It seems that functional lateralization is linked to the degree of manual asymmetry rather than the direction of manual asymmetry (Thomas and Campos, 1978).

The phenomenon of lateralization or bilateral asymmetry, is complex due to the link with the human brain, and touches the whole body in terms of morphology and physiology. It seems that the operating models of the brain's organization proposed at the beginning of this century have been abandoned, and justly so. The opinion widely accepted now is that there are a multiplicity of types of control and a heterogeneity of asymmetry (Vanden-Abeele, 1980). It is suggested that the direction of asymmetry is not unique but multiple in the individual, not to mention in a population.

CONCLUSION

We could have used only the summation of the moments of the right and left hands in the analysis. Instead, the use of principal components analysis has proved to be

of great assistance. This statistical method, as such, can be complex and difficult to use if not understood; yet, the use of multivariate statistical methods has the great advantage of providing easier interpretation of the data in our field. We do not suggest that use of these methods should be made compulsory, but rather that the mind should be open to their potential. In our case, the use of multivariate statistical methods did underline common elements and particularities of our data. The general characteristics is the general ability of our subjects in terms of performance (first components) and the lesser phenomenon is the bilateral asymmetry of performances (second components of both tests).

NOTES

1. I am deeply indebted to Gisèle Molgat for her assistance in the preparation of the manuscript of this paper. A version of this paper was presented at the 8th annual meeting of the Canadian Association for Physical Anthropology. Ottawa, Ontario, 1980.

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VARIATIONS IN DIFFERENTIAL LEUKOCYTE COUNTS IN RELATION TO AGE AND BODY BUILD IN A RURAL POPULATION OF WEST BENGAL, INDIA¹

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Abstract: The possible relationships between differential leukocyte counts and age, as well as two anthropometric indicators (Kaup index and sum of triceps and subscapular skinfold thicknesses) of body build, were investigated in male and female samples from the population of the village of Mirpur, Midnapore District, West Bengal, India. The analysis shows that in the case of males the variations of neutrophil and lymphocyte counts can be explained in terms of age alone, while in the case of females the two body build variables, and presumably other presently unidentifiable ones, may have appreciable effects on these counts.

Résumé: Les relations possibles entre le nombre différentiel de leucocytes de l'âge, de même que deux indicateurs anthropométriques (l'index de Kaup et la somme des épaisseurs du triceps et du pli cutané subscapulaire) de la musculature, ont été étudiés à partir d'échantillons mâles et femelles de la population du village de Mirpur, district de Midnapore, Bengale Occidental, Indes. L'analyse démontre que chez les mâles, les variations dans le compte des neutrophiles et des lymphocytes peut s'expliquer en termes d'âge exclusivement, alors que chez les femmes, les deux variables de la musculature, et présumément d'autres actuellement non identifiables, peuvent avoir des effets appréciables sur ces comptes.

Key Words: Anthropometry, Leukocyte, Correlation, India.

INTRODUCTION

Differential leukocyte counts (DC) are generally believed to vary with age as well as certain anthropometric indicators of body build (Alexopoulos and Babis, 1976; De Grouchy, 1960; Rud, 1947), but the data are equivocal (Burr and Damon, 1970; Weksler and Hutteroth, 1974) and systematic studies involving appropriate statistical techniques are rare (see however, Polednak, 1978).

In view of this, a systematic study was undertaken on the possible relationships between the differential counts and age, on the one hand, and two commonly-used indicators of body build; the Kaup index (weight/height²) and the sum of skinfold thicknesses (triceps and subscapular). The relatively infrequent leukocyte types, monocytes and basophils, were not used in this analysis because of their low frequencies.

MATERIALS AND METHODS

A multidisciplinary biomedical study involving collection of demographic, anthropometric, genetic, haematological, intestinal parasitic, etc., data is being conducted on the small Christian village of Mirpur in coastal Midnapore District, West Bengal, India. Some of the data have been published (Basu *et al.*, 1980; Bharati *et al.*, 1980; Bhattacharya, 1980; Gupta, 1978, 1980; Gupta *et al.*, 1977).

During the demographic survey, conducted on the entire population, the ages were recorded from parish registers of both Catholic and Protestant churches. Blood films were prepared and analysed for differential counts following standard techniques (Kolmer *et al.*, 1951). Several anthropometric measurements were also made using standard techniques (Weiner and Lourie, 1969), of which

TABLE 1
Correlation coefficients between age, and lymphocyte, neutrophil and eosinophil counts.

D.C. Age-Group	Number		Neutrophil		Lymphocyte		Eosinophil	
	Male	Female	Male	Female	Male	Female	Male	Female
Children (0-14 Yrs)	54	43	+0.22	+0.59*	-0.34**	-0.61*	+0.12	+0.20
Adults (15-44 Yrs)	37	54	+0.27	-0.06	+0.04	+0.01	-0.33**	+0.10
Elderly (45+ Yrs)	18	16	-0.07	-0.06	-0.03	-0.17	+0.46	+0.35
All ages	109	113	+0.51*	+0.32*	-0.36*	-0.27*	-0.30*	-0.09

* Significant at 1% level

** Significant at 5% level

weight, height, triceps and subscapular skinfold thicknesses were used in the present study. The analyses were done separately for the males and females.

RESULTS AND DISCUSSION

Some of the results have already been reported (Bhattacharya *et al.*, 1981) and are briefly recapitulated here. The correlation coefficients between age and neutrophil, lymphocyte and eosinophil counts, set out in Table 1, show that the relationships are generally statistically significant in the "all ages" and 0 - 14 years age groups. The general lack of statistical significance in the adult and elderly age groups, particularly in the latter, may be due in part to the relatively small sample sizes, although the possibility of a general lack of age difference within each of the three age groups (as against the presence of such differences between these groups) cannot be ruled out.

The leukocyte counts were regressed on age (Table 2) in the cases where correlation coefficients (Table 1) were significant. However, Chi-square tests for goodness of fit between the observed distributions and the fitted lines suggest that the fit is not good for any of the regression equations given in Table 2, indicating that the variations in leukocyte counts cannot be explained by age alone and that, therefore, other predictor variables should be looked for.

A search for the other predictor variables was made in the following ways.

1. Partial correlation coefficients between leukocyte counts and age, eliminating the effects of each of the two possible anthropometric indicators of body build (Kaup index and sum of skinfold thicknesses) as well

as of both of them, were computed. If the body build variables were important predictors of leukocyte count independent of age, removal of their effects should reduce the correlations of the counts with age.

2. Correlation coefficients between leukocyte counts and each of the two body build variables, as well as partial correlation coefficients eliminating the effect of age, were computed. If body build variables were important predictors of leukocyte counts independent of age, the leukocyte count-body build correlations should be high, and removal of age effects should not substantially reduce these correlations. The analyses postulated above were done with respect to neutrophil and lymphocyte counts only, separately for males and females.

Table 3 shows that in males the correlation between neutrophil count and age is significant and it decreases only slightly (but still remains significant) when the effects of Kaup index and sum of skinfold thicknesses (separately and together) were removed, indicating that a possible effect, slight at best, of body build variables on neutrophil count is possible. The correlations between neutrophil count and the two body build variables, as well as the corresponding partial correlations, are insignificant in general, indicating that the body build variables do not have any detectable effects on neutrophil count. The multiple correlation coefficient of 0.96 between neutrophil count, and age, Kaup index and sum of skinfold thicknesses suggest that none other than the predictor variables already considered here need be postulated to explain the observed variation in neutrophil count.

TABLE 2
Regression equations (lymphocyte, neutrophil and eosinophil counts on ages)

		Age-group	
		All ages	0-14 Yrs.
Neutrophil count	M	$Y_n = 44.32 + 0.27x^*$	
	F	$Y_n = 48.50 + 0.22x^*$	$Y_n = 37.33 + 1.39x^*$
Lymphocyte count	M	$Y_l = 37.74 + 0.16x^*$	$Y_l = 43.98 - 0.82x^*$
	F	$Y_l = 37.45 - 0.17x^*$	$Y_l = 51.52 - 1.79x^*$
Eosinophil count	M	$Y_e = 17.40 - 0.12x^*$	

* Regression coefficient significant at 1% level

TABLE 3
Correlation and partial correlation coefficients (male)

Correlation	Correlation Coefficient	Partial Correlation Coefficients		
Neutrophil and age	$r_{12} = 0.49^*$	$r_{12.3} = 0.46^*$	$r_{12.4} = 0.45^*$	$r_{12.34} = 0.46^*$
Neutrophil and Kaup index	$r_{13} = 0.21$	$r_{13.2} = 0.07$	$r_{13.4} = 0.09$	$r_{13.24} = 0.36^*$
Neutrophil and skinfold	$r_{14} = 0.20$	$r_{14.2} = 0.04$	$r_{14.3} = 0.07$	$r_{14.23} = 0.04$
Lymphocyte and Age	$r'_{1'2} = -0.37^*$	$r'_{1'2.3} = -0.37^*$	$r'_{1'2.4} = -0.38^*$	$r'_{1'2.34} = -0.37^*$
Lymphocyte and Kaup index	$r'_{1'3} = -0.10$	$r'_{1'3.2} = 0.11$	$r'_{1'3.4} = -0.11$	$r'_{1'3.24} = 0.06$
Lymphocyte and skinfold	$r'_{1'4} = -0.04$	$r'_{1'4.2} = 0.10$	$r'_{1'4.3} = -0.06$	$r'_{1'4.23} = -0.03$

x_1 = Neutrophil; x_1' = Lymphocyte; x_2 = Age; x_3 = W/H² (Kaup Index)

x_4 = Triceps + subscapular skinfold thicknesses

* significant at 1% level

Table 3 further shows that the correlation between lymphocyte count and age is also significant but it remains virtually unchanged (and significant) when the effects of the two body build variables, taken separately and together, are removed, indicating little or no effect of these variables on lymphocyte count. Correspondingly, the correlations between lymphocyte counts and the two body build variables, as well as the corresponding partial correlations are insignificant, indicating that the body build variables did not have any detectable effects on lymphocyte count. Thus, the lymphocyte count agrees with the neutrophil count in showing very little or no effect of the body build variables on its magnitude. The multiple correlation coefficient of 0.72 thicknesses, however, is smaller than in the case of neutrophil, indicating that other predictor variables in addition to those considered here may have some effects. The small differences in the neutrophil/lymphocyte count-age correlation coefficients as given in Tables 1 and 3 may be due to slightly different samples having been used in the two sets of analyses.

The female sample shows somewhat different results (Table 4). For instance, in the case of neutrophil count, the correlation with age decreases considerably (and becomes statistically insignificant) when the effects of Kaup index and sum of skinfold thicknesses, taken singly or

together, are removed, indicating that unlike in the case of males, the body build variables may have appreciable effects on neutrophil count in females. On the other hand, the correlations between neutrophil count and each of the two body build variables are significant unlike in the case of males, but they decrease considerably (and become statistically insignificant) when the age effects are removed, confirming age as a significant predictor variable, as in the case of males. The lymphocyte count shows a similar trend in general: (a) the correlation with age decreases when the effects of the body build variables are removed; and (b) the correlations with the body build variables are significant but they decrease considerably when the age effects are removed. The small differences in the neutrophil/lymphocyte count-age correlation coefficients as given in Tables 1 and 4 may be due to slightly different samples having been used in the two sets of analyses, as in the case of males. The multiple correlation coefficients of 0.60 and 0.51 in the cases of neutrophils and lymphocytes, respectively, suggest that predictor variables in addition to those considered here need be postulated to explain a major part of the observed variation of the two leukocyte counts.

While in males, the variations of neutrophil and lymphocyte counts can be largely explained in terms of age alone, with the body build variables having little or no

TABLE 4
Correlation and partial correlation coefficients (female)

Correlation	Correlation Coefficient	Partial Correlation Coefficients		
Neutrophil and age	$r_{12} = 0.33^*$	$r_{12.3} = 0.14$	$r_{12.4} = 0.23$	$r_{12.34} = 0.13$
Neutrophil and Kaup index	$r_{13} = 0.37^*$	$r_{13.2} = 0.21$	$r_{13.4} = 0.27^{**}$	$r_{13.24} = 0.20$
Neutrophil and skinfold	$r_{14} = 0.28^*$	$r_{14.2} = 0.13$	$r_{14.3} = 0.11$	$r_{14.23} = 0.10$
Lymphocyte and Age	$r'_{1'2} = -0.35^*$	$r'_{1'2.3} = -0.16$	$r'_{1'2.4} = -0.25^{**}$	$r'_{1'2.34} = -0.15$
Lymphocyte and Kaup index	$r'_{1'3} = -0.37^*$	$r'_{1'3.2} = -0.21$	$r'_{1'3.4} = -0.30^*$	$r'_{1'3.24} = -0.23$
Lymphocyte and skinfold	$r'_{1'4} = -0.27^*$	$r'_{1'4.2} = -0.11$	$r'_{1'4.3} = 0.15$	$r'_{1'4.23} = 0.14$

x_1 = Neutrophil; x_1' = Lymphocyte; x_2 = Age; x_3 = W/H² (Kaup Index)

x_4 = Triceps + subscapular skinfold thicknesses

* significant at 1% level

** significant at 5% level

predictive value, in females the two body build variables, and presumably other presently unidentifiable predictor variables, may have appreciable effects. Differences between males and females in respect of the pathophysiological processes determining the differential leukocyte counts may have led to such sex-differential leukocyte count-predictor variable relationships, but we do not presently possess suitable data to investigate this possibility.

ACKNOWLEDGEMENTS

We are indebted to the authorities of Geonkhali High School, and the sub-divisional authorities, Tamluk Sub-division, Midnapore District, West Bengal, for providing organizational help in the field; to Mr. N. Maitra, Mrs. M. Roy and Mr. B. Dey for providing technical assistance in the lab; to Mr. P. Adhikary for typing the manuscript; and, last but not least, to the people of Mirpur for their unhesitating cooperation with our work.

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HUMAN BIPEDALITY AS A CONCOMITANT OF DENUDATION¹

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Abstract: Highly K-selected catarrhines channel enormous investment into extensive care of highly dependent infants. Selection favouring denudation would have required that the mother's forelimbs be constantly available for the support of her infant. Loss of hair explains why the postural transformation to bipedality was a rapid one, and why bipedalism became a biological imperative.

Résumé: Les catarhiniens démontrant une forte sélection du facteur K déversent une somme d'énergie énorme dans les soins importants apportés aux nouveau nés encore grandement dépendants. Une sélection favorisant la dénudation aurait requis que les membres supérieurs de la mère soient constamment disponibles pour le soutien du nouveau-né. La perte du poil peut expliquer pourquoi la transformation de la posture vers le bipédalisme fut si rapide, et pourquoi le bipédalisme devint une nécessité biologique.

Key Words: Hominid, Bipedalism.

The emergence of early hominids from the rest of the higher primates can be characterized in a number of significant ways. The various morphological features which set them apart as a group taxonomically distinct among the hominoids have been enumerated by LeGros Clark (1959). The suite of hominid dental traits may be recognizable as far back as 15 million years ago (Leakey, 1962; Simons, 1972). After dentition, probably the first distinctly hominid morphological parameter identifiable in the fossil record is bipedality. Most researchers agree that the interpretation of the skeletal modifications associated with habitual bipedal locomotion is crucial to our understanding of hominid evolution. The bio-mechanical complexities involved in the transition to upright posture and gait have already been extensively discussed (Lovejoy, Heiple and Burstein, 1973), and need no further elaboration. The anatomical consequences of this radical change in locomotor habits is not of primary interest in this discussion; rather, attention will be focused on the initial reasons for such a development.

Bipedal locomotion itself is not unique to humans; ample evidence of such behaviour has been documented for several species of primates, including the gibbon (Carpenter, 1964), the chimpanzee (Goodall, 1971), and the gorilla (Schaller, 1963). What is unique to humans, however, is obligatory, orthograde striding. While one cannot make direct analogies between modern-day primate behaviour and that of a hypothetical hominid or pongid ancestor, it is not unreasonable to assume that the latter also possessed some bipedal preadaptation. For the sub-human primate, such pre-adaptive traits probably conferred only slight, if any, selective advantage. Entirely different circumstances existed, however, in the case of

the emerging hominid, making orthograde bipedality obligatory. The task, then, is to isolate and to account for the factors that were responsible for bringing this incidental behaviour to the forefront of the selection equation.

Moving on two legs is energetically inefficient, for it creates unnatural stresses on the skeleton and musculature, stresses which result in a "terrific mechanical imbalance" (Krogman, 1951). This, in time, produced problems associated with the birth process. In addition, the curtailment of speed when the animal was in flight must also have posed serious difficulties. The physical infirmities caused by orthograde posture, many of which mankind is to this day heir, have led Hewes to conclude that "selection for bipedalism . . . must have been rapid and ruthless" (1961). We suggest that the rapidity of this change is a key factor which has not been adequately accounted for in the explanations for bipedality that have thus far appeared in the literature. The apparent accelerated pace of the transition to habitual bipedalism, in spite of its obvious disadvantages, points to the occurrence of a major change in the biosphere of the prehomnids, the influence of which was so pervasive that the traditional plantigrade manner of moving around, with proven survival value, was speedily and irrevocably abandoned. Tool use (Washburn, 1960), food transport (Hewes, 1961), agonistic display (Westcott, 1967), changes in foraging techniques (Jolly, 1970), or gathering (Tanner and Zihlman, 1976) seem unlikely to have exerted an influence powerful enough to account for such a rapid behavioural modification. While such factors would certainly have served, secondarily, to reinforce and promote the development of bipedalism once it had already begun, all

indications are that the prime mover of the process must have been of a much more compelling nature - one so compelling that the prehuman had no alternative other than to walk upright.

There are many other fascinating problems concerning hominid development, such as those involving structural changes in the masticatory apparatus, progressive increase in cranial capacity, and the acquisition of language. In comparison to the interest raised by these developments, relatively little attention has been generated by that of hair loss. Most of the literature on the subject supports a theory that is predicated on an adaptation to a hunting way of life upon the open savannah. This theory postulates that increased energy expenditure and problems of overheating, generated by the new method of moving under a hot, tropical sun, resulted in a sudden decrease in hair density over most of the body (Montagu, 1964; Morris, 1967). More recently, however, this assumption has been questioned. Newman points to evidence which suggests that the "glabrous state is a marked disadvantage under high radiant heat loads, rather than the other way around" (1964: 226) and that "the obvious time and place where progressive denudation would have been least disadvantageous is the ancient forest habitat" (1964: 232). This, of course, dates hair loss at a much earlier period than present estimates allow. If, however, Newman's speculations prove to be well-founded, we may at last be in a position to solve the enigma of bipedality. Bipedality might well have been an inevitable consequence of hair loss; moreover, loss of hair can explain both why the postural transformation was such a rapid one, and why bipedalism became a biological imperative.

The phylogenetic development of the primates has been marked by several evolutionary trends (LeGros Clark, 1959). Those that are pertinent to our discussion revolved around the care and nurture of infants. Increasing parental investment, one of the major evolutionary trends among animals, culminates in the eutherian mammals, most species of which have thrust the entire burden of infant care on the females, who are specialized for placentation and lactation (Daly and Wilson, 1978). This trend is particularly prominent in the primate order in which there has been a progressive tendency towards giving birth to infants that are less mature than those of other mammalian species. There has also been a trend towards the prolongation of the dependency period. Primates, while they do build sleeping nests, do not typically utilize these to house their young. The primate mother carries her infant with her whenever and wherever she moves. In this sense she is indeed the "locomotory organ" of her infant (Lancaster, 1975). The infant is supported by the mother's forelimbs when she is sitting and, in the case of the very young infant, for the first few steps when she moves (Carpenter, 1964). However, when any great distance is to be covered, and especially when the mother is in full flight, her infant must support itself. It needs to cling - and cling tenaciously - if it is to survive. Thus, the selective retention of the quadrumanus (four-handed) condition is obviously, of great advantage to the primates;

but the facilitative agent without which the infant would be hopelessly lost is, of course, the mother's pelage.

If the hair of the prehuman did, indeed, become increasingly reduced, then the care and protection of infants would have been in serious jeopardy. One might as well wonder how the species could have survived under these unprecedented circumstances. The mothers, however, would not have been entirely without resources, as bipedal capabilities were, in all probability, already a part of their behavioural repertoire. Once denudation had progressed to the point at which the transportation of infants was seriously hampered, mothers would still have been able to pick up children in their arms, and walk. Thus would selective pressures have been brought to bear on a behaviour that was, until then, only incidental and sporadic. Recently Tanner and Zihlman (1976) have suggested a hominid emergence model based, in part, on maternal infant transportation. The shortcomings of their interpretation of bipedality include their failure to take into account the significance of denudation and the circular nature of their logic. In effect, they suggest that the increasing bipedal adaptation of the infant foot, through loss of its prehensile capabilities, would have led to a greater reliance by infants on being carried by their mothers, which would, in turn, have resulted in selective pressure favouring an increasingly bipedally adapted, non-prehensile foot.

Observations of gorillas (Schaller, 1963) have revealed that in the first six weeks of life the infant is supported by one hand while the knuckle-walking mother uses a three-legged gait. This locomotor pattern appears to be highly functional in the special case of a long-armed knuckle-walker who is required to support her newborn infant fully for only a few weeks. Contra Washburn (1968), there is no evidence to support a knuckle-walking stage in human evolution (Tuttle, 1969; Oxnard, 1967, 1968). More to the point, Howells has suggested that "knuckle-walking . . . would have tended to become an adaptive trap, difficult to escape from" (1973:37); furthermore, it has now been established that Pliocene hominids possessed humero-femoral indices of approximately 84 (Johanson and Taieb, 1976).

Prolonged infant dependency has reached its quintessence in hominids, probably the most K-selected of all primates, if not of all mammals, and the human infant's neuro-muscular development is the most retarded of any newborn in the animal kingdom. If such developmental retardation characterized early hominids, it would have been sufficient to account for obligatory bipedality. This is because hominid infants compared to other anthropoid infants would have had a considerably reduced capacity for clinging to their mothers for a protracted period. A denuded mother would, however, present a challenge to the most precocious infant. Even if we are to assume that a certain degree of three-legged locomotion were possible, the mother, once her infant reached a reasonable size, would have been required to provide two-limbed support during any movement.

This discussion would not be complete without some

reference to the possible causes of hair loss. Schultz (1950) has called hairlessness one of humanity's most conspicuous specializations and has noted among primates an evolutionary trend towards a less hirsute condition. Platyrrhines, it seems, exhibit the greatest hair density whereas catarrhines, particularly the great apes, manifest progressively less hair density. In humans, of course, this primate trend reaches its extreme. We know neither what factor or factors are responsible for this, nor when, nor why the final denudation took place. There are a few lines of enquiry that might eventually prove fruitful. Schultz (1950) has noted, for instance, that the newborn primate infant is virtually devoid of hair. The possibility exists that, for some reason, selection may have favoured the retention of this neotenus condition, perhaps because the radiant energy that does penetrate the forest canopy is "exactly the energy best reflected by human skin" (Newman, 1964: 232). Climatic changes, alterations in diet, chance mutation, gene drift, or any combination thereof are other factors that may have contributed to hominid denudation.

In conclusion, we suggest a probable sequence of events that led up to and followed upon the emergence of the hominids. Geological and climatic changes at the time of the Burdigalian and Vindobonian interface resulted in a significant decline in the once abundant tropical forests. This in turn led to increased competition among arboreal primates for available food resources. Several species were thus driven to explore the tropical forest floor as an alternative ecological niche. Once established in the new habitat, at least one, and perhaps more, of these species underwent a dramatic change. Selection, for reasons as yet unknown, favoured a rapid reduction in body hair. It is tempting to correlate the increase in tactile stimulation afforded by a naked skin with possible changes in both the size and complexity of the brain. Whatever the case, the reduction of hair seriously interfered with the usual mode of infant transport, thereby forcing the mothers to capitalize on a behaviour that had previously been used only on occasion and for short distances. Selection would then have favoured those individuals who were successful in improving their bipedal capabilities. However, the female, encumbered by an infant requiring the full support of both her arms whenever she moved, and by a method of locomotion as yet awkward and clumsy, would have found herself confined to a much smaller area than had previously constituted the extent of her range. This would have put serious restrictions on her foraging abilities; her survival and that of her infant would then have depended on selection within the group, and especially among the males, for altruistic behaviour in matters of food sharing and defence. This is consistent with the general concept of inclusive fitness and greater paternal involvement implicit in increased K-selection (Daly and Wilson, 1978).

Among higher primates, if not most mammals, the primary behavioural role model for all offspring is their mother (Harlow, 1965). Further documentation supports the view that, at least in some higher primates, young females show a greater tendency for innovative behaviour

than do older males, and that this behaviour can, eventually, permeate the whole troop (Frisch, 1968). A reasonable assumption, given the obvious survival advantage accruing from such a behavioural shift, is that a troop of relatively naked hominoids in which the highly fecund young females were bipedal would be in possession of a marked selective advantage. Such behaviour could appear in a single generation, and would probably be fixed within a very few generations, as a result of infant imitative behaviour. It has been well documented that idiosyncratic and innovative behaviours of the kind under discussion, readily spread from deme to deme via what has been termed "tradition drift" (Burton and Bick, 1972).

Over the years it has been repeatedly suggested that tool fabrication necessitated bipedality (Washburn, 1960). This position is no longer tenable. The fossil record and the archaeological evidence demonstrate that by the time the early hominids were fully adapted to orthograde bipedal locomotion, the earliest stone tool industries were still millions of years in the future. The first "steps" on the road to humanity were taken by individuals operating under an infinitely more compelling need than the desire to kill and butcher an animal. The first bipedal hominids were mothers desperately clinging to their helpless infants; the survival of our lineage depended on the success of their efforts.

NOTES

1. We wish to thank Professors Frances Burton, Susan Pfeiffer, Shelley Saunders, and Emöke Szathmari, and Mrs. Deirdre Breton for valuable and stimulating discussion and comments. Deirdre Breton's consummate editorial skills were most helpful and deeply appreciated. A version of this paper was presented at the 9th annual meeting of the Canadian Association for Physical Anthropology, Banff, Alberta, 1981.

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COMPONENT PATTERNS IN GESTURE FORMATION IN *Macaca sylvanus* OF GIBRALTAR¹

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Abstract: Past research in primate communication has frequently concentrated on species- or genus-wide manifestations of vocal/ gestural behaviour. My work with *Macaca sylvanus* of Gibraltar indicates that, although species-specific gestural patterns do occur, there are other patterns at the level of populations which allow differentiation of classes such as age, sex, and kin group. The recognition of these patterns may provide both evidence about the communication system and empirical evidence about the social structure of the group as perceived by its members.

Résumé: La recherche dans la communication des primates a fréquemment concentré sur les manifestations de la conduite vocale et de geste basées sur le genre ou l'espèce. Mon travail avec *Macaca sylvanus* de Gibraltar indique que, même si des modèles de gestes spécifiques à l'espèce existent, il y a d'autres modèles au niveau des populations qui permettent une différenciation des classes comme l'âge, le sexe, et la famille. Une connaissance de ces modèles peut donner de l'information sur le système de communication des singes entre eux-mêmes, et de l'évidence empirique sur la structure sociale du groupe comme aperçue par ses membres.

Key Words: Macaque, Communication, Gibraltar.

The whole field of communication has burgeoned in recent times. To a large extent this is due to the developing controversy concerning the amount and kinds of difference that exist between human and animal communication. In the early years of primate research the distinction was very simple. Humans talked and animals expressed their emotions by means of non-verbal cries or non-vocal gestures. This simplistic dichotomy has gone the way of most dichotomies with the discovery of human paralinguistic, or non-verbal, channels of communication, and with the realization that a great deal of information is transmitted through completely non-vocal channels (Argle, 1972). On the other side, primates are challenging the human assumption that only humans can utilize arbitrary coded signed systems to converse about the world, i.e., "talking apes". Part of the reluctance to accept the possibility that primates might learn to use such a communication format stems from the assumption that non-human primate communication systems are not based on principles of pattern (Cullen, 1972). This argument is based on the kinds of research that were common until recently on primate communication systems.

A very large proportion of previous communication studies has been concluded for one of three purposes. The earliest work looked at lists of components (e.g., eyes staring) that occurred during a communication and attempted to make phylogenetic assessments of various genera. The idea was that if you could trace an expression

such as the "grin" through several genera you might be able to trace the evolutionary connections between genera. Andrew (1963a, 1963b) and Van Hoof (1962, 1967) carried out this type of work. Another approach was to collect a list of the gesture components for a particular species in an effort to define the "normative expression" of that species, as was done by Hinde and Rowell (1962). The third type of study was a description of the ontogenetic development of particular gestures as was attempted by Chevallier-Skolnikoff (1973, 1974).

Unfortunately these descriptive approaches gave us very little information about how the communication system actually works. We know that one of its major functions in group-living animals is to provide group cohesion. Communication is the mechanism that enables animals to make use of the adaptive niche that is characterized by learned responses and shared information. Even very solitary species of animals must be able to communicate their readiness to mate, and must reduce the distance, both physical and social, between them (Rowell, 1972). More social animals, and particularly primates, have a very flexible mode of response. They can deal with problems such as food surpluses or shortages by reducing or expanding their personal space, by investigating new foods, or by moving out of their accustomed ranges. Young animals learn from observation and example what foods are considered edible by their group and what are not. Young animals are much more ready to try new foods than older

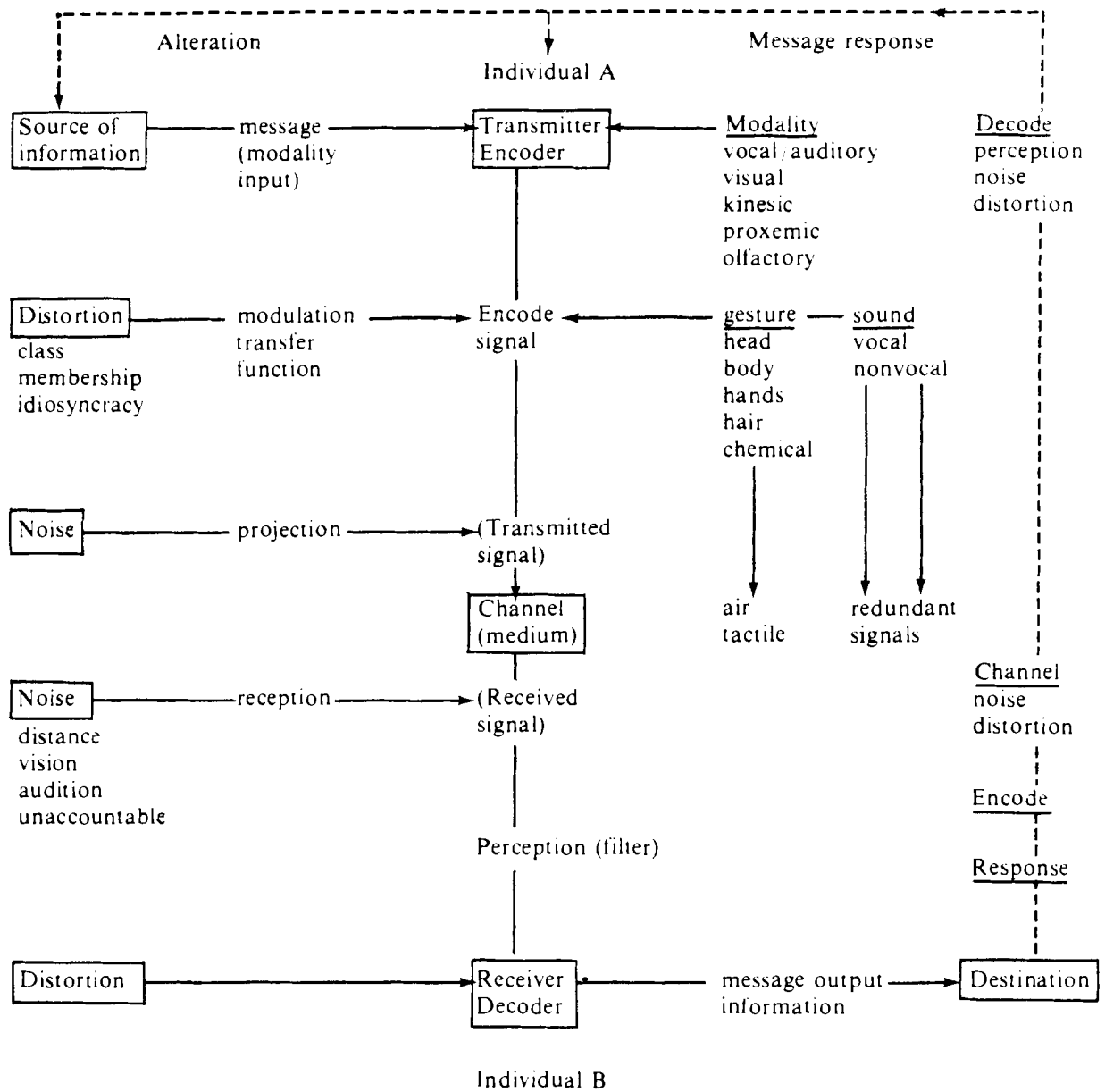


Fig. 1 Diagrammatic representation of information transmission with variables present. (Adapted from Corso, 1967: 463).

Simple Information transfer Model

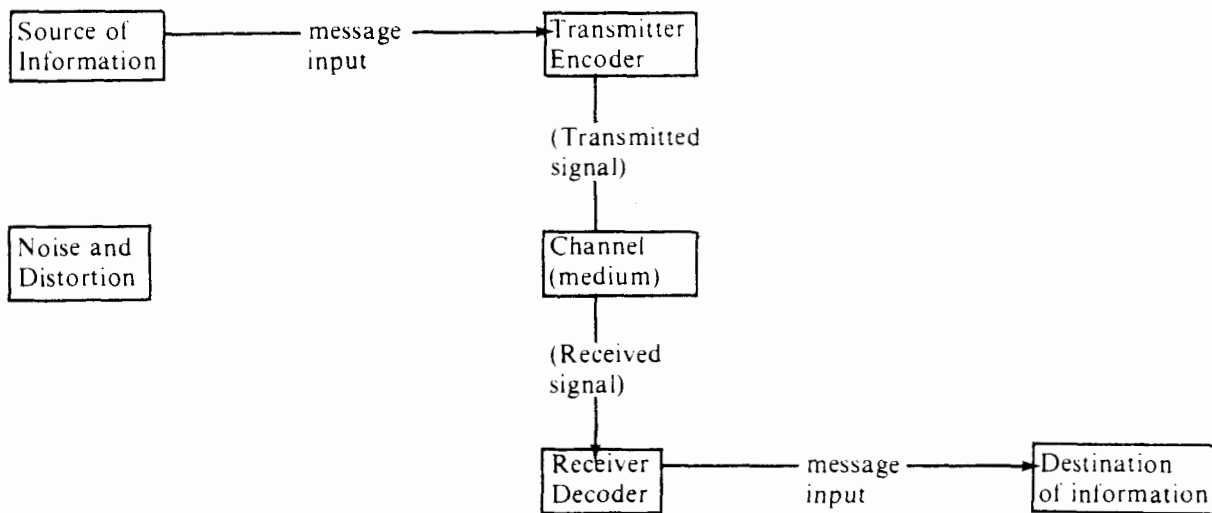


Fig. 2 Diagrammatic representation of information transmission. (taken from Corso, 1967:463).

ones, but are quick to follow indications of acceptance or rejection that adults emit. Japanese macaques, with their population differences in food lists and acquisition patterns are a good example of this (Kawamura, 1963). Another is my own experience with *Macaca sylvanus* of Gibraltar. I introduced dried fruit to some young animals on one occasion. The juveniles picked it up, sniffed it and began eating. The head male came over, picked some up, sniffed it and threw it down. Within a few seconds all the young animals had dropped their pieces. They ignored the fruit that day and on subsequent occasions. The adult did not threaten the juveniles at all, but merely indicated the non-acceptance of dried fruit as a food item.

Dangerous situations can also provide the opportunity for animals to learn how to respond adaptively. Baboons can stand off some predators while others evoke a flight response from all members of the group. Communication is also the mechanism of social survival; how to interact with peers, older animals, younger animals and particular individuals. Previous research has lacked both a focus on the individual sender and respondent, and a technique that would enable us to differentiate between one manifestation and another. These types of information would allow us to understand much more clearly how the structure of communication is tied to its function, and to the individual's place in the social network.

As an analogy, it is rather like listening to music and realizing that some music produces one effect and some another, without realizing that there are such things as notes and chords and timing or how they are put together. You might be able to extract one note at a time under lab conditions and describe it, but 1) you can't get all of them, and 2) you can't hear the single occurrence in the field anyway. All you get is the end result of how it is put together. So, although as Altmann has said, we want to

find out who does what to whom and in what order, we are still working on the "who does what" phase (Altmann, 1965a).

For certain primates, by using film as a recording device, we are beginning to get some ideas of the great range of components that can be used to create a gesture. My work with *Macaca sylvanus* has focused on the number and kinds of components that are used in the expression of a gesture by individual macaques, and on the amount of information produced. For this paper I have concentrated on threat behaviour, but my analysis of friendly and fearful gestures is continuing. I have extracted a list of components used that includes eleven more than have previously been recorded (Table 1). When the data were analysed one of my first major intuitions was substantiated. There are wide differences between animals in terms of which components are used in structuring the same gesture. The next question that comes in mind is what might have caused these differences. The model in Figure 1 is an indication of the complexity and constant feedback that characterizes the communication process between non-human primates. However, for purposes of this discussion, I have utilized the stripped-down model represented in Figure 2. This is a simple information transfer model with a sender, encoder, channel decoder and receiver. As can be seen by comparing Figures 1 and 2, multiple channels are often in use during communication. Since film is designed to pick up material only on the visual channel, this is the channel on which I have concentrated. Even on this one channel a great deal of information and variation were present. The aspect that particularly interested me was to discover what influences the code so that the form or morphology of the gesture varies from individual to individual. In other words, what kinds of factors would interfere with the coding process. I

postulated three potential sources of interference, divided into two major types. The first type was "noise", which is random change affecting the code. This kind of random interference often disturbs the system because there is no way of reversing the process. The major adaptation to noise in most information systems is a degree of built in redundancy in the message. The second type of interference is distortion, which is predictable change. Distortion is much easier to deal with or allow for in a message because the application of a constant modifier will enable the message to be decoded without difficulty. Of course the 'modulating transfer function' (Corso, 1967) will be different for every different type of distortion, but as long as it is predictable it will not affect the message. The two types of distortion under discussion here are "individual idiosyncrasy" and "class-based" distortion. Animals who use unique components when performing a gesture are adding their own individual marker to a gesture, much in the way a bird might use a signature tune (Thorpe, 1972). Class-based distortion on the other hand involves commonalities in the use of certain components based on common membership in a class such as age, sex or kin group.

Since I have indicated some of my results from analysis of the model in other publications, (1978, 1981) I will concentrate here on class-based distortion. In passing I will mention that almost no noise or random variation was found in the signals produced. The signals appear to be quite tightly structured and, although there is a lot of variability, very little of it appears to be random. In addition, individual usage of components is minimal. This was quite unexpected because previous general observation led me to think that various components might be individually idiosyncratic. As an example, slightly outside the confines of this paper, one old female *Macaca sylvanus* regularly used an inhale-exhale vocalization as part of her threat sequence. This animal was often spatially peripheral to the group, but the vocalization insured that when she made a threat she was noticed by all the group members. Within a year, however, this pattern of vocalization had spread to many more members of the group (Burton, 1973) and by the end of the next year it was not being used. Another example was a peculiar movement of the asymmetrical mouth opening which was thought to be idiosyncratic to the head male, but was found on film to be utilized by other animals also. The major source of

TABLE 1
List of components in descending order of use

	Frequency of 67	Frequency of Units (%)	Overall Frequency (%)
1. Eyes staring	65	97.0	51.9
2. Eyebrows raised	64	95.5	46.4
3. Piloerection	62	92.5	85.0
4. Eyebrows forward	61	91.0	37.4
5. Ears back	58	86.6	52.9
6. Mouth open threat	56	83.6	20.2
7.* Mouth stretch	55	82.1	14.4
8. Nostrils flared	52	77.6	22.9
9. Head raised	52	77.6	27.8
10. Eyelid flicker	50	74.6	20.5
11. Head forward	50	74.6	40.0
12.* Lower jaw protrude	44	65.7	10.8
13. Ears forward	43	64.2	24.9
14. Mouth closed	40	59.7	6.9
15.* Mouth forward	30	44.8	10.7
16.* Mouth protrude	26	38.8	7.9
17. Upper jaw protrude	25	37.3	9.5
18. Mouth open grimace	17	25.3	2.1
19.* Skin around eyes back	11	16.4	1.5
20. Incisors show	8	11.9	1.5
21.* Upper lip puffy	7	10.5	0.7
22.* Mouth puffy	6	9.0	0.5
23. Tongue protrude	6	9.0	0.5
24. Lower canine	5	7.5	1.0
25. Tongue show	5	7.5	0.7
26.* Rear crouch	3	4.5	0.5
27.* Mouth open wider right	3	4.5	0.2
28.* Mandrill mouth	2	3.0	0.1
29.* Mouth open wider left	2	3.0	0.1
30. Upper canine	2	3.0	0.3
31.* Lower jaw displaced right	1	1.5	0.1
32.* Body crouch	1	1.5	0.6

* Indicates the 14 components discovered by detailed observation of the data.

TABLE 2
List of classes and within-class division.

Sex	Age	Age/Sex	Kin Group	
Male	Subadult	M. Subadult	Kin	W
Female	Young adult	F. Subadult	Kin	B
	Old adult	M. Young adult	Kin	M
		F. Young adult	Kin	0
		M. Old adult		
		F. Old adult	Non-kin	A

variation, however, came from class-based differentiation of component use.

The variation was analysed in two ways. In the first analysis a count was made of how many units (each unit is one complete expression of a gesture) contained each component. In other words, if one animal made a threat gesture it would be composed of a number of different components. The next time he or she made the gesture, it might look somewhat different because different components were used. I was trying to ascertain in how many units any one component was used. This was labelled "unit-used analysis", and gave an idea of the frequency of each component. The second type of analysis scored the number of frames per unit in which a component occurred. This was converted to a percentage score that allowed units of different length to be compared. The information provided by this "overall-use" analysis was the rate of component use, (i.e., how many times a component was used per unit).

The data from all eleven adult and subadult animals were analysed. This sample was close to optimal, since it included animals of most age/sex classifications, and a number of kin groups. Juveniles and infants were not included because it is possible that variation in their gesture patterns might be more closely related to deficiencies of learning or practice than to a tight control of their component use. Another factor was that the smaller, highly active young were not as easy to film, and obtaining film of a quality comparable to that obtained for the older animals was more difficult.

One of the most striking features of this analysis was that no component was used 100% of the time by every animal. This means that there is no irreducible minimum of components necessary to define threat. There were four components that were used with a high frequency by every animal, but even these were absent on some occasions. These four were "eyes staring", "eyebrows raised", "eyebrows lowered" and "piloerection". Because these were so frequent none of them played a part in discriminating between classes of animals by unit use. This discovery of the absence of an absolute pattern for threat is of great theoretical importance since it indicates that the concept of threat exists without a particular pattern of components being necessary to express it.

The four classes which were chosen for analysis were age, sex, age/sex and kin group. These classes seem to cover a fairly wide range of attributes which might be considered socially relevant to the animals. The integration of the age and sex categories was included because it seemed possible that the differences between the sexes might be obscured by age or those of age by sex. In fact this division by age/sex was not clearly discriminated in both techniques of analysis. However, as an example it did allow some distinctions to be drawn between subadult males and subadult females. The kin group class was included because it seems very clear that matriline membership is an important factor of a primate's life. There were four kin lines present in this group, and one non-kin individual A (whose mother had died). At this particular time there were no immigrants to the group. Each class was broken down into the relevant subdivisions as indicated in Table 2. One of the subdivisions, the young adult male category, was vacant.

Tables 3 and 4 indicate the differences within and between the classes according to the type of analysis used. The unit use, or frequency, analysis gave results that differed somewhat from the rate, or overall use, analysis. The overall use analysis (Table 3) provides a more extensive discrimination within the various classes than does the unit use analysis. This is reasonable because there are only a fixed number of components that can be used or not used, but the rate analysis can vary by being either much lower or higher than the group mean. Unit use analysis for example is not sufficiently complex to distinguish within the age/sex category.

Some of the discriminations in the unit use table are based on the fact that one of the subclasses has no distinguishing component while the other(s) have at least one.

Tables 3 and 4 also provide another type of information. In these tables those components that distinguish within classes are listed as "W", while those that distinguish both between and within classes are indicated with a "B". These "B" components provide two types of information. They indicate within-class distinctions, as well as the types of components that discriminate between classes, and thus provide a structured focus or variability in the gesture. The most noticeable difference between

TABLE 3
Summary of overall use that discriminates between and within classes: age, sex, age/sex and kin

Components	Age Category			Age Category		Age/sex Category				Kin Category			
	OA	YA	SA	M	F	AM	SAM	OF	YAF	W	B	M	O
Ears Forward						W					W		
Nostrils Flared	W							W		W			
Eyes Staring	W							W					
Head Raised	W									W			
Lower Jaw Protrude	W									W			
Mouth Open Threat								B					
Ears back			W	W									
Mouth Closed			W	W			W						W
Mouth Open Grimace							B						
Incisors Show							B						
Rear Crouch				W			W						
Eyelid Flicker										B			
Upper Jaw Protrude										B			
Mouth Stretch										B			
Mouth Protrude												B	
Mouth Forward												B	
Eyebrow Forward	W							W				B	
Mouth Open Grimace			B										

W refers to components which distinguish categories within classes.
B refers to components which distinguish between classes.

"W" and "B" components is that "B" components are to a large extent mouth components while the within-class discriminators tend to be non-mouth components (Table 5).

The breakdown in Table 5 indicates that there is a significant difference in the use of mouth and non-mouth components in discriminating within and between classes. This finding corroborates another previous discovery (1981) about the differential use of mouth and non-mouth components. In Table 6 and 7 the numbers of constant and variable components are divided between the categories of mouth and non-mouth. The constant components are the ones used by various animals at 100% frequency, while the variable components are subdivided into those used several times, and those used only once (unique components) by various individuals. I found that

the constant components were significantly more often non-mouth components $X^2 P^2 < .05$. This was true for a list of component types. In Table 7, the actual total incidences of mouth and non-mouth components were compared and revealed a significant association of non-mouth components with consistent aspects of threat, and mouth components with the most variable aspects of threat.

It seems that much of the variation in threat gestures occurred through differential movement of mouth regions. In one interpretation of this, differential use might occur because within-class markers are held more constant. In other words, in order to indicate kin group affiliation or age status, an individual would use a fairly consistent marker. The between-class differential components would then be open to the potential of expressing more variability. One of the important features of this dis-

TABLE 4
Components used by Age, Sex, Age/Sex and Kin classes which distinguish within and between classes by unit use

Components	Age Category			Age Category		Age/Sex Category				Kin Category				
	OA	YA	SA	M	F	AM	SAM	OF	YAF	SAF	W	B	M	O
Head Raised				W							W			
Mouth Stretch					B									
Piloerection					B									
Nostrils Flared		W			W									
Eyelid Flicker			B											
Mouth Closed			W					W						W
Ear Forward												B		
Lower Jaw Protrude								B						

covery is the idea that the variation is structured not only by the class of the animal, but also by the kind of component by which consistency and variability are expressed.

The third major feature of this analysis is the discovery that kin group is the most clearly differentiated class. It is well demarcated in both types of analysis, but the overall-use analysis is particularly interesting.

TABLE 5
Division of Non-Mouth and Mouth Components

	Non-Mouth	Mouth	Total
Between Class	3	10	13
Within Class	9	3	12
Total	12	13	25

Fischer's Exact test $p = .0015729$ $p < .025$

Table 8 presents information concerning which components occur preferentially in each kin group. One can see how clearly even A, the non-kin individual, is separated from the others. Thus, in the search for patterns of component use, it seems very clear that animals are not just using any components which come to mind. Their ages, sexes, and kin groups clearly provide a significant constraint on the shape of the gesture. The fact that kin group is so clearly defined indicates that it is undoubtedly a very important aspect of primate group life. It is perhaps surprising that kin group differentiation is more clearly indicated than age and even sex, but this may indicate something about how primate groups structure themselves.

In addition to giving primatologists a window into group social structure, this complex communication system also may permit incoming animals to become aware of the group's organization. This is of inestimable value for integrating new group members. Some animals immigrate into groups as adults and must quickly learn the social situation. This task would be facilitated by the presence of a pattern element to communication which indicates the kin affiliation of each member. Young animals growing up in a large group certainly learn their communication and interaction patterns by observation and imitation of their mother. They would also benefit from having access to a meta-communicative level of information which would serve to inform and remind them of group relations.

TABLE 6
Number of components in mouth and non-mouth categories

	Constant Components	Variable Components	Unique Components
Mouth	4	20	16
Non-Mouth	11	8	4
	15	28	20
	X ² 6.94	X ² 1.52	X ² 3.33
	*X ² 8.40		
	$p < .05$	NS	NS

* Yates correction for small sample size applied

TABLE 7
Incidence of component use in mouth and non-mouth categories

	Constant Components	Variable Components	Constant Components
Mouth	6	107	40
Non-Mouth	38	50	7
	44	157	47
	X ² 39.77	X ² 4.35	X ² 12.34
	X ² c 39.04	X ² c 4.42	X ² c 12.58
	$p < .001$	NS	$p < .05$

c Yates correction for small sample size applied.

Other interesting possibilities for research into social structure arise if future work substantiates consistencies in the types of components which separate various age categories. The potential exists to turn the results of this research into a method of investigating social organization. One area of primate studies which has not been accessible to us until now is the area of self perception. How can we tell how non-talking primates perceive themselves within the social organization of the group? If we are able to discern differences in communication patterns between various age classes, this might enable us to answer some questions about self perception.

TABLE 8
Separation by Kin Group on basis of overall use

Component	Kin Group				Individual
	W	B	M	O	Af
Head Raised	X				X
Lower jaw protrude	X				
Nostrils flared	X				
Eyelid flicker	X				
Ears forward		X			
Upper jaw protrude		X			
Head forward		X		X	
Mouth Stretch		X			
Ears back			X	X	
Mouth Protrude			X		
Mouth forward			X		
Mouth closed				X	
Eyes staring					X
Mouth open grimace					X
Incisors show					X
Rear crouch					X
Mouth open threat					X

If a younger animal began to use patterns associated with older ones this might be an indication of a shift in its age positioning. For females the assumption of adult status has been defined by primatologists as the birth of an infant (Burton, 1972). It is clear, however, at least from personal observation, that some nulliparous females "act like adults" and are of a similar age to other adult females. They may have utilized the communication pattern of older animals to help their interactive status in their groups. An alternate situation might be operating in the case of some males. Generally it takes male primates more years to become adult than females. They are often

physiologically capable of breeding at four years, but even in groups which are characterized by the presence of only one breeding male, they are often tolerated until age six or seven. It is possible that this tolerance might be based on a continuation by these young males of a subadult pattern of communication. In other words, to use an interpretation, if the young males perceived themselves as subadults and acted as such, they would be in less danger of provoking the head male to chase them out of the group. Another possible corollary of this might be a way to define what is meant by social maturity for males. In many primates, social maturity is a tenuously defined term indicating that a male is allowed the prerogatives and roles of male adulthood. This may include free access to whatever females will accept him as a mate, and a place in the respect ranking of the group. Males have often been physiological adults for a number of years before they acquire this social adulthood, e.g. chimpanzees. It would be interesting to note if differences in communication patterns were correlated with this difference in age class. I would suspect that there might be a distinct difference.

In conclusion, it is evident that primate gestures are quite complex methods of information transfer. The system provides information about the age, sex and kin group of the sender. The model used had predicted some randomness in the variability observed, based on noise and individual idiosyncrasy in the system. Instead it was found that most of the variability was tightly structured, even when some components were not used often. Insights were also provided about information at a meta-communicative level. The kinds of components used indicated consistent and variable aspects of the message, providing a potential for a higher level of information than merely proximal level survival data. Among exciting potentials is the possibility of using the communication system to get an inside look at social behaviour. We already get an indication that kin group is a very important aspect of life and is recognized by a social group. Another area of research, which I am presently investigating, is the calculation of the weighted uncertainty of various components to provide an estimate of the amount of information they add to a message. This would begin to give us the power of predictability and a real grasp of how information transfer in a non-vocal system might work.

NOTES

1. A version of this paper was presented at the 9th annual meeting of the Canadian Association for Physical Anthropology, Banff, Alberta, 1981.

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TUBERCULUM SUBCONDYLOIDEUM LATERALE AND THE LATERAL GUTTER OF THE TEMPOROMANDIBULAR FOSSA AMONG SOME HIGHER PRIMATES

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Abstract: Analysis of approximately 500 hominoid crania leads inferentially to an explanation of the occurrence of the subcondylar tubercle in the mandible and of the lateral gutter of the temporomandibular fossa. Statistically, neither of these traits is associated with habitus characteristics of chewing, nor are they sexually dimorphic. Both traits appear to be the result of phylogenetic differences in the musculature governing lateral motion of the mandible.

Résumé: L'analyse d'environ 500 crânes d'hominidés permet d'inférer l'explication de la présence du tubercle subcondylien de la mandibule et de la gouttière latérale de la fosse temporo-mandibulaire. D'un point de vue statistique, on ne peut pas associer ces traits à l'habitude de mâcher ou à un dimorphisme sexuel. Ces deux traits semblent être le résultat de différences phylogénétiques dans la musculature gouvernant le mouvement latéral de la mandibule.

Key Words: Temporomandibular Joint, Hominoid.

INTRODUCTION

Observation of a minute phenomenon can lead into a complex of related phenomena, which in turn can unite to suggest a partial explanation of broader enigmas. Such is the case with the tuberculum subcondyloideum laterale (Weidenreich 1936:76) and the lateral gutter of the temporomandibular fossa. Attention given to the former led to the awareness of the latter, and their interrelatedness; this paper suggests that these two "anomalies" may relate to the development of the entire temporomandibular joint.

While T.D. Stewart was constructing a cast of the Shanidar I Neandertal cranium, he observed a massive exostosis situated on the lateral aspect of the mandibular ramus immediately beneath the condyle. He brought this to my attention and allowed me to use the skeletal collections of the U.S. National Museum for comparative analysis. During my examination of some 500 crania and mandibles I gradually became aware of a related phenomenon – a guttering or channeling of the lateral border of the temporomandibular fossa, so that the limits of that depression extend to the base of the insertion of the zygomatic muscle into the temporal fossa. Incidence of these two alterations was observed in gorillas, orangutans, Neandertals, and modern humans.

MATERIALS AND METHOD

Since a search of the literature revealed no comparative work in regard to the tubercle, nor any mention of the

lateral gutter, I undertook such a study. To this end, I examined random samples of crania and associated mandibles of 30 orangutans, 30 gorillas, 32 Australians, 50 Eskimos, 50 Mongoloids, 28 Polynesians, and archaeological skeletal materials from Florida (50), South Dakota (54), and New Mexico (50) (all from the U.S. National Museum collections), randomly-selected crania and associated mandibles of 50 Blacks in the Howard University collections, and some 50 Black and White cadavers at the University of Michigan. The samples from the first two institutions are random only in the sense that no sorting or selection of individual crania and mandibles was involved, other than avoidance of specimens with damaged temporomandibular regions when possible. A search of the literature on the australopithecines, *Homo erectus*, and Neandertals, and examination of casts in the U.S. National Museum collections, produced a sample of eight Neandertals and one Erectoid with undamaged temporomandibular regions. Applying the chi square test for significant association to all these data, I found a strong relationship between the occurrence of the tubercle and the lateral gutter.

Noted in recording the observations were sex, age (sub-adult, adult), side and size of the tubercle (left or right ramus; absent, slight, medium, marked), condylar pathology, depth of fossa, alterations of the anterior border of the fossa (Newman, 1957:215), the insertion of the zygoma in relation to the position of the fossa, the degree and direction of toothwear, the antero-posterior and

TABLE 1
Incidence of Tubercle in Samples
(Figures in parenthesis refer to percentages)

Category	Orangutan	Gorilla	Neandertal	Australian	Eskimo	Mongoloid	Polynesian	Florida	Sioux	Zuni	Black
Sample	30	30	9	32	50	50	28	50	54	50	50
Age:											
Adult	26	28	8	30	47	49	28	49	50	49	50
Subadult	4	2	1	2	3	1		1	4	1	
Sex:											
Male	15	17	8	19	18	28	12	28	27	22	26
Female	15	11	1	13	32	22	16	22	24	28	24
Indet.		2							3		
Tubercle:											
Individuals:	9 (30)	20 (67)	9 (100)	12 (38)	28 (56)	19 (38)	16 (57)	25 (50)	39 (72)	27 (54)	26 (52)
+ R. Ramus only:	(30)	(5)	(11)	(25)	(14)	(11)	(24)	(28)	(21)	(14)	(12)
Male	2			2	2	1		5	4	2	1
Female	1		1	1	2	1	4	2	4	2	2
Indet.		1									
+ L. Ramus only:	(44)	(5)	(22)	(25)	(14)	(11)		(16)	(5)	(14)	(19)
Male	1	1	2	1	3	1		3	2	2	2
Female	3			2	1	1		1		2	3
+ Both sides	(26)	(90)	(67)	(50)	(72)	(78)	(76)	(54)	(74)	(72)	(69)
* Prominence:											
Absent	50	20	5	45	54	66	28	61	34	54	56
Slight	9	25		14	28	26	11	26	42	39	27
Medium	1	11	2	3	9	6	9	9	20	6	14
Marked		4	11	2	9	2	8	4	4	1	3

+ Percentages are based on their values in relation to the total number of occurrences of the tubercle, not the total sample.

*Absence, or degree of development, by side. Thus in a sample of 50, there could be 100 possible occurrences or absences of the tubercle.

medio-lateral shapes of the condylar head, and the presence or absence of the lateral gutter in the fossa. In examining cadavers, the nature of attachment of the lateral external ligament to the ramus was noted at the time that University of Michigan medical students conducted dissections of the temporomandibular region.

Tuberculum subcondyloideum laterale

Le Double attributes the first mention of the tubercle to Albrecht (apophyse hypocondylienne). While Albrecht did not explain the tubercle, Le Double felt that it was an anomaly created by the "... ossification of the inferior fibers of the lateral external ligament of the temporomaxillary articulation, causing an enlargement in the height and mass of the region where the fibers attached" (1906:338). Boule (1913:96) agreed with Le Double's explanation. Kramberger (1906:165) pointed out the presence of the tubercle, but suggested that it was the result of arthritis, in mandible "J" from Krapina. He termed it the subcotyloid protuberance. Martin (1923:131), in describing the La Quina crania, also mentioned the tubercle, attributing its presence to the external lateral ligament. McCown and Keith (1939:220) also mentioned the tubercle, stating that it served as a point for ligamentous attachment. Weidenreich (1936:67, 76, 77) designated it as the tuberculum subcondyloideum laterale, and felt that: "... it represents only the superior end of the crista ec

tocondyloidea" (1936:67). Patte (1955:257) felt that the tubercle was due to the pressures of the external lateral ligament, but that it had no phylogenetic value. Some mention that they have observed the tubercle in gorillas, orangutans, chimpanzees, and modern humans. In their studies of modern humans, Sullivan (1922), Krogman (1932), Wood Jones (1931) and Oettking (1930) do not mention the tubercle.

The tuberculum subcondyloideum laterale most commonly appears as a rough ridge paralleling the long axis of the mandibular ramus. Although form varies, it is usually from 2 to 6mm in length and less than 3mm in width. It is quite prominent on Neandertal mandibles, being more pronounced on these than is the case with modern humans. In the gorilla and the orangutan, the tubercle appears as an unroughened conical exostosis of medium development.

Le Double (1906:338) observed that the shapes which the tubercle assumed were those of a hook, a straight thorn, a truncated thorn, etc. Kramberger (1906:165) noted that the tubercle was separated from the capitulum by a groove. Weidenreich (1936:67, 76, 77) also mentioned that a sulcus separated the top of the tubercle from the capitulum, and described it as an oval exostosis on the Peking *Homo erectus* jaws. He observed its occurrence on some Australian and Chinese jaws, on gorilla and orangutan jaws, but not on chimpanzee jaws. Patte (1955:257)

felt that the tubercle would be better designated as the tuberculum pterygoideum superius, even though the external lateral ligament enters at this point.

My observations conform to the sizes and shapes already noted. In the gorilla sample, although the tubercle was quite marked, it was not developed to the degree seen in the Neandertal materials in relation to the overall robusticity of the mandible. The gorilla tubercle form differs from that seen in all other instances save the orangutan. As seen on the gorilla jaws, it is in the form of a symmetrical, conical projection immediately beneath the condyle. The apex of the cone and its entire surface are smoothed, lacking the roughening that characterizes the Neandertal and *Homo sapiens* examples.

In the orangutan sample the tubercle is much more gracile than the form seen on the gorilla mandibles. When the tubercle is present on orangutan mandibles, it is situated much lower on the ramus than is the case with gorilla tubercles. It usually appears as a slight swelling more analogous to the form seen in the gorilla sample than to the Neandertal or modern human samples.

The casts that show an undamaged temporomandibular joint are Peking G2, the La Quina male, La Chapelle, Ehringsdorf, Krapina J, Teshik Tash, La Ferrassie, and Shanidar I. In these, the tubercle is always present, elongate, and "marked" in development. Although there are a few samples on mandibles of modern humans that are "marked" in their development, none can compare with the robusticity seen on the Neandertal casts. Even the jaw of the child from Teshik Tash displays a very well-developed tubercle.

In modern humans the tubercle also assumes an elongated shape. However, there is a much wider variation in form and degree of prominence among the modern human samples than is seen in any of the others. Table 1 shows that, while the tubercle is present in about one-third of the observations on orangutan jaws, two-thirds of the observations on gorilla jaws, and in all observations on the Neandertal jaws, it is present in only half the cases in the modern human samples. Furthermore, at times in the modern human samples, the tubercle was not present but replaced by a pit. Since the position of this pit is not at variance with the position of the tubercle, I am inclined to believe that both serve the same function and are due to the same causes, but whether they are piezoelectrical responses (cf. Eyman, 1970) is unknown. Table 1 indicates that the variation in the frequency of the tubercle is not significant among modern humans.

The tubercle can appear on only one side, or simultaneously on both sides. In the latter instance, the degree of development of the two tubercles is usually unequal.

Lateral gutter of the temporomandibular fossa

To my knowledge this feature is not mentioned in the literature. Observation of a "normal" fossa reveals a clearly-defined depression in the base of the skull. Lateral to it, the bone is flat or convex. When the gutter is present, the fossa no longer is a well marked depression. The lateral border of the fossa disappears and the depression is

channeled laterally so that it has a U-shape. Usually the gutter maintains the maximum depth of the fossa, although sometimes it becomes more shallow as it extends laterally. When no "border" could be detected on the lateral side of the fossa proper, but instead a gutter could be both seen and felt, then the gutter was recorded as present.

The gutter seems to occur somewhat independently of the tubercle. Table 2 shows that the gutter occurs in all cases in the orangutan sample, about one-half the cases in the gorilla sample, three-fourths of the cases in the Neandertal sample, and about one-half the time in the modern human samples. At times there is a gutter but no corresponding tubercle; at other times the reverse is true. Often a gutter will appear on the left side and a tubercle on the right side, or the reverse. There can be a gutter on both sides, but no tubercle, or a single tubercle; or the gutters can be absent, with a tubercle present on one or both sides.

In the orangutan sample, all of the crania had a gutter and the fossa was quite shallow, almost to the extent of being absent. In some cases the gutter was deeper than the rest of the fossa. The channel in the gorilla crania seems more analogous to the condition seen in the Neandertals and modern humans than it is to the condition seen in the orangutan crania. This situation parallels that seen for the tubercle.

STATISTICAL ANALYSES

As can be seen from Table 3, chi-square tests and Fisher's Exact Tests (cf. Siegel, 1956) were applied to the data. The probabilities are derived from Pearson and Hartley (1958). All tests involved an assumption of a one-tailed test corrected for continuity; where applicable, they involve contingency coefficients as well as the corrected contingency coefficient.

In all of the Fisher's Exact Tests, only one (#12) necessitated Coult's (1965) modification. Table 3 indicates 34 tests that surpassed the initial assumption that the criterion level for significance should exceed the 5% probability level. It might also be noted that of the 34 tests that met this criterion, 5% could provide "spurious" (random-chance "significance"). Translated into the 34 significant tests this means that at the minimum 1.7% are due to random sampling error. This is more pertinent with respect to tests #27, #30, and #34 where the results seem, to me, invalid.

In Table 3 I have grouped the data and their significances in rank-order form. I present to the reader a point-by-point summary of the salient interpretation of these data.

It should be obvious from column 3, Table 3, that the bilateral presence or absence of the tubercle is striking when the orangutan and gorilla samples are compared. The same is true for the gutter. Simply put, comparatively gorillas are evolutionarily closer to modern *Homo sapiens sapiens* than are orangutans in this regard. Obviously this has been noted before in other contexts.

TABLE 2
Incidence of Gutter in Samples
(Figures in parenthesis refer to percentages)

Category	Orangutan	Gorilla	Neandertal	Australian	Eskimo	Mongoloid	Polynesian	Florida	Sioux	Zuni	Black
Sample	30	30	9	32	50	50	28	50	54	50	50
Age:											
Adult	26	28	8	30	47	49	28	49	50	49	50
Subadult	4	2	1	2	3	1		1	4	1	
Sex:											
Male	15	17	8	19	18	28	12	28	27	22	26
Female	15	11	1	13	32	22	16	22	24	28	24
Indet.		2							3		
• Gutter:											
Absent		33 (55)	1 (11)		47 (47)	64 (64)	10 (18)	48 (48)	52 (48)	59 (59)	48 (48)
Present	60 (100)	27 (45)	7 (78)		53 (53)	36 (36)	46 (82)	50 (50)	54 (50)	41 (41)	52 (52)
+ R. Fossa only:		2 (7)			2 (4)	2 (4)		5 (10)	11 (20)	4 (8)	4 (8)
Male								2	5	8	8
Female		2			2	2		3	6	1	2
+ L. Fossa only:		5 (17)	1 (11)		13 (26)	20 (40)	10 (36)	11 (22)	10 (18)	17 (34)	6 (12)
Male		3	1		4	8	4	8	6	10	4
Female		2			9	12	6	3	4	7	2
+ Both fossae	(100)	(76)	(89)		(70)	(56)	(64)	(68)	(62)	(58)	(80)

+ Percentages are based on their values in relation to the total number of occurrences of the tubercle, not the total sample.

* Absence, or presence, by side. Thus in a sample of 50, there could be 100 possible occurrences or absences of the tubercle.

With respect to the gutter, the same column indicates a remarkable difference between orangutan and gorilla (the orangutan has a more "shallow" temporomandibular fossa and more pronounced "guttering" than the gorilla). It also indicates that the guttering is variable within modern human groups.

Bilateral presence or absence of both tubercle and gutter is interesting when orangutan and gorilla are compared, but also a unilateral presence/absence is notable. For *Homo sapiens sapiens*, the Fisher's Exact Test suggests that there is considerable bilateral/unilateral variation with respect to the gutter when comparing apes with humans. Also, the presence/absence of the gutter among extant human groups should be noted, but in the same vein recall that the recording of the presence of the gutter was done on a subjective basis.

In effect then, it would appear from the sample that the presence/absence, association/non-association, bilateral/unilateral, side and tooth-wear differences reflect evolutionary and habitus responses to mastication. *Why* remains a question in terms of these two variations and is outside the scope of this paper.

The age of the individual, condylar pathology, depth of the fossa, alterations of the anterior border of the fossa, the relations of the insertion of the zygoma to the position of the fossa, the degree and direction of tooth wear, and the antero-posterior and medio-lateral shapes of the condylar head, do not seem to have any significant bearing on the occurrence of either the tubercle or the gutter. Admittedly, the small size due to inadvertent sampling bias of the Neandertal sample has probably affected both the acceptance and rejection of certain of the premises tested.

DISCUSSION

In the series examined, it soon became apparent that the concept of the tubercle as a response to condylar pathology (such as arthritis) was untenable. Only a very few of the occasional pathological mandibles and crania showed either the tubercle or the gutter.

Furthermore, as the statistical tests indicate, neither of the two phenomena is associated with sex difference. The possibility that the features were the result of habitus characteristics of chewing was also discounted. The Zuni and Eskimo samples, for example, do not indicate that the dietary effect is expressed in this way. This tenet was further discounted when the lack of sexual difference and the seeming lack of influence of tooth wear were taken into consideration.

The medio-lateral and antero-posterior shapes of the condylar head, and the depth of the fossa, may have some influence on the occurrence of one or both of the anomalies. However, the ensuing discussion suggests that these factors are negligible.

Finally, age would seem to have some bearing on the problem. This is particularly well-illustrated by the Teshik-Tash Neandertal child, where the tubercle and the gutter are both prominent. The presence of either or both conditions was seldom noted in subadult *Homo sapiens*.

The sample may be ranked with the apes at one end, the Neandertals somewhere in the middle, and the *Homo sapiens* samples at the other end. The Neandertal sample, small as it is, represents a transitional point between the two poles, in terms of the temporomandibular changes

TABLE 3
Summary of Statistics

✓ = corrected for continuity
 * signif. at .05
 ** signif. at .01
 *** signif. at .001

Test Group	✓	N	D.F.	X ²	<P	>P	Fischer's Exact	Exact P	C	C _{max}	Corrected C
1. Bilateral pres.-abs. tubercle, orang-gorilla (sexes pooled)	✓	50	1	17.278***	—	0.001	—	—	0.507	0.707	0.717
2. Bilateral pres.-abs. tubercle, modern humans (sexes pooled)		292	7	12.364	0.10	0.05	—	—	0.200	0.935 (asymmetrical)	0.214
3. Bilateral pres. abs. gutter, orang-gorilla (sexes pooled)	✓	53	1	11.501***	0.001	—	—	—	0.422	0.707	0.597
4. Bilateral pres.-abs. gutter, (no Australians) modern humans (sexes pooled)		212	6	28.510***	0.001	—	—	—	0.310	0.926 (asymmetrical)	0.335
5. Bilateral pres.-abs. tubercle and gutter together, orang-gorilla (sexes pooled)		15	1	—	—	—	one-tailed	0.524	—	—	—
6. Bilateral pres.-abs. tubercle and gutter together, modern humans (sexes pooled, no Aust.)		117	6	13.591*	0.05	0.025	—	—	0.323	0.926 (asymmetrical)	0.349
7. Bilateral tub-pres/gutter abs. and reverse, orang-gorilla (sexes pooled)		29	1	—	—	—	one-tailed	0.001***	—	—	—
8. Bilateral tub-pres/gutter abs. and reverse, Esk.-Mong., Poly.-Neg., Fla-Sioux-Zuni (sexes pooled)		63	2	5.888	0.10	0.05	—	—	0.292	0.816 (asymmetrical)	0.358
9. Unilateral pres., tub. vs. gutter, orang-gorilla (sides and sexes pooled)		16	1	—	—	—	one-tailed	0.006**	—	—	—
10. Unilateral pres., tub. and gutter, modern humans (sides and sexes pooled)		169	6	3.559	0.75	—	—	—	0.144	0.857 (asymmetrical)	0.168
11. Unilateral tub. and gutter pres., same side, R. vs. L., Esk-Mong, Fla-Sioux-Zuni (sexes pooled, no Poly or Neg)		14	1	—	—	—	one-tailed	0.308	—	—	—
12. Tub. L. only, gutter R. only vs. tub. R. only, gutter L. only, Esk-Mong-Poly, Fla-Sioux-Zuni (Neg., Aust. out)		11	1	—	—	—	one-tailed	0.012**	Coul't's note used		—
13. Pres/abs. tub., apes vs. Neand. (side, sexes pooled)	✓	69	1	5.650*	0.025	0.01	—	—	0.275	0.707	0.389
14. Pres.-abs. tubercle, Neand. vs. Sapiens (sides, sexes pooled)	✓	373	1	5.520*	0.025	0.01	—	—	0.121	0.707	0.171
15. Pres.-abs. gutter, Neand. vs. Sapiens (sides, sexes pooled)	✓	373	1	2.290	0.025	0.10	—	—	0.001	0.707	0.001
16. Pres.-abs. gutter, apes vs. Neand. (sides, sexes pooled)	✓	69	1	0.510	0.50	0.25	—	—	0.001	0.707	0.001
17. Bilat. vs. unilat. gutter, apes vs. Sapiens (sexes pooled)	✓	424	1	40.820***	0.001	—	—	—	0.296	0.707	0.419
18. Tub. present-absent, humans by sample (sexes pooled)		364	7	13.820	0.10	0.05	—	—	0.191	0.926 (asymmetrical)	0.206
19. Pres.-abs. tubercle, apes vs. humans (sides, sexes pooled)	✓	424	1	0.110	0.75	0.50	—	—	0.001	0.707	0.001
20. Tub. pres.-abs. (abs. bilat.), sapiens by sex (side, groups pooled)	✓	351	1	0.360	—	0.75	—	—	0.001	0.707	0.001
21. Gutter pres. abs. bilat., sapiens, by sex (side, group, Aust. ignored)	✓	332	1	4.410*	0.05	0.025	—	—	0.114	0.707	0.161
22. Tub. pres.-abs. (abs. bilat.), apes, by sex (side, group ignored)	✓	59	1	0.010	—	0.75	—	—	0.000	0.707	0.000
23. Gutter pres.-abs. (abs. bilat.), apes, by sex (side, group ignored)	✓	60	1	0.080	—	0.75	—	—	0.000	0.707	0.000
24. Gutter pres.-abs., humans by group (sexes pooled, Austr. ignored)		332	6	17.690**	0.01	0.005	—	—	0.225	0.926 (asymmetrical)	0.243
25. Tub. sl.-mkd., apes vs. humans (side, sexes pooled)		187	2	1.040	0.75	0.05	—	—	0.001	0.816	0.001

TABLE 3 (continued)

Test Group	✓	N	D.F.	X ²	<P	>P	Fischer's Exact	Exact P	C	c _{max}	Corrected C
26. Gutter pres.-abs. bilat., by sex, Mong. sample		28	1	—	—	—	one-tailed	0.027*	—	—	—
27. Gutter pres.-abs. bilat., by sex Poly. (none abs. bilat.)		18	1	—	—	—	one-tailed	0.0000***	—	—	—
28. Gutter pres.-abs. bilat., by sex, Zuni sample		29	1	—	—	—	one-tailed	0.257	Coult's note used		—
29. Bilat. tub.-gutter pres.-abs., by sex, Mong. sample		17	1	—	—	—	one-tailed	0.421	—	—	—
30. Bilat. tub.-gutter pres.-abs., by sex, Poly. (none totally abs.)		6	1	—	—	—	one-tailed	0.0000***	—	—	—
31. Tubercle pres.-abs., by sex, Mong sample (sides ignored)	✓	50	1	1.578	0.25	0.10	—	—	0.175	0.707	0.248
32. Tubercle pres.-abs., by sex, Sioux	✓	52	1	4.824	0.25	0.025	—	—	0.291	0.707	0.412
33. Gutter pres.-abs., by sex, Mong. sample (side ignored)	✓	50	1	0.058	0.90	0.75	—	—	0.000	0.707	0.000
34. Gutter pres.-abs., by sex, Poly. sample (side ignored; none abs.)		28	1	—	—	—	one-tailed	0.0000***	—	—	—

observed. The curious discrepancy in the occurrence of the tubercle and the gutter between the two ape samples, the complete appearance of the tubercle among the Neandertal sample, and the moderate occurrence of tubercle and gutter among the modern human sample reinforce this view.

Perhaps the major point of interest in regard to the two phenomena being considered is neither their relative frequency from group to group, nor a description of either feature; rather it becomes the genetic and muscular force that may have contributed to the formation of the gutter and the tubercle.

Although a great deal of work has been devoted to the temporomandibular joint, neither the tubercle nor the gutter was mentioned. At first glance the statements of Le Double (1906), Boule (1913), Martin (1923), McCown and Keith (1939), Weidenreich (1936), and Patte (1955) — that the tubercle served only for ligamentous attachment — are sufficient. But the questions that immediately arise are: Why does the tubercle not appear on all mandibles? Why does the tubercle seem not to be associated with the gutter? Why do both phenomena occur at all? Clearly, the answers to these should lie not in the presence or absence of pathological conditions, but in the workings of the joint itself. And since the temporomandibular joint is operated by muscles, the answer must lie in the realm of the genetic origins and learned behavior of the muscle action. If this assumption is correct, then the possible implications of the tubercle and gutter become more apparent, in that they might serve as an insight into the muscular differences between the apes, Neandertals, and modern humans. With this concept is the observation that here is at least part of a genetic bundle that is expressive of evolutionary change.

When I was able to observe dissections of the temporomandibular joint, I saw that in the cases where the tubercle was present, the posterior band of the external lateral ligament shifted back along the edge of the ramus,

pulling the anterior band back also. This may or may not be the case, and I feel that further exploration could yield some interesting data. If the ligamentous point of attachment on the ramus is shifting, then possibly there are similar variations in the temporal, masseter, and/or pterygoid muscles also (not necessarily a shift in points of attachment; possibly it is reflected in points of stress). Hylander (1975) provides a detailed discussion of this point.

Angel (1948:231) thinks that heredity is the main factor in the mass and bony relationships of the external and internal pterygoids and the masseter, but that during childhood the use of these muscles can equally reflect learned chewing habits. Bone and muscle structure, and chewing method, shape the joint mainly through their functional effects; but Angel further points out that small muscular and ligamentous forces can strongly mold the bone, and that "... at least a rough blank for a given bone formation develops even in the absence of function ..." (1948:232). He thinks that genetic control is even more important than environment in the formation of the joint, since it is more responsive to the genetically-determined total facial pattern than to the fewer learned chewing patterns (1948:242).

According to Sicher (1952:175), rotatory components of chewing are gradually penumbrated by translatory components as attrition increases. Angel (1948:238) thinks that changes in condylar form and deepening of the fossa are due to loss of vertical height through tooth wear or occlusal changes. He also thinks that it is the articular eminence, rather than the fossa, that bears the slight stress of the condyles during chewing (1948:227). Furthermore, Sicher (1951:6) says that the medial articular lip of the fossa prevents medio-lateral displacement of the condyle. Again, Hylander (1975) has summarized these and other issues. In all of the cases I observed, the medial lip was undamaged. I am confident, therefore, that this factor (in addition to those of attrition, habitus factors,

tooth wear, and the articular eminence) does not play a strong part in the formation of the tubercle and/or the gutter.

Many of the non-human primates possess almost horizontally sloping articular eminences and short pterygoid processes; these indicate that the pull of the external pterygoid is more horizontal than oblique (Angel, 1948:234-235). The muscles responsible for closing the jaws also pull more upward and backward than they do in humans, and there is little lateral movement. Sicher (1952:169-171) observed that jaw-opening among chimpanzees is effected through a purely hinge movement; but that characteristically in humans the jaw is opened by a combination of rotary and translatory movements, since the presence of the mastoid narrows the retromandibular fossa. Likewise the forward bending of the posterior part of the cranial base further narrows the fossa in humans.

Coon (1955:269) has pointed out the strong temporal development seen in the Neandertals and in the Rhodesian skull, and that this muscle is situated far back on the parietal and temporal. He further notes that the masseters and the zygoma are poorly developed. In the Neandertals the internal pterygoid is strong. Contrasted to these conditions, says Coon, is the jaw musculature of modern man; here the temporal muscles are located more anteriorly on the parietal and the temporal muscle bundles pass under a strong zygoma, and the masseters are powerful. Thus Coon feels that in regard to the manner of temporal attachments, the more developed masseter in modern humans, and the total jaw musculature, the difference between the jaw musculature of the Neandertals and modern humans is not phenotypic (1955:270). Indeed, Coon points to the more powerful jaws of modern humans compared with the Neandertals, and suggests that tonal and qualitative muscular differences may provide an explanation (1955:270).

Recalling Angel's remarks about the responsive rather than the directive role of the muscles, it is interesting to note Sicher's (1952:26) statement that mandibular movements are directed much more by muscle than by bone shape and ligaments, partly as a result of the uniqueness of the temporomandibular joint itself. Since the articular disk slides with the motion of the condyle, the former does not alter the form of the articular eminence functionally (Angel, 1948:224).

In my estimation, the muscle that most strongly bears upon the problem of the tubercle and gutter is the external pterygoid. Its force is directed down, in, and forward, thus pulling the mandible forward. Sicher has remarked that the action of only one of the external pterygoids "... will shift the mandible to the other side by pulling one condyle forward, inward, and downward" (1951:19). Forcible clamping of the jaws endangers the position of the condyle and disk on the slope of the articular eminence, and by contraction the external pterygoid prevents their displacement backwards and upwards; thus the condylar-disk-articular eminence relationship is unharmed (Sicher, 1951:27). The point of insertion for the external pterygoid muscle fibers into the disk becomes important

in this regard for, until the teeth come into mutual contact during chewing, the external pterygoid must assume responsibility for avoiding mandibular displacement (Sicher, 1952:177).

The role of the ligaments in chewing (notably the temporomandibular, or lateral external ligament) is to tighten as the jaws open, thus forcing the condyles to begin a sliding motion (Angel, 1948:226). The ligaments by themselves are not a sufficient fulcrum for these movements and must work together with the external pterygoid. Zimmerman (1951:88), like Sicher (1952:161), states that the temporomandibular ligament strengthens the articular capsule being "... the only accessory ligament of the joint directly associated with the capsule". The zygoma provides attachment for the lateral wall of the joint capsule and the temporomandibular ligament, but it does not protect the lateral edge of the fossa (Zimmerman, 1951:202). Sicher notes that the sphenomandibular and stylomandibular ligaments lack any great influence on mandibular movement (1952:163).

As to lateral and rotary movements of the jaw, Sicher (1952:171) points out that the reduction of the free space behind the mandible creates constriction of movement, necessitating a forward movement of the mandible in chewing. Thus, the "external pterygoid muscle was utilized in the acquisition of the protrusive component of the opening movement . . . Since this intricate movement is not necessitated by the shape of the articulating bodies or by the course of ligaments, the two basic movements can be enacted independently" (1952:171). A lateral shifting of the mandible occurs only when one condyle and disk are pulled toward the articular tubercle, during which action the mandible moves on a vertical axis running a few millimetres behind the condyle on the side towards which the chin is moving. Thus, in moving the chin to the right, the axis is behind the right condyle, and the left condyle and disk move forward, medially, and downward. In right lateral movements the right condyle does not rotate in place; it moves a little *outward and forward* (Bennett's movement), because such a lateral shift demands that the right condyle be held in place by muscle fibers to some degree (Sicher, 1952:171). Sicher calls attention to the fact that the external pterygoid is prominent in moving the mandible because of its role in so many different movements, but cautions that it cannot be termed the sole opener of the jaws (1952:173). As to lateral movements, Sicher states:

The lateral rotation . . . is an asymmetrical variation of the forward thrust; . . . one external pterygoid muscle combines forces with the slightly contracted elevators. It is . . . necessary that the elevators assist in this movement by holding the "resting" condyle in its position. . . by preventing it from deviating anteriorly to any great extent. The participation of the retracting fibers is in all probability responsible for the movement of the "resting" condyle; that is, for the Bennett movement. This seems the more probable because of the possibility of a lateral rotation from a forward position of the mandible, a movement which entails a retraction of that condyle to this side of which the chin deviates, whereas the other condyle is kept immobilized in its forward position (1952:174).

CONCLUSIONS

Some explanations for the subcondylar tubercle and the lateral gutter can now be proposed. The comments by Coon, Angel, and Sicher allow for the elimination of habitus characteristics as a causal factor of any appreciable influence. The marked appearance of the tubercle on the mandible of the Teshik Tash Neandertal child is relatively proportional in keeping with the development seen on adult Neandertal mandibles. This condition applies to the relative development of the tubercle on the mandibles of subadult *Homo sapiens* and their adult counterparts. Comparison of samples from populations with known dietary differences as indicated above further reinforce this view.

The anatomical glimpses of Neandertal musculature that are afforded through bone study suggest a most interesting genetic bundle involved with their morphological development. Coon's remarks on the jaw musculature of modern humans and the Neandertals, plus Sicher's comments on chimpanzee jaw musculature, are enlightening in regard to the extreme development of the tubercle among the Neandertals.

Since the shape of the bone components of the temporomandibular joint seem to depend more upon the musculature than anything else, and since the musculature seems to dictate the chewing pattern, I am left with the conclusion that the gutter is caused by a lateral elongation of the articular disk. This elongation seemingly occurs as a response to a lateral force placed on the disk by the temporomandibular ligament and the insertion of the fibers of the external pterygoid, which, it will be recalled, work together in opening-closing movements anyway. The tubercle would appear as a result of the same stresses and by the same agents.

Zimmerman has commented on the role of the zygoma in forming an attachment for the lateral edge of the disk and the temporomandibular ligament, and that it does not provide lateral protection for the fossa. Coon has stressed the greater strength of the zygoma in modern humans.

Perhaps a weaker jaw musculature and zygoma in the Neandertals are the causes for the prominence of the tubercle among them. A weakened lateral attachment for the disk and ligament might have allowed for a more lateral movement, expressing itself through both the tubercle and the gutter. The Bennett movement, in this regard, would explain a possibly greater stress being placed on both the articular disk and the ramus, in order to counterbalance a greater tendency towards lateral movement. In modern humans the stronger zygoma and jaw musculature might decrease such lateral stresses and thus the appearance of the gutter and the tubercle but this might be counterbalanced by the growth of the mastoid process and a shift of the posterior part of the cranio-facial axis, which, we have seen, diminishes the antero-posterior space available for the expansion of the fossa. This could conceivably be one expedient for avoiding condylar displacement over the edge of the articular eminence. I am not necessarily attributing any greater power to the temporomandibular ligament and the external

pterygoid fibers relative to their attachment into the disk and below the condyle; I am merely suggesting that the different orientation of the jaw musculature, and structural differences in the joint, might have placed a different stress on those fibers. This would tend to reinforce Coon's suggestion of differences in muscle tone.

Among the ape samples, it can be seen by consulting Tables 1 and 2 that the tubercle is present on both sides far more commonly on gorilla jaws than on orangutan jaws, which closely approximates the condition seen when contrasting the Neandertals with modern humans. Conversely, the gutter is much more frequent among the orangutans than among the gorillas, which is paralleled to a lesser degree when the Neandertals are compared to modern humans. Perhaps these conditions are indicative that, initially, greater stress is placed on the disk, causing the gutter to become an actuality prior to the tubercle.

If the small size of the Neandertal sample can be considered as affording a dependable inference, then the temporomandibular region of the Neandertals is curious indeed. The continual appearance of the tubercle in a marked state of development among the Neandertals is in strong contrast to both the ape and the modern human samples. The latter two are similar in that, when the tubercle is present, it is most commonly slight in development, less frequently is of medium expression, and but rarely is marked in appearance. The similarity in expression of both features jointly by side among the Neandertals and modern humans has already been discussed. Again, the occurrences of the gutter in both of the fossae at the same time among the apes and modern humans, but not among the Neandertals in relation to either or both of these two, is quite interesting.

Kramberger and Weidenreich both mention a sulcus separating the mandibular condyle from the tubercle. Perhaps this is indicative of a nerve, or nerve injury, which produced the tubercle. I am inclined to discount this explanation, but research along this line might be of interest.

It appears that the weaker musculature among the Neandertals, existing as it were in a state of indecision in terms of the transition from an ape temporomandibular region to that of modern humans, is the explanation for the discrepancy they present. If the assumption is correct that antero-posterior constriction of the fossa is caused by the development of the mastoid process, then the bilateral symmetry of the presence of the gutter among the apes becomes apparent. In this case a balance between the medio-lateral and antero-posterior stresses has been attained, with no great demand that additional ligamentous attachment be provided by the tubercle. Modern humans, on the other hand, lack this antero-posterior freedom for expansion of the fossa, but increased muscular development, shift in the direction of muscular pull, alteration of the cranio-facial axis, and the Bennett movement produce both the tubercle and the gutter. Perhaps one can postulate a series of conditions between these two extremes that are expressed by both the tubercle and the gutter among the Neandertals. Here the relative increase

of the mastoid process has begun to reduce the amount of antero-posterior expansion available to the fossa but there is no longer sufficient stress to produce a constant bilateral channeling. Balance is achieved by reinforcing the points of ligamentous attachment, producing the massive tubercle and frequently the lateral gutter.

ACKNOWLEDGEMENTS

I am indebted to Dr. T.D. Stewart, Division of Physical Anthropology, U.S. National Museum; Dr. M.A. Cobb, Department of Anatomy, Howard University; Dr. R.T. Woodburne, Department of Anatomy, University of Michigan; Dr. W.M. Dempster, Department of Anatomy, University of Michigan and others, for their helpfulness and advice pertinent to this study.

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C-LINE POLYMORPHISM OF THE PALMAR DERMATOGLYPHICS AMONG THE GAUR BRAHMINS, INDIA

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Abstract: C-Line terminations of 161 male and 99 female Gaur Brahmins of Patiala City, Punjab have been studied. The difference between the two sexes for C-line terminations is not significant.

Résumé: Nous avons étudié les terminaisons de la ligne C (de la paume) dans un échantillon de 161 hommes Gaur et 99 femmes Gaur qui sont Brahmins de la ville de Patiala au Punjab. Nous n'avons pas trouvés de différences significatives entre les membres des deux sexes dans les terminaisons de la ligne C.

Key Words: Dermatoglyphics, Punjab, C-line polymorphisms, Sex differences.

INTRODUCTION

The Gaur Brahmins, an endogamous subcaste of the Brahmins, practising gotra (clan like organization) are distributed over Haryana, Punjab and Uttar Pradesh. They practice settled agriculture. Data for foot measurements, physical characters and finger dermatoglyphics have been reported elsewhere (Sharma et al. 1978; Garg, 1982; Garg and Chattopadhyay, 1981/1982 and 1984).

Among the four main lines, D,C,B and A, it has been noticed that the C-line is the only main line of the palm which shows true polymorphism in terms of direction as well as degree of transversality. Therefore, C-line termination has been used by physical anthropologists and geneticists as an important tool for population genetics studies (Rife, 1968; Plato, 1970; Bhattacharya, 1971; Bansal, 1972; Bhanu, 1972; Ghatge, 1974; Tyagi and Maseldan, 1974; Kazi, 1975; Bhanu, 1975; Chakravarty, 1979; Narahari, 1979; Krishan et al., 1979; Das Sharma, 1980; Veeraju, 1980; Naidu, 1980; Narahari, 1980 and Sengupta, 1983). The present study deals with the bilateral, bisexual and population differences exhibited by C-line termination among the Gaur Brahmins.

MATERIAL AND METHOD

The data analyzed in the present paper consist of bilateral inked impressions of 260 Gaur Brahmin children (161 male and 99 female) collected from government schools in the villages of Alona, Sone Mazra, Sagalpur, Sonalian, Lachrukalan, Kammi and Chammaru, Tehsil Rajpura, Patiala District, Punjab. Care was taken not to include any blood relations of the subjects. The prints were taken and analyzed according to the method described by Cummins and Midlo (1961). C-line terminations were classified into three model types as described by Bhattacharya (1971):

- Type I. Includes the terminations ending at 3, 4, 5, 6 and 7.
- Type II. Includes the terminations ending at 9, 10, 11, 12 and 13.
- Type III. Includes the terminations ending at 8, X, x and 0.

TABLE 1
Frequency distribution of C-line termination of palmar dermatoglyphics among the Gaur Brahmins

Type	Male					Female				
	Right		Left		Both	Right		Left		Both
	n	%	n	%		n	%	n	%	
I	51	31.68	78	48.45	40.06	38	38.38	56	56.57	47.47
II	97	60.25	62	38.51	49.38	36	56.57	32	32.32	44.44
III	13	8.07	21	13.04	10.56	5	5.05	11	11.11	8.08

RESULTS AND DISCUSSION

The percentage frequency distribution of the three types of C-line terminations among the Gaur Brahmins is presented in Table 1. The distribution of the three types shows the following trend in frequencies: II > I > III and I > II > III in males and females, respectively. Type III is the least frequent in both the sexes.

The bilateral distribution of the three types of C-line terminations shows that type II is more frequent on the right palm in both sexes, whereas type I and III show high frequencies on the left palm in both the sexes. The sex-wise classification in terms of these three types reveals that males exhibit type II, whereas, females show type I as the common type. Thus, it indicates that in males the radial terminations are most frequent, whereas in females ulnar terminations are more common. The bimanual differences in both sexes are significant, but the difference between the sexes for three types of C-line terminations are not ($X^2=2.99$ df=2.).

Table 3 compares the occurrence of the three types of C-line terminations among Gaur Brahmins with some of the Northern Indian populations. Types I and II range from 27.00% to 58.33% and 29.00% to 58.08%, respectively, while type III ranges between 2.50% to 23.5%. This indicates that maximum variability is in type I followed by type II and type III. Chi-square has been calculated to test if any of the compared castes differ significantly from the Gaur Brahmins. Since there is no sexually specific difference in the three types of C-line terminations in the present study, the pooled sample of Gaur Brahmins was utilized for the purpose of comparative evaluation. Gaur Brahmins show significant differences only from Rajputs, Brahmins, Sah, Ahirs, Jats, Khatri, Rajput of Kulu and

Rastogi while in all other castes the differences are insignificant.

TABLE 2
Chi-square test for the bilateral and bisexual comparison of C-line termination among the Gaur Brahmins

	X^2	df	at 5%
<i>Bilateral</i>			
Male	14.40	2	S
Female	12.24	2	S
Both	115.78	2	S
<i>Bisexual</i>			
Male/female	2.99	2	NS

ACKNOWLEDGEMENTS

I thank the staff and students of Government Middle School, Alona, Government High School, Lachrukalan, Government Primary School, Sone Mazra, Sogal pur, Chammaru, Kammi; District Patiala for their cooperation during collection of the data. I am also grateful to Dr. P.K. Chattopadhyay, Reader in Forensic Science, Department of Chemistry, Punjabi University, Patiala for his valuable suggestions. Thanks are also due to Professor I.P. Singh, Dr. M.K. Bhasin, Dept. of Anthropology, Delhi University, Delhi and Dr. I.J.S. Bansal, Head, Department of Human Biology, Punjabi University, Patiala.

TABLE 3
C-Line termination in some of the northern Indian populations

Population	sex	n	Type			X^2	Source
			I	II	III		
1. Rajput, U.P.	♂	100	53.00	29.00	18.00	11.5423**	Tiwari, 1963
2. Brahmins, U.P.	♂	155	41.60	40.32	18.07	6.4699**	Tiwari, 1963
3. Sah, U.P.	♂	40	42.50	33.75	23.75	8.6945**	Tiwari, 1963
4. Artisan caste, U.P.	♂	60	39.17	45.00	15.83	0.8233	Tiwari, 1963
5. Gujars, Delhi*	♂	152	—	—	14.56	—	Chattopadhyay, 1971
6. Rajputs, Rohtak*	♂	187	36.36	50.27	13.36	2.7810	Chattopadhyay, 1978
7. Ahirs, Gurgaon*	♂	100	27.00	55.50	17.50	9.2053**	Chattopadhyay, 1978
8. Jats, Rohrak*	♂	100	29.00	53.50	17.50	7.6840**	Chattopadhyay, 1978
9. Muslim, Kashmir	♂	48	58.33	38.34	3.12	4.1652	Sen, 1966
10. Khatri, Patiala*	♂ & ♀	254	35.43	48.43	16.14	6.2101**	Khushwaha, 1972
11. Banyias, Patiala*	♀	100	38.00	53.75	8.25	1.4059	Ahuja, 1972
12. Mohammedans, Rajasthan*	♂ & ♀	100	49.00	45.00	6.00	1.7192	Kumbhani, 1963
13. Khatri, U.P.	♂ & ♀	120	40.41	43.33	16.26	3.3253	Tyagi & Maseldan, 1974
14. Bengali Brahmins, Lucknow	♂ & ♀	100	41.00	49.50	9.50	0.2101	Tagi & Shuki, 1973
15. Brahmins (Palampur)	—	192	53.64	37.67	8.68	5.1264	D.U.
16. Rajput (Kulu)	—	156	55.00	42.50	2.50	10.4856**	D.U.
17. Rastogi	♂ & ♀	300	30.66	57.84	11.50	9.2821**	Rastogi, 1972
18. Punjabi	♂ & ♀	145	37.88	58.08	4.04	5.5671	Bansal & Bhattacharya, 1972
19. Punjabi (Khatri and Brahmins)	♂ & ♀	100	46.00	42.00	12.00	0.9845	Sharma, 1962
20. Bengali Kayastha, Lucknow	♂ & ♀	100	47.00	55.50	7.50	0.5402	Tyagi & Shukl, 1973
20b. Khatri, Hoshiarpur	♀	186	—	—	18.38	—	Sharma, et al., 1980
21. Ramgarhias*	♂ & ♀	200	42.25	45.25	12.50	1.0036	Singh & Bansa, 1982
22. Gaur Brahmins	♂ & ♀	260	43.08	47.20	9.62	—	present study

* Frequency calculated by present author
** Significant at 5% level

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SIMULTANEOUS OCCURRENCE OF DISCONTINUOUS CRANIAL TRAITS: SOME THEORETICAL AND PRACTICAL CONSIDERATIONS FOR POPULATION STUDIES

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Abstract: The interaction among 27 discontinuous cranial traits in 1040 southern Ontario Woodland crania representing 17 population samples is investigated using the phi coefficient. At the .01 level of significance a greater frequency of positive correlations occurs than is expected by chance. Correlation levels throughout the matrix are, however, low. It is suggested that the inclusion of all variants yielding biologically meaningful correlations, such as those occurring between accessory sutural bones, clino-clinoid and carotico-clinoid bridging and the supraorbital foramen and frontal grooves, is theoretically unsound because it violates the independence assumption for the use of these data in biological distance studies. An empirical study is used to support this contention. Additional correlation matrices are computed for male and female crania and for four of the largest population samples. Twice as many significant correlations were detected in male versus female crania, a result which has important implications for biological distance studies and for studies investigating the association between skeletal variability and residence practices. When the individual population samples are used to determine intertrait correlation the null hypothesis is accepted in each case. It is concluded, that the best estimate of intertrait correlation in the population is achieved by pooling samples of the same deme rather than testing them individually.

Résumé: Les interactions de 27 caractères craniens discontinus sur 1040 crânes, tirés de 17 populations du sud de l'Ontario, étaient analysées avec le coefficient Phi. Un plus grand nombre de corrélations significatives (≥ 0.01) en sortaient que prédit par l'hasard. Cependant le niveau de ces corrélations positives étaient bas. Parce qu'il viole la présomption de l'indépendance des mesures statistiques, l'usage de tous les variants donnant des corrélations d'une signification biologique, ne semble pas justifié dans les calculs de la distance biologique entre populations. Une étude empirique soutient cette constatation. D'autres matrices de corrélation étaient construites et pour les crânes d'hommes et pour ceux des femmes des quatre plus grandes populations étudiées. Deux fois plus de corrélations significatives sortaient de l'analyse des crânes masculins que celle des crânes féminins. Ce résultat soulève d'important possibilités pour l'étude de la distance biologique et aussi pour celles des rapports entre la variabilité squelettique et les groupements de résidence. Quand les mesures tirés de chaque population sont utilisé séparément, pour calculer les corrélations entre les caractères, l'hypothèse de nul effet est toujours acceptée. La conclusion tiré de ces analyses est que l'on réalise la meilleure estimation des rapports entre les caractères d'une population en mettant ensemble les échantillons du même deme, plutôt que de les analyser individuellement.

Key Words: Discontinuous Cranial Traits, Populations, Theory.

INTRODUCTION

Physical anthropologists have traditionally used different classes of human biological data (e.g. blood groups, discontinuous and continuous variates of the skeleton and dentition) to estimate the degree of divergence between human populations. Germane to measuring biological affinities among population samples, regardless of the class of data used, is the detection and treatment of correlated variates, since the fundamental premise of computing distance statistics is that the variates occur independently of each other (Mahalanobis, 1936; Grewal, 1962; Berry and Berry, 1967). Detection in this case implies a statistical search for positive or negative correlations and involves, a) sample size, b) the selection of an appropriate statistical test and c) the selection of a confidence level for deciding significance. Treatment concerns the handling of correlated variates in terms of deciding to include or exclude correlated traits in the computation of distance coefficients. In this paper the intercorrelation of discontinuous cranial variants in a large number of southern Ontario Woodland crania is presented to examine the issues involved in this critical area of population research.

BACKGROUND

The general lack of correlation between non-metric traits in the skeleton of *Mus musculus* (Truslove, 1961; Gruneberg, 1963) led to the analogy that these variants were independent of each other in *Homo sapiens*. Berry and Berry (1967) were first to test this assumption in *Homo sapiens* using a sample of 99 Egyptian crania scored for 30 discontinuous cranial variants. They found 10 significant correlations in 378 pairwise tests at the .01 level (correlation coefficient/its standard error ≥ 2.5 and concluded:

These ten significant values can best be interpreted as showing extremely little inter-correlation particularly since four of the ten involve variation at the lambda or in the lambdoidal suture. Furthermore, there was no trend towards association among the 368 non-significant correlation coefficients which were calculated . . . The virtual absence of correlation between variants makes it permissible to sum individual measures of divergences without having to perform the complex adjustments necessary in computing similar statistics from skeletal measurements, which tend to be more highly correlated (Berry and Berry, 1967: 373-394).

This, plus the results from *Mus musculus*, led to the assumption that a discontinuous cranial trait develops through the cumulative interaction of many genes and epigenetic factors under the influence of a threshold mechanism (Truslove, 1961; Gruneberg, 1963; Berry and Berry, 1967). Because so many genetic and nongenetic effects are involved, it is reasonable to assume that the underlying variable (e.g. size of a rudiment) operated on by the threshold mechanism is normally distributed (Sjøvold, 1977). Therefore, in the epigenesis of most traits a certain degree of positive correlation exists due to common genes and environmental factors, with the degree of correlation being a function of the proportion of common factors influencing paired variants. It is not sur-

prising, then, with the large number of genetic and non-genetic factors influencing trait development, that previous studies have found low levels of correlation between traits (e.g. Corruccini, 1974; Suchey, 1975). Yet it is necessary to emphasize that, in most studies employing adequate sample sizes, the null hypothesis of intertrait correlation has been rejected on statistical grounds.

It is germane to note that in previous studies certain traits were repeatedly found to be correlated and this prompted speculation on causality. The developmental tendencies towards hypostosis and hyperostosis showed the most pervasive effects on intertrait correlation (Korey, 1970). Hypostosis, particularly as evidenced by the pattern of interaction between accessory sutural bones, showed the greatest influence (Berry and Berry, 1967; Ossenberg, 1969, 1974, 1976; Korey, 1970; Buikstra, 1972). A regional effect which produced higher correlation levels between adjacent versus non-adjacent traits has also been suggested as a major determinant of intercorrelations (Hertzog, 1968). Population differences in the pattern of intertrait correlations have also been reported (Korey, 1970). The important point is that some variants are correlated for reasons that are biologically meaningful, while other significant correlations may have little biological significance. The latter, which include significant negative correlations, can be regarded as stochastic associations for the purpose of population studies. Significant correlations with reasonable biological explanations are a potential hazard to distance studies since essentially they provide redundant information in the real population. Given this, it is in the area of detecting and treating correlated traits of biological significance that previous studies should be closely analysed.

Much research on intertrait correlation has focused on the selection of appropriate statistical tests. This topic has been discussed thoroughly by Sjøvold (1977) who supports Benfer's (1970) argument for the use of phi over the much used chi square statistic (see Buikstra, 1972; Suchey, 1975). Sjøvold (1977) emphasizes that the problem of measuring the association between traits is secondary to the question of whether the degree of association differs significantly from zero. Phi, because of its close approximation to the chi square distribution ($df = 1$), is more sensitive to this task than other coefficients of association that have been used (e.g. Yule's Q), but possesses an advantage over chi in that it is far less sensitive to sample size. Another advantage of phi is that it is mathematically equivalent to the Pearsonian r which is used to test correlation for metric variants, thus facilitating comparisons of results based on the two classes of variables. Had Corruccini (1974), for example, used phi instead of Yule's Q he would have had a legitimate basis for comparison and perhaps might not have been led to question his results showing that nonmetric traits were less strongly correlated than cranial measurements. A related statistical issue concerns using factor analysis of non-parametric coefficients like phi to investigate the pattern of trait interaction (e.g. Saunders, 1977). While one of the most common applications of phi is as an entry into

matrices to be subjected to factor analysis, the theoretical legitimacy of this approach has been challenged by Sjøvold (1977). The mathematical arguments are beyond the scope of this paper but I am in agreement with Sjøvold's view. I also feel that factor analysis complicates rather than simplifies the issues involved in inter-correlation analyses of discontinuous traits.

A related but more crucial statistical issue concerns the sample size necessary to estimate intertrait correlation in the population. Only Korey (1970) has suggested that sample size has important implications, noting that the population differences in the degree of intertrait correlation he found may have been partly a function of his disparate sample sizes. For the most part, those few researchers who have tested their data for intertrait correlation have followed the lead of Berry and Berry (1967) by using a single sample of approximately one hundred crania. The effects of sample size on the correlation levels have yet to be empirically tested, although, in view of Korey's (1970) data, Type II errors may be characteristic of previous studies.

In addition to differences in statistical methods of detection, researchers vary in their methods of treating correlated variants. The literature is characterized by two opposing models: the inclusive and reductionist. Each of these is governed by its own hypothetical constructs. Advocates of the inclusive model argue that because the overall interaction between discontinuous traits is low, it is unnecessary to omit traits that are significantly correlated, even if the number of significant correlations exceeds chance (Berry and Berry, 1967; Sjøvold, 1977). They propose that the benefits of including a few significantly correlated traits in the computation of distance coefficients outweigh the disadvantages because a large trait battery samples a great proportion of the genome and, in theory, reduces the potential effects of disrupting factors such as genetic drift and small sample size. Proponents of the reductionist model (e.g. Buikstra, 1972; Ossenberg, 1976) argue that positively correlated variants with biological meaning produce redundant information when summed for use in distance formulae. They recommend the exclusion or differential handling of traits to produce a trait list that fulfills the independence requirement. The procedures followed in reducing trait lists must be objective and must be defined within the context of a given research design. For example, Ossenberg (1976) found that all sutural ossicles were significantly correlated with each other and she scored the presence of sutural ossicles per cranium regardless of their location. Essentially, then, she treated sutural ossicles as a single trait. This procedure, however, requires intact crania, since with fragmentary samples the incidence of ossicles in the population samples would be considerably underestimated. As yet, no study has tested the strengths of the inclusive versus the reductionist approach.

The present study examines the effects of sample size on intertrait correlations and tests the merits of the inclusive versus reductionist models. In addition, because many traits are influenced by sex and most researchers

now recommend treating male and female data separately (Milne *et al.*, 1983), intertrait correlations are computed for males and females to determine if differences exist. The present analysis follows Sjøvold (1977) by using the .01 confidence level for deciding significance of phi.

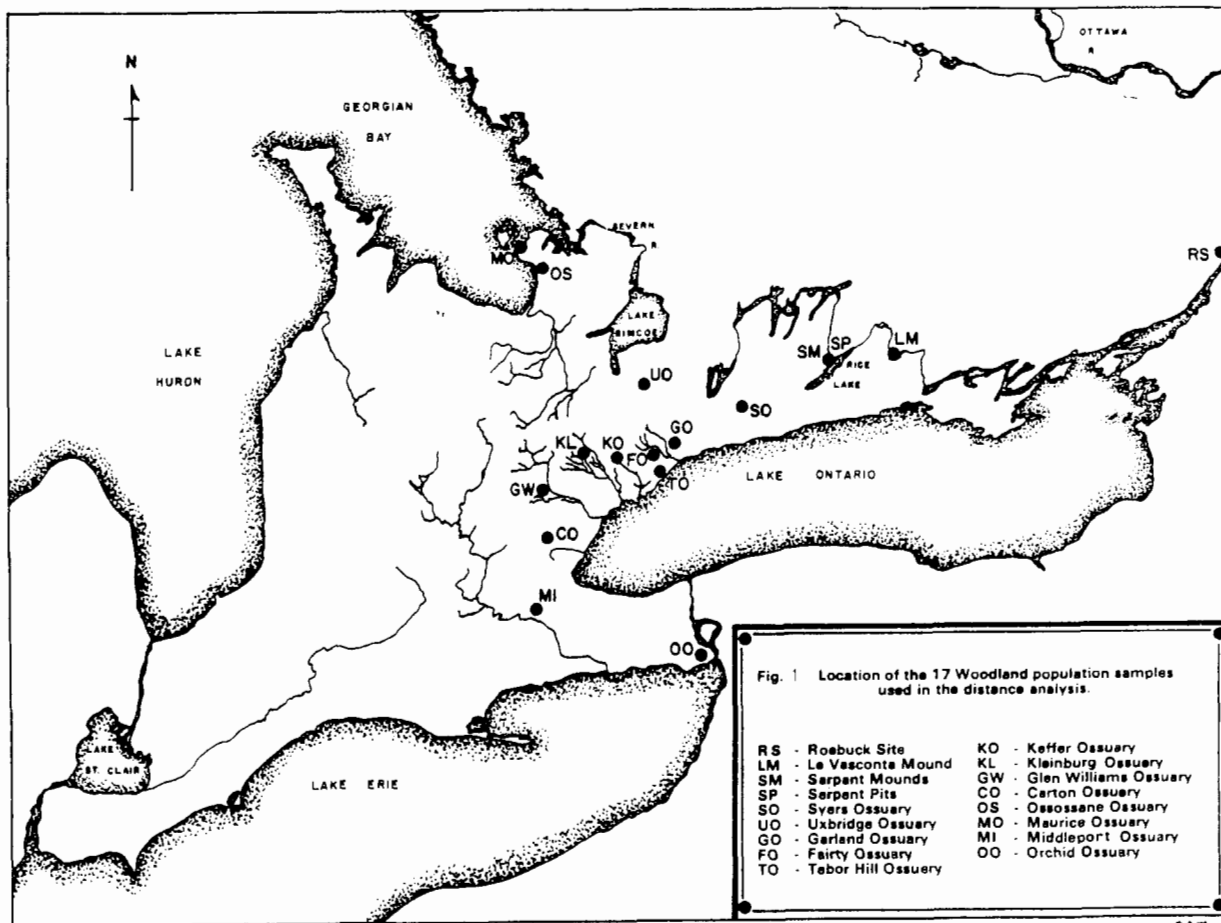
SAMPLES AND METHODS

The study sample consists of 1040 adult Iroquois crania from 17 southern Ontario Woodland sites (Figure 1). Biological distance coefficients between these samples, plus archaeological data, support the hypothesis that these sites represent a common deme (Molto 1980). The large conglomerate sample, composed of 371 males, 342 females and 345 crania of unknown sex, therefore serves as a sample population to determine intertrait correlation. The skulls were scored for 27 discontinuous traits using the individual as the unit of observation for bilateral variates.

Correlation matrices were computed for the conglomerate sample and for each of the largest population samples, namely Orchid (N=135), Kleinburg (N=103), Carton (N=81) and Glen Williams (N=79). These individual samples are used to test the effects of sample size on the correlations. Additional correlation matrices were calculated for the male and female data to test if the pattern of intertrait correlation is 'sex-influenced'. Mean Measure of Divergence Coefficients comparing the Syers Ossuary to the other Woodland sites using composite (27 traits) and reduced (21 traits) trait lists were computed to test the effects of correlated traits on distance coefficients.

RESULTS

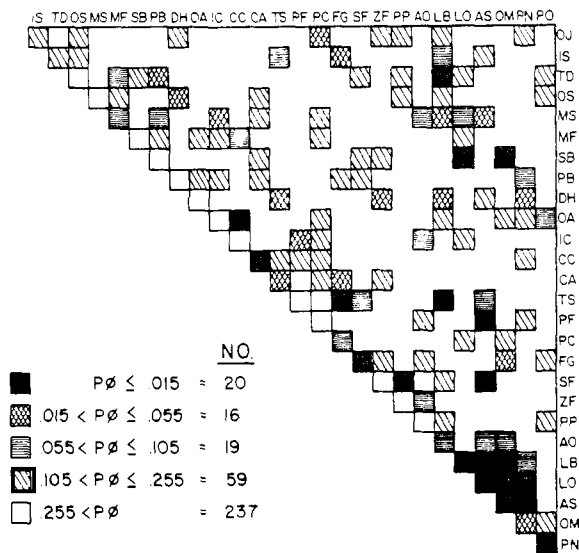
In the correlation matrix for the composite sample (Figure 2) there are 20 significant coefficients ($p \leq .01$). Of these, 4 are negative and may be disregarded (Sjøvold, 1977). Since four times the expected number (4) of significant correlations occurred, the null hypothesis is rejected. Overall, however, correlations between these traits are low, as 67.5% of the interactions exceed $p = .255$. Of the positive significant coefficients it is noteworthy that 75% (12/16) involve accessory sutural bones and, among the sutural ossicles, all the coefficients are positive and 60% (9/15) are significant (Table 1). The pterionic ossicle is least involved in the ossicle associations, being statistically independent of all the accessory bones except the parietal notch bone ($p \leq .01$). Of the significant correlations not involving accessory ossicles, two correlations have reasonable biological meanings, namely, clinoclinoid and carotico-clinoid bridging (because they are hyperostotic manifestations of the same trait) and the supraorbital foramen and frontal grooves (because of regional and developmental factors).



In a previous study (Molto, 1980), I used these results to assist in selecting a final battery of 21 traits to compare the 17 southern Ontario Woodland samples. The procedures by which the correlated variates were treated in the latter study are reviewed briefly here, since they relate directly to the results and discussion that follows. Using a reductionist approach, all ossicles except those at pterion and lambda were eliminated, since these two variates were totally independent and the lambda bone is highly associated with all the other ossicles. In handling the other associations, the carotico-clinoid bridge and frontal grooves were retained rather than their correlates (i.e. clino-clinoid bridge and supraorbital foramen respectively) because they are more variable and provided better discriminatory potential between the Woodland samples. The final battery included three significant associations which is approximately equal to chance expectations in this trait list. The associations are; tympanic dehiscence with ossicle at lambda and the trochlear spur with both ossicle at lambda and frontal grooves. Only the first association makes biological sense since both are hypostotic traits. However, as there appears to be no developmental explanation for these associations they were treated as stochastic events.

From the outset in the above study a reductionist philosophy was followed in that traits were omitted to satisfy the independence requirement. The question emerges as to the nature of the results if the inclusive approach had been used. To address this MMD's were computed between the Woodland samples using two trait lists; a composite list of 27 variants and a select list of 21. The latter had the following traits removed; clino-clinoid bridge, supraorbital foramen, lambda ossicles, asterionic ossicles, occipito-mastoid ossicles and pterionic ossicles. Due to the numerous problems inherent in interpreting a large distance matrix (136 MMD's) in light of regional anthropological theory, comments will be restricted to comparisons involving a single sample, the Syers ossuary. Table 2 shows the MMD coefficients between Syers and the other Woodland samples using both trait lists. With the composite battery each MMD is larger and the mean coefficient is greater than twice that produced by the select list. More important is the fact that 81% (13/16) of the MMD's are significant using the composite battery whereas 38% (6/16) are significant with the select list. In terms of interpretation, the results of the select list are considerably more meaningful relative to our current knowledge of Iroquoian prehistory. The select list shows

Fig. 2 Shaded matrix of intertrait correlation between 27 discontinuous cranial traits based on the probability of phi ($P\phi$).



that Syers is closest to its neighbouring groups and is considered part of their deme. Interpretation of the composite list not only contrasts the latter interpretation but also does not produce any clear affinity patterns. The disparity between the two matrices can be better understood if the contributions of the correlated traits are considered (Table 3) in the interpretation of these results the principle of equal additivity is utilized, that is, it is assumed that each trait of a given battery contributes equally to a given MMD. In the composite list, each trait is expected to contribute 3.7% to each MMD whereas in the select list the expected contribution is 4.76%. Note that the six correlated traits collectively contribute 35.4% to the MMD's whereas their expected contribution is 22.2%. Further analysis shows that both the clino-clinoid bridge and the supraorbital foramen provide close to their expected values. This is logical since the percentage incidence for each of these variants in Syers is close to the overall mean for the Iroquoian data and both incidences fall close to the midpoint of the variation in the Iroquoian samples (Table 3). A variant pattern emerges for accessory ossicles. Collectively these traits almost double their expected contribution to the MMD's (29.0 versus 14.8%). Further, each trait dramatically exceeds the Iroquoian mean, with each representing the highest incidence among the Woodland samples (Table 3). Interestingly the same holds for both the lambdic bone and ossicle at pterion, the traits that were retained in the select list. In the Syers data, accessory ossicles were present in 23 of 25 crania with the following distribution: one had a single ossicle type present, seven had two types present, three had three types, nine had four types and one had five types. Clearly, the ossicle correlations in Syers obscured relationships with the other sites when the composite trait battery is used.

The results of the intertrait correlations for the four largest Woodland samples is summarized in Table 4. The null Hypothesis is accepted in each case. Furthermore, the smaller samples are not consistent with each other or with the conglomerate sample in terms of the traits found to be positively correlated. For example, in the Glen Williams sample (Table 4) a significant positive correlation occurred between pterionic and lambdic ossicles, yet these variants were highly independent (actual probability = .97) in the large sample. There are numerous additional examples that could be cited, but the salient point is that if the correlation results were based on any of the smaller samples, the estimation of intertrait correlation in the Iroquoian population, as inferred through the results of the conglomerate sample, would have been misrepresented.

Table 5 summarizes the results of the male and female correlation matrices. In males, 6.3% (22/351) of the correlations are significant compared to 3.1% (11/351) in females. While this difference is slightly exaggerated due to the presence of four negative coefficients in the male data and none in the female data, a variance still exists that requires explanation. The fact that the male, female and conglomerate samples are close in the number of positive significant correlations suggests a minimal role for sample size. There is also no sex difference involving accessory sutural bones or hypostotic traits, although the correlations are somewhat higher in females. It is with the hyperostotic traits that sexual dimorphism is evident. In males, seven of the significant correlations involve hyperostotic traits whereas in females only one pair of hyperostotic traits is significantly correlated. The latter association, between the clino-clinoid and carotico-clinoid bridges, is also better explained in terms of these variants being expressions of a similar manifestation rather than being influenced by sex. It seems, then, that the sex differences found relate to a general tendency towards hyperostosis in male Iroquoian crania.

DISCUSSION

Consistent with previous studies, the results reported here indicate that correlation among discontinuous cranial traits is low, but significant (e.g. Berry and Berry, 1967; Corruccini, 1974; Suchey, 1975; Sjøvold, 1977). However, the higher incidence of significant positive correlations in this study probably reflects the larger sample size used. When the four smaller Woodland samples were used, the null hypothesis was accepted in each case, the pattern of intertrait correlation varied from sample to sample, and each of the latter samples produced disparate results compared to the conglomerate sample. The pattern of trait interaction revealed by the latter is far more meaningful and consistent with the craniological literature. These results indicate that sample size, even when phi is used, has a pervasive effect on detecting intertrait correlations. It follows that researchers should try to use as large a homogeneous sample as possible to determine intertrait correlations. Using small samples, as many have

TABLE 1
Summary of the significant ($p < .015$) intertrait correlations in southern Ontario Woodland crania.

Traits	0	01
Tympanic dehiscence-Lambdaic ossicle	.090	.008
Spinobasal bridge-Lambdaoidal ossicle	-.121	.015
Spinobasal bridge-Occipito-mastoid ossicle	-.114	.013
Ossified apical ligament-clino-clinoid bridge	.151	.023
Clino-clinoid bridge-carotico-clinoid bridge	.284	.081
Frontal grooves-Trochlear spur	.104	.011
Trochlear spur-Lambdaic ossicle	.133	.018
Parietal foramen-Asterionic ossicle	.094	.009
Frontal groove-Supraorbital foramen	.200	.040
Supraorbital foramen-Parietal process of temporal	-.103	.011
Supraorbital foramen-Asterionic ossicle	-.141	.020
Lambdaic ossicle-Lambdaoidal ossicle	.290	.084
Lambdaic ossicle-Asterionic ossicle	.204	.042
Lambdaic ossicle-Occipito-mastoid ossicle	.165	.027
Lambdaoidal ossicle-Asterionic ossicle	.164	.027
Lambdaoidal ossicle-Occipito-mastoid ossicle	.168	.028
Lambdaoidal ossicle-Parietal notch ossicle	.112	.013
Asterionic ossicle-Occipito-mastoid ossicle	.141	.020
Asterionic ossicle-Parietal notch ossicle	.171	.029
Parietal notch ossicle-Pterionic ossicle	.117	.014

TABLE 2
MMD's between the Syers Ossuary and 16 southern Ontario Woodland sites using composite (27 traits) and select (21 traits) trait lists. An asterisk above the coefficient indicates at $p < .05$.

	Composite List	Select List
Roebuck Site	.0646*	.0338*
Le Vesconte Mound	.1454*	.1129*
Serpent Mound	.1202*	.0963*
Serpent Pits	.0772*	.0368*
Tabor Hill Ossuary	.0255*	.0056
Fairty Ossuary	.0377*	.0107
Keffer Ossuary	.0200	-.0020
Uxbridge Ossuary	.0425*	.0062
Glen Williams Ossuary	.0417*	.0266*
Kleinburg Ossuary	.0347*	.0179
Garland Ossuary	.0443*	.0112
Carton Ossuary	.0381*	.0048
Ossossane Ossuary	.0407*	.0109
Maurice Ossuary	.0174*	.0277
Middleport Ossuary	.0325*	-.0093
Orchid Ossuary	.0785*	.0336*
MEAN MMD	.0538	.0266

TABLE 3
Percentage incidence of six discontinuous traits in the Syers Ossuary Relative to the Woodland data in southern Ontario

Trait	% incidence Syers Ossuary	Iroquois P/N	Mean %	Sample (%) Range N = 17	Mean % Contribution to MMD's (N = 16)
Clino-clinoid bridge	10.4	107/944	11.3	6.1 - 20.2	3.1
Supraorbital foramen	64.0	930/1634	56.9	44.8 - 78.6	3.3
Lambdaoidal ossicles	87.5	401/671	59.7	33.3 - 87.5	8.3
Asterionic ossicles	47.5	194/701	27.7	10.0/47.8	7.3
Occipito-mastoid ossicles	43.5	106/577	18.4	9.1 - 43.5	6.9
Parietal Notch ossicles	50.0	167/729	22.9	9.2 - 50.0	6.5
					35.4

TABLE 4
Frequency of significant correlations using different sample sizes. Number of pairwise comparisons per comparison base on the interaction of 21 traits is 351.

Sample	Number of crania	Significant Correlations		
		No.	%	
Glen Williams Ossuary	79	2	.006	Mendosal suture - Ossified apical ligament
Carton Ossuary	81	1	.003	Pterionic ossicle - Lambdic ossicle
Klienburg Ossuary	103	5	.014	Pterionic ossicle - Parietal notch ossicle
				Spinobasal bridge - Parietal process of temporal
				Trochlear spur - Lambdic ossicle
				Supraorbital foramen - Posterior condylar canal (absent)
				Frontal grooves - Parietal process of temporal
				Lambdic ossicle - Lambdoidal ossicle
Orchid Ossuary	135	2	.006	Clino-clinoid bridge - Carotico-clinoid bridge
				Mendosal suture - Lambdic ossicle
Total Male	371	22	.063	
Total Female	324	11	0.31	
Total Sample	1040	20	0.57	

TABLE 5
Significant intertrait correlations in male and female Iroquois crania. An asterisk indicates a negative phi coefficient

<i>Males</i>	<i>Females</i>
Tympanic dehiscence - Lambdoidal ossicle	Os Japonicum - Mendosal suture
Marginal foramen - Ossified apical ligament	Trochlear spur - Lambdic ossicle
Spinobasal bridge - Lambdoidal ossicle*	Lambdic ossicle - Occipito-mastoid ossicle
Divided hypoglossal canal - Lambdic ossicle*	Mendosal suture - Lambdic ossicle
Divided hypoglossal canal - Asterionic ossicle*	Lambdoidal ossicle - Occipito-mastoid ossicle
Divided hypoglossal canal - Parietal notch ossicle*	Occipito-mastoid ossicle - Asterionic ossicle
Divided hypoglossal canal - Intermediate condylar canal	
Ossified apical ligament - Marginal foramen	
Ossified apical ligament - Clino-clinoid bridge	
Marginal foramen - Tympanic dehiscence	
Supraorbital foramen - Asterionic ossicle*	
Lambdoidal ossicle - Asterionic ossicle	
Lambdoidal ossicle - parietal notch ossicle	
Tympanic dehiscence - Lambdic ossicle	
Open sinusum - Lambdic ossicle	
Pterygobasal bridge - Carotico-clinoid bridge	
Optic foramen - Lambdic ossicle	
	<i>Both Sexes</i>
	Clino-clinoid bridge - Carotico-clinoid bridge
	Frontal grooves - Supraorbital foramen
	Lambdic ossicle - Asterionic ossicle
	Lambdic ossicle - Lambdoidal ossicle
	Asterionic ossicle - Parietal notch ossicle

done, is equivocal in light of the present results. The question emerges as to a satisfactory minimum sample size for this type of analysis. Considering the similar results in the number of positive correlations produced between the conglomerate sample and the male-female subsamples, each of the latter containing approximately three hundred crania if allowances are made for missing data, I recommend 300 as a baseline sample size. Since most prehistoric samples are considerably smaller than this, samples have to be combined to increase the number. Samples that are pooled necessarily must represent the same deme, in light of the data showing population variability in the pattern intertrait correlation.

A question germane to these studies is the treatment of positively correlated traits. The apparent distorting influence of the correlated variants (i.e. accessory sutural ossicles) on the MMD coefficients between Syers and the other southern Ontario Woodland samples, suggests that, in distance studies, a reductionist approach is empirically, as well as theoretically, superior to the inclusive one. Inclusionists may argue that relative to the Iroquoian data, Syers is atypical in its pattern of intertrait correlation. While this view undoubtedly has merit, it is important to emphasize that distance matrices are nonorthogonal and even one unrepresentative sample can profoundly influence the results and concomitant interpretations. This is

particularly applicable to the hypothesis testing of distance matrices or if interpretations are based on taxonomic constructs of distance coefficients, such as cluster analysis. Those following an inclusive design, should, in light of these results, specify the relative contributions of the correlated traits to distance coefficients.

The reductionist approach creates an additional problem, namely, that of deciding which of the paired traits to eliminate. A general theoretical rule to follow is to exclude the trait with the least between sample variance, since the trait with the greater variance is a better measure of sample divergence (Sjøvold, 1977). This assumes that the correlated traits are otherwise similar in terms of epigenetic factors (i.e. effects of age, sex, nutrition, etc.), scoring precision and sample size (number of observations). These conditions are rarely attained. Moreover, because patterns of intertrait correlation can vary between populations, it is expected that the trait lists used will also vary. It is important, then, that the methods used to select traits based on intertrait correlation are precisely stated. In this way effective theoretical standards can be established.

Since many discontinuous cranial traits consistently yield significant sex differences, many researchers compute separate distance coefficients for males and females using the same trait battery (e.g. Corruccini, 1974; Larach and MacIntosh, 1970; Milne *et al.*, 1983). In these studies, if intertrait correlations are determined, they are usually based on pooled data for the sexes. To my knowledge, no study has tested male-female data separately prior to computing and interpreting their separate matrices. Yet, this procedure seems necessary, based on the sexually dimorphic pattern of intertrait correlation described here for the Iroquois. With the Iroquoian data several hyperostotic variants would have to be removed from the trait list prior to comparing the male and female distances. Otherwise, a potential bias would be introduced because so many hyperostotic traits are significantly correlated in males. This, in theory, could increase the homogeneity in the male versus female coefficients. Often such male-female variances, both for individual traits and distance coefficients, are used to infer social practices pertaining to residence (Spence, 1974; Kennedy, 1981). A note of caution for such research designs seems in order if the data presented here can be used as an interpretive measure. Further research is required to determine if most populations of *Homo sapiens* are characterized by sexual dimorphism in the pattern of intertrait correlation.

CONCLUSIONS

Intercorrelations between discontinuous cranial traits, while low, seem strong enough to influence biological distance coefficients and their significance levels. It appears, from this analysis, that 'reduced' trait lists that satisfy the independence assumption, are better suited to population research. The scientific interests of future studies would be best served if correlation testing of discontinuous variants were integral to their research designs.

As part of this proposal I make the following recommendations.

1. Large samples, preferably greater than 300 crania should be used to detect intertrait correlations (and even this may be inadequate for rare traits).
2. To obtain a large sample to test for intertrait correlation only samples from the same deme can be pooled since populations vary in their correlated traits.
3. The phi coefficient should be used to test for correlations between discontinuous traits that are scored dichotomously (absent/present).
4. With samples that are large enough, intertrait correlations should be determined separately for males and females, particularly if separate male-female distances are computed.
5. In omitting one of a pair of correlated traits that are otherwise similar in terms of epigenetic influences, scoring precision, and the number of observations recorded, the trait removed should be the one with the smaller between sample variance.
6. In circumstances for which it is impossible to detect correlations due to inadequate sample size for that deme, researchers should avoid using too many accessory ossicles since their intercorrelation is a consistent feature in *Homo sapiens*.

In closing, I would like to emphasize that the concept of distance is a theoretical mathematical concept that has been borrowed and applied to population biology. Debate continues as to the meaning and/or legitimacy of distances computed using biological data (Sjøvold, 1977). In view of this, the very least researchers can do, is to obey the assumptions outlined by mathematical theory. This means that biological distances should be computed using variates that, except for an acceptable number of chance associations, are statistically independent of each other.

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THE COURTSHIP BEHAVIOUR OF FEMALE JAPANESE MONKEYS

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Abstract: The estrous behaviour of semi-free ranging female Japanese monkeys was observed, in order to investigate the role of the female in the establishment of mating pairs. It was concluded that the females play a very active role in the formation of mating pairs, showing three times more solicitation behaviour than males. They also reject more than 30% of the advances they do receive. Female courtship behaviour is described, with emphasis on proceptive or solicitation behaviour. Further analysis based on socio-demographic variables revealed that the age of the female had an effect on behaviour, with older females behaving in a more calm, sophisticated manner when soliciting a male. Age was also the most significant male variable, with females showing more rejections to younger males. Other than age related findings, it must be concluded that the socio-demographic characteristics are not predictive of the females' courtship behaviour.

Résumé: Pour éclaircir le rôle de la femelle dans l'établissement des couples pendant la saison des amours, le comportement d'un échantillon de singes japonaises a été étudié pendant leurs périodes d'oestrus. Il s'est avéré que les femelles jouent un rôle actif dans la formation des couples car elles exécutent trois fois plus des comportements dits de sollicitation (s'approcher, se présenter, suivre, etc.) que les avances qu'elles reçoivent des mâles. Cette description de la cour que font les femelles souligne l'importance des comportements proceptifs, c'est à dire, les comportements qui indiquent la recherche active d'un partenaire pour l'accouplement. L'analyse des variables socio-démographiques démontre que les femelles plus âgées étaient plus habiles, calmes et subtiles dans leurs cours que les plus jeunes, et que l'âge était important aussi chez les mâles. Les femelles rejettent les avances des jeunes mâles plus fréquemment que celles des mâles plus âgés. Outre l'âge, les variables socio-démographiques utilisés dans cette étude ne se montraient aucune capacité à prédire les comportements de la cour chez les singes japonaises.

Key Words: *Mucaca fuscata*, Courtship, Mateship, Age and behaviour.

INTRODUCTION

The theory of sexual selection is usually divided into two processes: epigamic selection, which is interaction between the sexes (usually female choice) and intrasexual selection, which is interaction within one sex (usually male competition). There has been a great deal of controversy over the relationship between these two forces, and over the issue of whether it is males or females that are the "creative force in sexual selection" (Fedigan, 1982). Most discussions of sexual selection in mammals stress the importance of intrasexual selection; aggressive male behaviour is seen as more important than female choice (Ralls, 1977). Another pervasive notion is that the females are essentially passive, simply accepting male sexual initiations. This concept, however, seriously misrepresents the normal mating sequence and encourages a biased concept of feminine sexuality (Beach, 1976).

Until recently, the subject of female choice has been largely overlooked in primate research, even in studies of Japanese monkeys, where reports of male-male competition are rare, and reports of females exercising choice of partners are common (Tokuda, 1961-2; Wolfe, 1979; Enomoto, 1974). Due to recent theoretical developments concerning sexual selection, various researchers are now interested in the factors that affect partner choice. For

example, one popular issue under investigation is the relationship between male dominance rank and mating success. The results of these investigations are mixed. A positive correlation between male rank and mating success in macaques has been reported by Tokuda (1961-2), but Drickamer (1974) and Eaton (1974) reported no correlation. Other studies had mixed results (Hanby *et al.*, 1971; Fedigan and Gouzoules, 1978). This research, however, is generally done from the perspective that high rank in males allows greater access to estrous females, rather than from the perspective that the female's choice of partners may reflect a preference for males of higher status.

Other studies try to correlate various male behaviours and mating success. For example, Modahl and Eaton (1977) and Wolfe (1981) have shown a correlation between male displays and mating success (as measured by ejaculation frequency). Enomoto (1981) reports a correlation between aggressive behaviour toward the female, such as chasing, and mating success. Presumably these studies say something about the factors that influence female choice as a mechanism of sexual selection, however, the evidence is indirect – inferred by male behaviour and mating success. The authors themselves recognize that the data offer only preliminary support (Modahl and

Eaton, 1977) and that the females' reactions to the displays must be defined (Enomoto, 1981).

Notably absent from the literature are studies which focus on female behaviour during the mating season – specifically female behaviour prior to the actual consort and mating. Clearly, studies such as these are essential to our understanding of pair formation. Morris defines courtship as “the heterosexual reproductive communication system leading up to the consummatory act” (1956:12). He points out that courtship helps to construct the male-female bond that is necessary for a successful consort. A true understanding of female choice would necessarily involve a focus on the courtship behaviour of females, that is, the behaviour that precedes or leads to a consort pairing.

The objectives of this study were: (1) to describe the repertoire of female courtship behaviour in *Macaca fuscata*; (2) to compare females on the basis of age, parity, rank, number of offspring and presence of a recent infant, to test for differences in courtship patterns; and (3) to relate female courtship behaviour to some socio-demographic characteristics of the interacting males.

MATERIALS & METHODS

Behavioural data were collected on a troop of approximately 300 semi-free ranging Japanese monkeys during the 1982 mating season (September-December). Approximately 700 observation hours were spent in the field, during which 140 hours of focal animal data were collected.

The subject animals were sexually mature females, and an attempt was made to sample evenly; based on age, parity, rank, presence of an infant and number of offspring. At least five hours of data were obtained on as many females as possible. The total number of subject animals was 40.

Focal animal data sheets were used and thus the frequency, duration, sequence, direction and recipient of behaviour were recorded. Focal animal sessions were one hour in length. The ethogram was designed to include any possible behaviour, however sexual behaviours predominate. Both male and female behaviours were included since behaviour directed at a female by a male is included in the focal data. Only the behaviour of estrous females was recorded, and the behavioural sequences were later classified into copulatory or non-copulatory. Only the non-copulatory behaviour sequences were considered to be courtship sequences, regardless of whether the female was soliciting or rejecting a male. Courtship in this study is any behaviour received or directed by an estrous female who is not engaged in a mount sequence. It is not possible, at least in the field situation, to *know* which animal initiated a sexual interaction. As Eaton (1978) pointed out, what appears to be a female initiation may have been preceded by a courtship behaviour by the male over a week ago. It is also often impossible to know whether a given pair are just entering a consort or whether they are simply between copulations within a consort. In order

to avoid making faulty assumptions, no distinction was made between pre- and post-copulation or between established consorts and newly forming ones.

The analysis of all 95 different behaviours would be methodologically and conceptually impossible, therefore it was necessary to combine the ethogram units into higher level categories. This was done heuristically on the basis of the obvious function or purpose of the behaviour. For example, approach/follow/sit near/estrous hack and many other behaviours were grouped into the higher level category of “proceptive behaviour”. Thirteen general categories of non-mounting estrous behaviour resulted (Table 1). Also, vocalizations were separated from proceptive behaviour for a second analysis to check the original results. This analysis revealed no new results, thereby confirming the correctness of including vocalizations in the proceptive behaviour category.

Since the role of the female in establishing mating pairs is of primary interest in this study, it was useful to analyze how females differed in the frequency with which they showed specific proceptive behaviours. For this analysis, the proceptive behaviours were analyzed as individual ethogram units. Likewise, in considering the effects of the interacting male, both higher level categories and specific behaviours were important. In this case, all sexual and aggressive behaviours that involved the males were separately analyzed. It was thus possible to determine whether different males received different behaviours from the females and whether different males directed different behaviours to the females. Non-directed behaviours (e.g. estrous scream or slap ground) were not considered.

The analysis was carried out in three steps. First, simple descriptive statistics and *t*-tests were used to meet the first research objective: the description of female courtship behaviour.

The second stage of the analysis was designed to meet the second research objective: to determine if different groups of females differ in the frequency, range or duration of various behaviours. The independent variables here were female age, rank, parity, presence of an infant and number of offspring. For rank, the population was divided into high, medium and low. Parity was divided into nulliparous, primiparous or multiparous. Presence of an infant was simply a 'yes' or 'no' score depending on whether or not the female had a live infant from the 1982 birth season. The dependent variable list includes the frequency of heuristically lumped ethogram categories (e.g. proceptive behaviour), the frequency of specific courtship behaviours (e.g. 'present'), the range of courtship behaviours displayed, and the duration of various states (e.g. 'groom'). The raw frequencies of each behaviour were adjusted to account for unequal sample hours on the females. A Pearson Correlation was used when testing the continuous variables of age and number of offspring. A One-way Analysis of Variance was used to test for differences in behaviour based on rank, parity, and presence of an infant.

The third stage of the analysis was designed to meet the

TABLE 1
Heuristically grouped behaviour categories

DIRECTED	RECEIVED
<i>Proceptive/Solicitation Behaviour</i> follow/sitbeside/sit near/ventral sit against/embrace/approach/ increase proximity/lip quiver/walk by/walk past/walk around/ chase/genital inspect/contact call/estrous scream/estrous hack/ alarm call/hip touch/present/manipulate object/ threat to observer/slap ground/mount rub/attempt mount/body jerk/crouch	<i>Advances/Solicitations Received</i> receive a follow/receive a sit beside/receive a sit near/receive a ventral sit against/receive an embrace/receive an approach/receive an increase proximity/receive a stare/receive a lip quiver/receive a whiri pivot/ receive a walk by/receive a walk around/receive a walk past/ receive a chase/receive a genital inspect
<i>Rejection Behaviour</i> leave/decrease proximity	<i>Rejection Received</i> receive a leave/receive a decrease proximity
<i>Female Fear Indicators</i> flee/fear grimace/response move	<i>Fear Indicators Received</i> receive a fear grimace
<i>Dominant Behaviour</i> displace	
<i>Submissive Behaviour</i> receive a displace	
<i>Aggressive Behaviour</i> threat/lunge/aggressive chase/grab/bite/pin and bite/ defensive scream	<i>Aggressive Received</i> receive a threat/receive a lunge/receive an aggressive chase/ receive a grab/receive a bite/receive a pin and bite
<i>Affiliative Behaviour</i> groom/groom solicitation	<i>Affiliative Behaviour Received</i> receive a groom/receive a groom solicitation
	<i>Solitary Estrous Behaviour</i> walk/forage/run/self groom/sit/ manipulate nipples/peer/food call

third research objective: to test for differences in behaviour based on characteristics of the interacting male. Here the independent variables were male age, rank, and spatial status. Again, rank was represented by a score of high, medium or low. Spatial status refers to whether the animal was central or peripheral in the troop. This is a relatively straightforward geographic distinction. The dependent variable list for this stage of the analysis includes the frequency of heuristically lumped ethogram categories, specific male courtship and aggressive behaviours, and specific female courtship behaviours which involve males. Since males were not equally sampled, it was necessary to adjust the raw frequencies by dividing each frequency by the total number of entries on that particular male. Again the Pearson Correlation and the Oneway Analysis of Variance were used to test for significant results. In both the second and the third stage of analysis, all independent variables were tested against all dependent variables.

RESULTS & DISCUSSION

A very important consideration in the issue of female choice is the role that the females play in the establishment of mating pairs. Is it the males or the females that do most of the soliciting? A *t*-test comparing the number of female courtship behaviours (7173) to the number of male courtship behaviours (2085) observed was signifi-

cant ($t = 4.55$, $df = 39$, $p = .000$). This shows clearly that female Japanese monkeys do play a very active role in the establishment of mating pairs. In fact according to these data, females are much more active than the males. This supports the assertion by Tokuda (1961/62) that Japanese macaque males or females may solicit, but females solicit more frequently. Furthermore, in this study females did not accept all of the advances that they received. A comparison of total number of male advances and total number of female rejections revealed that females reject 33.14% of the advances they receive. Often an estrous female rejecting one male will be actively pursuing another (obvious aggressive competition between the males was never observed in such cases). Clearly, the females are not willing to mate with just any male, but are instead selective, actively soliciting in some situations and actively rejecting in others.

Female Japanese monkeys use a variety of courtship behaviours. Following Stephenson (1973) I was able to outline three stages leading to a mount series. The first is advertising and monitoring, the second is testing and closing of inter-individual distance, and the third is attempting to establish a mount series. While there is no 'typical' or uniform behavioural pattern among the females, there is a repertoire of behaviours which may occur at each stage.

The first stage was observed much less frequently than stages two or three. Females displaying estrous behaviour

usually seemed to be directing the behaviour to a particular male. When observed, however, this stage seemed to be characterized by a general high level of excitement and was often associated with a great deal of vocalization. The ethogram category of solitary estrous behaviour (sitting, walking, running, self-grooming, foraging, etc.) perhaps best represents this stage. This behaviour was observed in females who also showed other behavioural signs of estrous. The female would run through this repertoire of behaviour repeatedly, performing each only briefly before hurriedly going on to another. Estrous screams, estrous hacks and a variety of contact calls enhance the general impression of hyperactivity and agitation. These females will cover great distances and it seems obvious that they are either advertising or trying to select a potential partner. Certainly this noisy excited female draws a great deal of attention and she is often chased and occasionally bitten by a male. She may flee from the male and continue the behaviour pattern elsewhere or at this point she may begin to try to maintain proximity to the "chasing" male.

The testing and closing of inter-individual distance involves a different repertoire of possible behaviours. Most commonly the female will simply follow and sit near the male. She may or may not vocalize. If vocalizations are present they can vary in kind, frequency, rate and pitch. Basically the female will try to decrease the distance between herself and the male by subtly trying to inch her way closer, if they are already sitting in proximity, or by sitting a little closer to him each time she follows and sits near. Startled jumps and fear grimaces from the female are common at this stage, although occasionally the female will appear much more confident and simply walk right up and sit in body contact with the male. Either method may result in the female being chased and/or bitten by the male. Such aggression does not seem to discourage the females from further solicitation of that particular male.

Sometimes a female will employ a less direct, or more 'coy' strategy, walking in front of the male, presenting her hindquarters, lip quivering and moving on. Any or all of the above behaviours may be displayed and often this results in the female being followed by the male.

Once the female has established body contact with a male and appears to be comfortable and not expecting aggression, a new repertoire of behaviours will begin. These behaviours are clearly designed to establish a mount sequence. Vocalizations are very common at this stage, with estrous hacks and contact calls being most frequent. Estrous hacks usually involve a jerking of the body, although body jerks also occur in silence. As time progresses and the male has not yet mounted, the female's level of agitation increases. Manipulation of small objects in the environment, slapping the ground and even threatening the observer will occur. The purpose of these behaviours appears to be to coax and urge the male to begin mounting. Presenting the hindquarters is probably the most obvious action the female can take to prompt mounting. Some females will even go so far as to hip touch and mount the male. It should be clear that there is no one

standard behaviour pattern here. The female may exhibit any or all of the above behaviours, and may even just sit patiently waiting for the male to initiate mounting. One tendency does prevail though: the onset of a regular mount sequence will result in the cessation of 'prompting' behaviours.

On many occasions more than one female was observed soliciting the same male at the same time. On at least three occasions outright agonism between the two females was witnessed, and it appeared that the higher ranked of the two would start the encounter by threatening and/or chasing off the lower ranked one.

The notable feature of the courtship behaviour is variation. Each proceptive behaviour has a different overall frequency of expression. Some are much more commonly used than others. Furthermore, there is a great deal of variation between individuals in the expression of proceptive behaviour. This includes both the total frequency of all proceptive behaviour and the frequency of specific solicitation behaviours.

In an attempt to account for this variation, females were compared on the basis of age, rank, parity, number of offspring and presence of a recent infant. Both overall rate of solicitation (proceptivity) and differences in specific courtship behaviours were considered. It was first hypothesized that the variability in the overall frequency of proceptive behaviour might be due to the above mentioned socio-demographic variables. Despite the great individual variability, however, this analysis revealed remarkable homogeneity in the frequency of proceptive behaviour among the sociological groupings (see Tables 2 and 3) although there was a trend ($p = 0.08$) for primiparous females to exhibit more proceptive behaviour than nulliparous and multiparous females. On the basis of this analysis, the hypothesis that socio-demographic differences between the females will explain different solicitation rates must be rejected. The explanation for the extreme individual variability in frequency of proceptive behaviour must lie elsewhere.

One possible explanation could be that the high 'proceptors' were sampled at different stages of the menstrual cycle than were the low. Presumably female receptivity and proceptivity would correlate with the fertile phase. Unfortunately, complete estrous data on each female were not collected so it is impossible to investigate this at this time. But as Fedigan points out, in primates the correlation between motivation or willingness to mate and the ovarian cycle is not clear and "all primate sexual behaviour seems to be relatively emancipated from direct hormonal controls" (1982:144). The explanation for the great variability observed in the expression of overall proceptive behaviour must be idiosyncratic variation or, more likely, some as of yet undefined variables.

While the sociological variables of age, rank, parity, presence of an infant and number of offspring do not explain total frequency and rate of proceptivity they do shed some light on differences in the expression of other courtship behaviours. In other words, some of these factors do seem to influence how the females interact with

TABLE 2

Results of the analysis of variance on the frequency of proceptive behaviour by parity, rank and presence of infant

	Mean Frequency of Proceptive Behaviour	Standard Deviation	F Ratio	Probability
Parity				
Nulliparous	54.84	24.89	2.613	0.08
Primiparous	67.13	47.41		
Multiparous	38.14	28.59		
Rank				
High	45.20	43.24	0.075	0.92
Medium	50.44	26.64		
Low	46.34	30.67		
Presence of Infant				
Yes	47.06	29.46	0.000	1.00
No	47.10	37.10		

potential mates.

The analysis revealed a number of significant behavioural differences between females with an infant and females without an infant (Table 4). These include both higher level categories (rejection received and solitary estrous behaviour) and specific behaviours (ventral sit against, alarm call, body jerk, follow). Females with an infant received more rejections from males, showed less solitary estrous behaviour, were less likely to sit ventrally against a male, alarm called more, body jerked less, and followed more than did females without an infant. Most of these differences can be explained by the physical presence of the infant. For example, females with infants show a greatly reduced frequency of ventrally sitting against a male. This is understandable since the infant, if with the mother, is usually at the nipple. Also, the mean frequency of solitary estrous behaviours is low for females with infants, and this is not surprising since this non-sexual behaviour category represents the stage where the female is doing the most running about. It seems reasonable to expect that a mother could not monitor her infant's activities while moving rapidly throughout the enclosure.

The other variable which yielded a number of significant behavioural differences was the age of the female (Table 4). In this case most results involved specific behaviours, the only significant result for a higher level category involved rejections received (see below). The frequency of the following behaviours showed a significant positive correlation with age: follow, walk past, approach, genital inspect, and alarm call. Significant results based on the number of offspring are also relevant here since age and number of offspring are themselves highly correlated ($r = 0.9261$, $p = 0.000$). The number of offspring was positively correlated with the frequency of alarm calls, follow, walk past, and rejections received. The number of offspring showed a significant negative correlation with the frequency of sexual presentation.

These age related influences on behaviour can be understood as part of the socialization process. In social animals such as Japanese monkeys, and primates in general, learning is an important, if not crucial factor in the development of behaviour. It is clear that many behaviour patterns change as an animal grows up, observing the behaviour of others as well as experiencing life itself. In terms of solicitation behaviour, the predominant change seems to be an increased level of sophistication, a tendency for the females to calm down and behave in a more self-assured, less frantic manner than when they were young and inexperienced. For example, the 'coy' courtship pattern is best represented by the "walk past". Both age and number of offspring show a significant positive correlation with the frequency of "walk past". This pattern usually results in the male following the female, and it seems less likely to result in the female being attacked in some way by the male. Through a process of trial and error, and by observing the courtship behaviour of older female monkeys, the maturing animal may become more likely to copy and eventually to adopt this behaviour into her own repertoire.

Further support for the idea that females become more efficient as they get older involves the frequency of presenting. In Japanese monkeys, sexual presentations are relatively rare; the common practice is for the male to hip touch the female when he is ready to mount. Nulliparous females who are generally young animals, show

TABLE 3

Results of the Pearson Correlation of frequency of proceptive behaviour with age and number of offspring

	Correlation Coefficient	Probability
Age	-0.1468	0.183
Number of offspring	-0.1108	0.248

significantly more sexual presentations. This is in line with the overall appearance of agitation and impatience. Frequent sexual presenting would be expected of animals who have not yet learned that there are other, less obvious, ways of prompting a male to mount. These young females may learn that mounting will start without excessive presentations and it is therefore a waste of energy to do so. Furthermore, it appeared that the more agitated the female was, the more likely she would be to annoy her partner and subject herself to attack. The notion that the frequency of obvious and possibly agitating behaviours decline as the female matures is further supported by the tendency ($p = 0.659$) for nulliparous and primiparous females to slap the ground more than multiparous females, and by the tendency ($p = .0732$) for nulliparous females to threaten the observer more than primiparous or multiparous ones.

These findings support those of Wolfe (1978) who also discussed sexual immaturity in young females. She stated that "the attainment of sexual maturity by adulthood can be viewed as a learned process leading to efficiency and prowess" (1978:55).

The effect of age (and therefore learning) as well as the predictable effect of an infant, are the most informative of

the socio-demographic variables analyzed, in terms of explaining female courtship behaviour. Certainly other factors must be investigated in order that we further our understanding of the role of the female in the establishment of consort bonds. The physiological basis of proceptive behaviour, as mentioned earlier, is not believed to be a direct or even important indirect predictor, however, it is possible that this issue needs to be reconsidered. At least in rhesus monkeys, new evidence suggests that underlying endocrine factors strongly influence female solicitation behaviour, and social variables such as rank do not appear to override this effort (Cochran, 1979). Possibly a more complete understanding of the physiological basis of reproduction and sexual behaviour is a necessary consideration for future research, despite the apparent emancipation from hormonal control. In Japanese monkeys this will be a particularly great challenge, since there is no apparent cyclicality to the occurrence of estrous (Wolfe, 1979) and since not only are the external indicators extremely variable, but also their relationship to internal events is not clear.

It is reasonable to consider that the interacting male may have an effect on the courtship behaviour of the female. The suggestion here is that females might behave

TABLE 4
Significant Behavioural Differences Between Females Based on Age, Number of Offspring and Presence of Infant

Higher Level Categories	ANOVA		Pearson Correlation	
	With Infant	Without Infant	Age	Number of Offspring
rejection received	$f = 8.820$ $p = 0.0052$			$r = 0.2834$ $p = 0.038$
solitary estrous behaviour		$f = 12.568$ $p = 0.0011$		
Specific Behaviours				
ventral sit against		$f = 4.678$ $p = 0.0367$		
alarm call	$f = 4.952$ $p = 0.0321$		$r = 0.3932$ $p = 0.004$	$r = 0.3841$ $p = 0.005$
body jerk		$f = 4.461$ $p = 0.0413$		
follow	$f = 5.340$ $p = 0.0264$		$r = 0.2281$ $p = 0.027$	$r = 0.3051$ $p = 0.021$
walk past			$r = 0.2812$ $p = 0.031$	$r = 0.2426$ $p = 0.054$
approach			$r = 0.2861$ $p = 0.028$	
genital inspect			$r = 0.2462$ $p = 0.052$	
sexual presentation				$r = -0.2433$ $p = 0.054$

differently towards different males. A number of studies have tried to approach the issue of female choice by investigating the relationship between the male's mating success and factors such as rank, aggressiveness, and tendency to display, but there has been no analysis of the behaviour of the female and how it might change depending on the interacting male. Exploring the basic behaviour differences that occur with different males is a crucial element in the study of female choice.

In this study it was hypothesized that some of the variability in female behaviour might be due to the sociological variables of male age, rank and spatial status. Contrary to what we might expect given the emphasis on rank in the literature, however, male rank does not seem to be significantly affecting the frequency of very many female behaviours. One clear result is that high ranking males leave females significantly more often than do either medium or low ranked ones. The other clear result is that females show fear indicators to medium and high ranked males more than to low (Table 5).

The other male variable that had a significant influence on behaviour is age. As was the case with the female variables, age of the male appears to be the most influential factor in terms of variability in courtship behaviour. First of all, age is positively correlated with a variety of male advances (Table 5). Older males showed a significantly greater tendency to follow, sit near, approach, increase proximity, lip quiver and walk past females. In other words, females are more likely to receive these behaviours from older males than they are from younger ones. Females also direct a variety of behaviours differentially to older males (Table 5). To older males the females show significantly more rejection behaviour and more indications of fear. Older males were also likely to receive significantly more of a few proceptive behaviours, specifically older males received more lip quivers, walk by and genital inspects from the females.

The influence of male age upon behaviour may also be interpreted in terms of learning. The differential behaviour exhibited by males of different ages is likely a func-

TABLE 5
Significant behavioural differences with characteristics of the interacting male.

	Male age	Male rank
<i>Behaviour Directed by Males to Females</i>		
follow	$r = 0.4736$ $p = 0.006$	
sit near	$r = 0.5763$ $p = 0.001$	
approach	$r = 0.5582$ $p = 0.001$	
increase proximity	$r = 0.4770$ $p = 0.006$	
lip quiver	$r = 0.4863$ $p = 0.005$	
walk past	$r = 0.4110$ $p = 0.017$	
leave		$f = 4.213$ $p = 0.0136$
<i>Behaviour Directed by Females to males</i>		
fear indicators*	$r = 0.3760$ $p = 0.027$	$f = 4.662$ $p = 0.0234$
rejection behaviour*	$r = 0.5441$ $p = 0.002$	
lip quiver	$r = 0.3234$ $p = 0.050$	
walk past	$r = 0.3144$ $p = 0.055$	
genital inspect	$r = 0.3583$ $p = 0.033$	

* indicates a higher level capacity

tion of the learning process. More importantly in terms of female choice, however, is the effect that the age of the male has on the behaviour of the female. Notably absent is any tendency for the females to show obvious and direct solicitation behaviours like "approach" and "follow" differentially to different aged males. There is no clear evidence that females prefer males differentially based on age. The tendency for females to show more rejection to older males may be a result of the greater number of advances received rather than an indication of an age preference.

The data indicate clearly that females are more likely to show indications of fear to older and higher ranking males. Whether it is age or rank that is the critical variable is not clear since they too are positively correlated. The courtship behaviour of the male Japanese monkeys does involve considerable "elements of intimidation" (Fedigan, 1982:145), so it is not surprising that the females are indicating fear. However, the results of this study do not indicate any tendency for the females to receive more courtship chases or other forms of aggression from older males.

Enomoto suggests that "there is a relation between female fear and the dominance rank order of the male" (1974:270). He points out that during the non-mating season there is little sexually related interaction and that behaviour such as sitting together or grooming occurs infrequently and only between established pairs. Since breeding season brings with it a need for contact between the sexes that is not otherwise occurring, new behaviour patterns are necessary. My results show fear on the part of the females toward older and higher ranked males. The data presented by Enomoto (1974) show a higher frequency of appeasement behaviour from higher ranked males. Both of these results support this notion. Furthermore, Enomoto reports that higher ranked males show a higher frequency of several types of positive behaviour. This is similar to my finding that older males show a higher frequency of a number of solicitation behaviours. While the true appeasement value of these behaviours is not known, it is very possible that something like "lip quiver", which is believed to function as a distance de-creeaser, may have an appeasement function in the courtship context.

It was expected that the sociological characteristics of the male would have a considerable influence on the courtship behaviour which they receive from the females, yet according to these data, the most clear cut results involve "female rejection" and "female fear indicators". Neither age, rank, nor spatial status of the male are responsible for any difference in the overall solicitation rate of the female. There was no indication that higher ranked males were more "popular" or received any more advances. Generally, this analysis suggests that we should rule out these sociological variables as the basis for the difference in female solicitation rates and courtship patterns. A viable alternative research pathway may be an analysis of the behaviour of the male and how this affects the courtship behaviour of the female.

SUMMARY AND CONCLUSIONS

The issue of female choice has been insufficiently dealt with in the primate literature and this has led to a view of the female as being essentially passive in the formation of mating pairs. This is a study of the courtship behaviour of female Japanese monkeys. Courtship behaviour is important in the construction of the male-female bond. The objectives of the study were to: (1) describe the repertoire of female courtship behaviour and the role of the female in establishing mating pairs; (2) compare females on the basis of age, parity, rank, number of offspring and presence of a recent infant to test for differences in courtship patterns; and (3) relate female courtship behaviour to the characteristics of the interacting males.

A comparison of the total number of female solicitations to the number of female advances received revealed that females play a more active role in soliciting partners than do the males and also reject more than thirty percent of the advances they do receive. There is a great deal of variety in the courtship repertoire, however, three basic stages leading to a mount sequence can be outlined. They are advertising and monitoring, testing and closing inter-individual distance, and attempting to establish a mount series. Among the 40 subjects, there was a great deal of variation in the total amount of courtship or solicitation behaviour shown.

An attempt was made to determine some of the female variables that affect the expression of courtship behaviours. The variables tested were age, rank, parity, number of offspring and presence of an infant. According to the data, none of these variables was responsible for the variability in overall frequency of proceptive behaviour. However, the age of the female did affect the frequency of specific proceptive behaviours. As the females get older they tend to become more efficient and sophisticated in their solicitation patterns. It is suggested that other variables, for example, the physiological stage of estrous, might be more important than sociological variables in influencing proceptive behaviour.

The age, rank, and spatial status of the interacting males were then tested in order to check for differences in the behaviour of the females. The results show that females express more fear indicators to higher ranked and older males. They also rejected older males more, but this could be due to the increased number of advances received by older males.

Having investigated the influence of some basic socio-demographic variables on female courtship behaviour, it is possible to go on to alternative lines of research. Suggestions for future research are: (1) multi-factoral analysis of male and female socio-demographic variables; (2) analysis of the effect of variation in male behaviour; (3) consideration of the possible differences in pre- and post-copulatory behaviour and in new vs. old consort pair behaviour; (4) detailed investigation of the relationship between female age and courtship behaviour; (5) a comparison of pre- and post-conception behaviour.

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SOME PRELIMINARY OBSERVATIONS OF VERVETS (*CERCOPITHECUS AETHIOPS*) FROM THE GREATHEEDS POND AREA ON ST. KITTS, WI.

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Abstract: Preliminary observations of vervets at Greatheeds Pond on St. Kitts show at least two distinct groups using the northern and western sides of the pond for most feeding and other activity. The animals live in a mangrove forest surrounding the pond and enclosed by a dirt tract linking several areas of moderate to intense human activity. Although the level of human disturbance seems high, preliminary observations show that the animals use certain aspects of human intervention in the forest and surrounding areas to their advantage.

Résumé: Nos études préliminaires de *Cercopithecus aethiops* à Greatheeds Pond, St. Kitts, W.I. nous suggèrent qu'il y a au moins deux groupes distincts qui emploient les côtés du nord et ouest de l'étang pour la plupart de ses activités. Les animaux se logent dans un forêt de mangrove autour de l'étang et ceint par un sentier enchaînant plusieurs centres de l'activité humaine. Malgré un niveau élevé de dérangement humain, nos études montrent que les animaux peuvent profiter de certains aspects de l'intervention humaine dans le forêt et environs.

Key Words: Vervets, Human, Disturbance, Feeding, Ranging.

Green monkeys (*Cercopithecus aethiops sabaues*) are thought to have arrived on St. Christopher and several other Caribbean islands with the African slave trade in the 17th and 18th centuries. (See McGuire *et al.* 1974; Coppinger and Maguire, 1980; or Poirier, 1972 for details). An estimated 30,000 monkeys live on the island today (McGuire *et al.*, 1974; Coppinger and Maguire, 1980).

St. Kitts is a volcanic island in the Leeward Islands (Lesser Antilles) centered on 17° 15' N and 62° 40' W (Poirier, 1972) consisting of a main island and a long, narrow peninsula extending to the southeast. On the main island the volcanic slopes are heavily forested, and the forest extends down to the sea coast in ravines between cultivated fields.

The peninsula is sandy and the vegetation is dominated by bush and scrub with some xerophilic species. The main part of the peninsula is uninhabited by humans. (For a more complete discussion of the ecology of the island see McGuire *et al.*, 1974; Poirier, 1972).

We concentrated our survey on a less well-known group around Greatheeds Pond – the most northerly of a series of marshes on the (Atlantic) northeast coast is located about 5 km from the capitol city, Basseterre and about 1 km north of the village of Conaree (Figure 1). An access

road circles the pond and surrounding forest which covers approximately 12.5 hectares. Nearly all trees within the forest are mangrove. Along the periphery acacia (*Acacia farnesiana*) and clammy cherry (*Cordia obliqua*) are important as food resources. Across the access road both the sea grape (*Coccoloba uvifera*) and the sugar cane are used as food resources.

We chose Greatheeds Pond for study because monkeys are rarely hunted there and because the forest is at least 1 km from known human dwellings. There were two main objectives of this survey. First, we hoped to determine which parts of the forest were used by the monkeys and with what intensity. Second, we hoped to identify the monkey population using the forest; and determine its size and composition.

SUMMARY OF OBSERVATIONS

Most observations were made from a single emergent tree (about 10m) on the water's edge that allowed us a view of about two thirds of the pond and surrounding forest (Figure 2). Secondary observations were made from a series of blinds within the mangrove forest. Several searches of the entire forest were conducted with the help of student volunteers from the two primate research centres on the island.

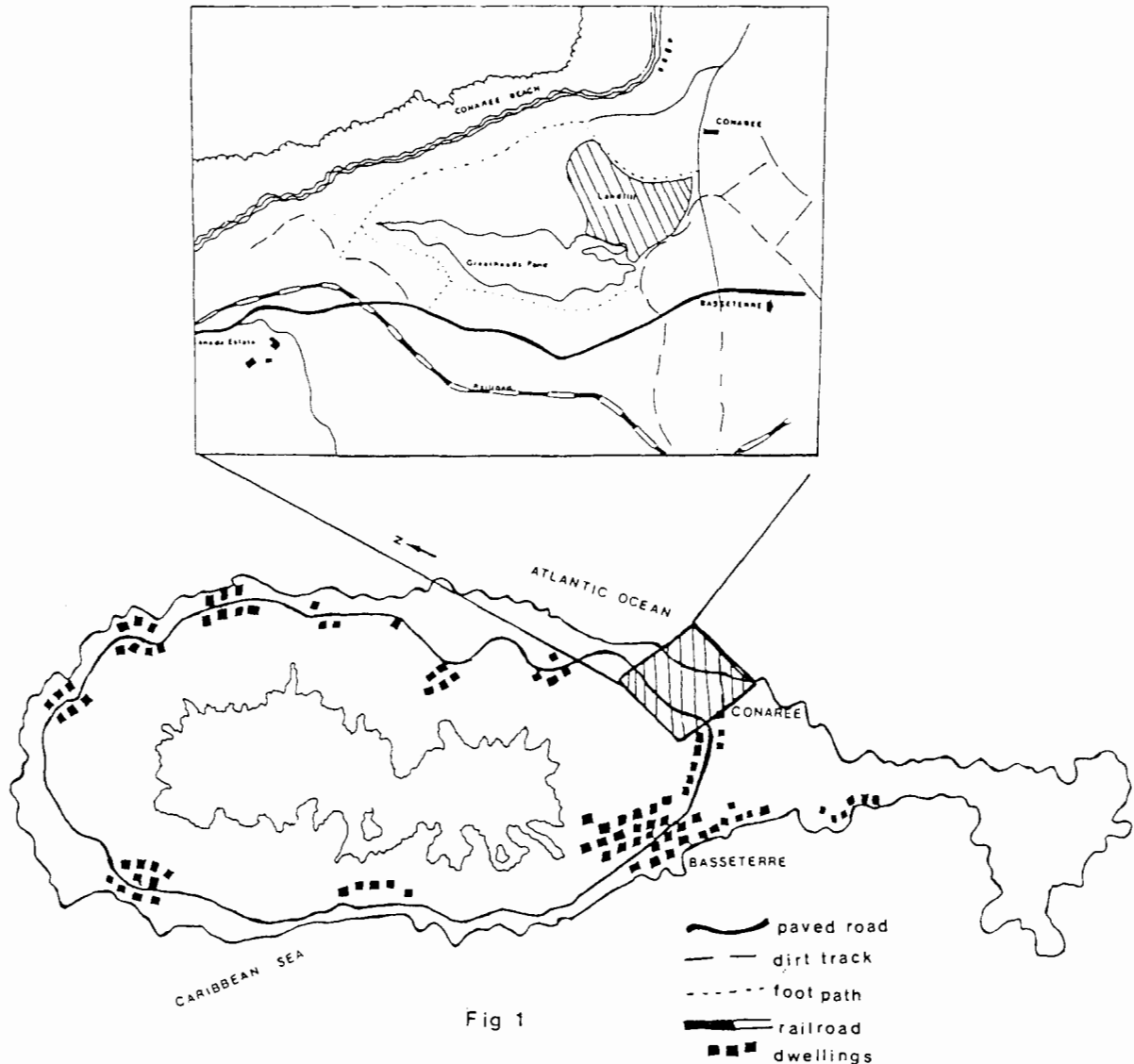


Fig 1

Fig. 1 Greatheeds Pond is located on the Atlantic side of St Kitts and is the northernmost of a series of shallow coastal ponds originating from the peninsular neck to the southeast. Details of the pond and vicinity are shown in the inset. The landfill to the southeast is a site of constant human activity. The railroad and cane fields are used seasonally by humans. The track around the pond is used daily, but predominantly in the morning and late afternoon.

Our observations on the pond site lasted from 23 June to 10 August, 1983, five or six days weekly. Direct observation of the animals' feeding area and travel routes was conducted from 0510 - 0830h and 1530 - 1845h daily. Searching various parts of the forest for traces of the animals was restricted to midday.

Monkeys became active in the predawn hours and moved into the feeding areas by 0600h and remained until 0800h. The animals generally returned to feed before 1600h. If undisturbed, they remained until 1800h. Nearly all of our contact and direct observation took place in the northwest corner of the forest (Figure 2), where the clammy cherry trees were most abundant, and there was easy access to sugar cane. We were able to observe monkeys feeding in the trees along the access road over a distance of about 100 to 150m.

The monkeys emerged from a low thicket on the northern end of the pond and crossed single-file over a series of fallen tree trunks before entering the feeding area (Figure 2). Just prior to crossing and after all the animals had entered, one individual sometimes would act as a sentry.

This crossing was the best time to observe the groups as they passed, but we later learned that an alternative route existed a little deeper in the forest (Figure 2) which was not visible from the observation post.

We made three types of sightings. Most frequently seen was a group of six monkeys. Despite the fact that the birth season was well under way, there were no infants in this group and no obviously pregnant females (although Fedigan [1982] reports that pregnancy may be hard to detect in vervets). We sexed the group by relative size and recorded its composition as one adult male, three proba-

TABLE 1
Approximate relative frequencies of sightings by area^a

		Northwest	Northern Border	Northeast	Southeast	Southwest
Direct Observation	(N)	56 ^b	12	2	0	3
	(%)	76.71	16.44	2.74	0	4.11
Traces	(N)	60	5	1	0	2
	(%)	88.24	7.35	1.47	0	2.94
Total	(N)	116	17	3	0	5
	(%)	82.27	12.06	2.13	0	3.54

^a The relative frequency of sightings in the five zones is computed as proportion of total sightings and by type. We included in the northwest zone sightings of animals moving into that zone along one of the travel routes from the rest or northern border zone. This might have distorted the relative frequencies or activity in each zone, but when compared to the proportion of indirect observations (traces) in the two zones, the difference is not significant ($p < .435$ for the northwest zone; $p < .41$ for the northern border zone.)

^b Includes observation of animals as they pass into this area from the northern border.

ble females and two juveniles.

Two adult males were consistently sighted alone or following at some distance behind the main group. These two males were observed several times at close range and identification of individuals was possible.

On two occasions we observed groups of 11 and 13 animals, respectively. It is likely that these other monkeys were not visible during most of the observations and that the actual group size is 12 or more.

FEEDING OBSERVATIONS

Most feeding occurred in a stand of clammy cherry trees along the access road on the northwest side of the pond (Figure 2 and Table 1). This road was well travelled, and the fruit trees are concentrated. Monkeys feeding in these trees fill their cheekpouches and then retreat to deeper parts of the forest to eat. We found a lot of pits, and pulp scattered on the ground and sticking to tree trunks up to 100m into the forest.

Animals used this same strategy when raiding the cane fields. They broke the stalk and then stripped out the pulp. Inside the forest dried stalks hang from the clammy cherry trees, and chewed pulp can be found on the forest floor.

We observed this activity daily except for a period of three weeks in July when no monkeys were seen in this area at all. There was also no indirect evidence of the monkeys during this time such as fresh feces, cane damage, or cane detritus in the trees. A careful search of the forest indicated that fruiting trees were not available elsewhere. This left us with two main questions. First, what other food resources may be available to these animals? Second, where are they located.

Several of the potential foods listed by McGuire *et al.* (1974) were abundant in the area. We saw many dis-

articulated crab shells. Large spiders, grasshoppers, and moths were abundant as well, and most trees showed new growth. Egg shells were found under trees in the main feeding area. The animals were not observed directly eating these foods, however, and most of the evidence for including them as dietary items comes from examining monkey feces.

All fecal samples recovered showed clammy cherry remains. Seeds are often found in the feces, but skins were always present. Some plant materials were identified, and some articles resembled insect hard parts. The frequency of the clammy cherry remains in the feces indicates that it is a favoured food. We looked for reasons why the animals might avoid this resource for such a long period of time, and considered that the pattern of the human disturbance of the forest may be an important factor.

The monkeys ranged throughout the forest. Table 1 shows the relative frequency of sightings in different parts of the forest. The fewest sightings were on the east side of the forest in the section near the landfill and in the southeastern section adjacent to it. In the northeastern section, there were two sightings. A local hunter also pointed out several traces of monkey hair on tree trunks there.

The northern border area appeared to contain the main resting and sleeping area. It was from here that the animals left to enter the feeding area and it was to this area that they returned after both morning and afternoon feeding. It was also the area where sentries were most often seen for up to two hours after the monkeys had entered it from other sectors.

In the northwestern sector we observed feeding in the trees and in the cane, travelling to and from the resting area, and some sentry behaviour. It was the only place where a whole group was observed feeding.

On three occasions several animals were observed feed-

ing on clammy cherry in the southwestern section. Dried fecal samples indicated that this part of the forest had been used before as well. How the monkeys travelled to this section was not clear, since there is a break in the forest cover both between the northwest and southwest and between the southwest and the southeast sectors.

HUMAN DISTURBANCE

Humans disturbed the forest in several ways. In the early morning and mid-late afternoon several groups of people would travel the road along the forest to the landfill. When they passed the feeding areas the monkeys would always flee into the forest. Morning and afternoon disturbances coinciding with the monkeys' feeding times also occurred as farmers came to tether or relocate their livestock grazing at the edges of the cane fields. These disturbances were temporary, and the monkeys often returned within an hour to the feeding site.

Humans accounted for the two persistent disturbances that we think may have been important determinants of forest utilisation. One local craftsman used the mangrove as a source for reeds for making baskets. On the occasions when he was there, he chose the relatively accessible western side of the forest, choosing and cutting materials over several days.

A second human lived on the forest's edge along the beach road to the north. He earned his livelihood from selling charcoal made from the trees in the forest, disturbing the forest in two ways. First, he cut down trees both to use as fuel and to clear trails into the forest. Later he would cover the logs with sand and burn them for several days to produce charcoal.

The charcoal maker and the basket weaver both began a round of activity in the same week – the first week that the monkeys disappeared (about 4 weeks after our observation began). It was a full week after the burning ended that the animals returned to the northwestern sector to feed, but the charcoal maker had a more lasting effect on the monkey group. The parts of the forest he cleared altered the routes available to them for travelling between sectors. Much of the northern border sector had been cleared so that there were narrow "highways" of vegetation over 10m high. The rest was under 3m.

It was along these highways that we made all the observations from blinds in the forest and most other sightings; and it was here that we found all our indirect evidence – fecal samples and dropped food – in the northern border area.

DISCUSSION

McGuire *et al.* (1974) describe the various types of human disturbances and their effects on the groups they were observing. Direct disturbance occurs when humans or their livestock come into contact with the monkeys, indirect disturbance occurs when activities outside of the areas used by monkeys affect the group.

Previous studies have reported that primate groups are sensitive to human activity in the forest, but they have

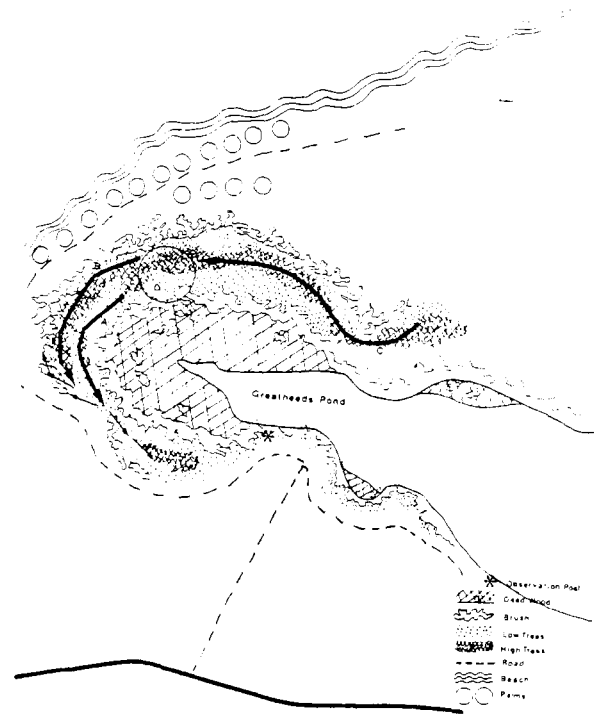


Fig. 2 The main contact area for this study was along the northern edge of the pond. From our observation post at the southern end of a cove, we could see the main travel routes used by vervets. A and B are the two routes usually taken to travel to the main feeding area in the northwest of the pond. Animals were observed directly using route A, while fecal and food remains identified route B. Route C was used by the satellite group on two occasions as they returned to the rest area (D). The animals usually traveled along the edge of tall trees to and from the rest area.

focused primarily on the effects of habitat destruction (Heltne *et al.*, 1970; Kano, 1982; Jones and Sabater Pi, 1971) or hunting of the primates by humans (Whitten and Whitten, 1982; Freese *et al.*, 1982; Jones and Sabater Pi, 1971). Our observations on Greatheeds Pond indicate that indirect effects of human activity patterns in the forest and surrounding fields may be more important.

The indirect effects of human disturbance are a new focus in primate ecology and conservation. Changes in forest utilisation due to human economic and subsistence activity are observed by Jones and Sabater Pi (1971) for lowland gorillas and common chimpanzees. Handler (personal communication) has reported similar changes in forest use patterns among pygmy chimpanzees in Zaire under pressure from logging industry. Human agricultural and forest management activity has been implicated also in altered patterns of habitat utilisation among pygmy marmosets (Soini, 1981), several species of New World monkeys in Venezuela (Rudran and Eisenberg, 1982), and vervets, Nilgiri langurs, and crab-eating macaques (Poirier, 1976).

Bishop *et al.* (1981) have proposed a four-point ordinal scale for estimating habitat disturbance. This scale measures four types of habitat disturbance. Disturbance to the habitat is a measure of direct human use of forest resources; disturbance to the animals measures the degree to which humans attempt actively to displace monkeys from these resources. The habitation scale records how accustomed the monkeys are to a human presence and the predation scale measures whether predators are naturally occurring prey species, domestic animals, or absent. A low score (1) indicates the least disturbance to the presumed "natural" habitat.

The Greatheeds Pond area is surrounded by land modified by human activity. Land on three sides of the pond is under continuous use for sugar cane cultivation and as a landfill. The northern border and northeast areas are used occasionally by humans, although at least one human makes his home in the northern border area. On the scale proposed by Bishop *et al.* (1981) the habitat disturbance is rated 2.5 (Table 2).

TABLE 2

Ordinal evaluation of human disturbances to monkey populations in the Greatheeds Pond area. Rankings follow Bishop *et al.* (1981). Details in text.

Disturbance to habitat	2.5
Disturbance to animals	2
Habituation to humans	1.5
Presence of predators	4
Total disturbance	10/16

Animals are rarely harassed by humans, except when seen in the cane fields. This would rate 2 on the animal disturbance scale. The monkeys are totally unhabituated, fleeing whenever humans approach, but returning within a short time (1.5 on habituation scale). Finally, there is a complete absence of predators in the Greatheeds Pond area (4 on the predator scale).

As Bishop *et al.* (1981) suggest, this ordinal scale may be useful for comparing the relative disturbance in different areas, but one cannot interpret the scores as any sort of definitive description of habitat disturbance. This method is proposed as an interim approach to be supplemented with further research into the problem. According to the scale, the Greatheeds Pond area is significantly disturbed, despite the absence of direct human predation. There are both short-term effects due to the presence of humans and their livestock in the forest and long-term effects due to forest destruction and regeneration. We were unable to predict the location of the monkey groups on the basis of food resources alone. They change their utilisation patterns based on the effects of human disturbance in two ways.

First, they disappeared from the areas where favoured food resources were abundant. Second, the monkeys began travelling before sun-up to the feeding areas. Chapman (personal communication) has also found that the

vervets from the peninsula moved to and from sleeping sites under the cover of twilight whenever pressure from humans was felt.

In the future we hope to be able to carry out long-term studies at Greatheeds, on alterations in foraging behaviours and travel routes caused by various human activities and the rate of recovery from these disturbances.

ACKNOWLEDGEMENTS

This research would not have been possible without the advice and support of Drs. Michael McGuire and D. Eugene Redmond and the staff and students at the St. Kitts Biomedical Research Foundation, and Dr. Frank Ervin and the staff and students at the Behavioral Sciences Foundation. We wish to thank Drs. Linda and Laurence Fedigan for their encouragement of this research and their advice on research problems and strategies. Colin Chapman gave us the benefit of his recent research experience on the island. Dr. Laurie Godfrey supported and encouraged the project and was responsible for our collaboration. We wish especially to thank Sarah Petto for logistical support throughout the summer and for the figures which accompany this report. This project was supported in part by a Graduate School Fellowship from the University of Massachusetts at Amherst.

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CONGENITAL ABNORMALITIES IN A PREHISTORIC IROQUOIAN VILLAGE: THE UXBRIDGE OSSUARY

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Abstract: The Iroquoian Feast of the Dead and associated ossuary construction created a single repository for the recently deceased members of neighbouring villages. As such, the ossuary provides an excellent vehicle for studying the prevalence of congenital abnormalities in a population. With this objective we examined the Uxbridge Ossuary, from Southern Ontario (N=457, ca. 1490 ± 80 A.D.). Five congenital conditions are identified and three of these show multiple occurrences. Congenital abnormalities include one case of hereditary multiple exostoses, one case of scoliosis, three cases of craniostenosis, two hemi-vertebrae, and four Stafne defects. It is argued that the study of congenital defects present in ossuary samples may be used to study the population's genetic relatedness.

Résumé: L'ossuaire associée à la fête de la mort des Iroquois forma une répositoire unique des membres récemment décédés des villages voisins. Donc l'ossuaire peut fournir un excellent échantillon type pour l'étude des anomalies congénitales de la population. C'est dans ce but que nous avons étudiés l'ossuaire d'Uxbridge dans le sud de l'Ontario (n = 457, ca. 1490 ± 80 après J.C.). Nous avons pu identifier cinq conditions congénitales, dont trois aux manifestations multiples. Parmi les anomalies congénitales se trouve un case des exostoses multiples, deux hemi-vertèbres, et quatre défauts de Stafne. Nous estimons que l'étude des anomalies congénitales trouvées dans les restes des ossuaires peuvent nous servir dans l'analyse du niveau d'apparenté de la population.

Key Words: Congenital Abnormalities, Ossuaries, Genetics, Iroquoian Feast of the Dead.

The ossuary, as found in Southern Ontario, presents a unique research situation to the paleopathologist. Through their funerary ritual, the Feast of the Dead, the Iroquoians created a repository for all deceased group members from the past 8-12 years (cf. Thwaites, 1896-1901; Trigger, 1969, 1976). If ethnographically documented practices were followed, the resulting sample is an almost complete representation of deaths taken from a deme during a discrete time interval. As such, it offers an excellent opportunity to study the incidence of congenital and developmental abnormalities within a population.

On the other hand, there are shortcomings. Some individuals, including very young infants, victims of drowning and perhaps warriors fallen in distant battlefields (Churcher and Kenyon, 1960) are not included, or have been cremated. The bone is thoroughly mixed and frag-

mented so that often age and sex cannot be attributed to an abnormal specimen, nor can the extent of skeletal involvement be ascertained from an isolated fragment.

With these limitations in mind, we set out to document the extent and type of congenital abnormalities found within one ossuary. We reasoned that whatever heritable conditions are seen may very likely be present in multiples if the sample is one of related individuals. Thus, examination of congenital abnormalities can support the assumption of genetic relatedness. It also gives a very general indication of the "load" of disabilities tolerated by the group.

There is some evidence that Iroquoians did not kill infants displaying physical defects. A complete cleft palate is documented in an adult from the nearby Kleinburg Ossuary, A.D. 1600 (Melbye, 1975). Individuals with severe disabilities such as femoral fractures appear to

have been maintained within the Uxbridge population (Pfeiffer, in press). Ethnographic accounts of the Huron indicate that "cripples and other deformed individuals were rare, but were not entirely absent" (Trigger 1969:7). Hence, we may hope to see a good representation of inherent skeletal defects.

Relatively common conditions (e.g. malalignment of the dentition, accessory cranial bones) and conditions of equivocal etiology (e.g. spondylolysis, rib abnormalities) are not included in this discussion. While conditions such as spondylolysis and cervical fusions may show a simple Mendelian etiology (McKusick, 1975), in an ossuary sample it is often impossible to rule out extenuating trauma. For example, the Uxbridge sample includes one vertebra with partial spondylolysis which is clearly the result of spinal trauma. Evidence of infection and trauma, while amply represented in the Uxbridge sample, are also excluded from this discussion.

MATERIAL

The Uxbridge Ossuary was excavated from 1975-1977 by Patsy Cook and members of the Ontario Archaeological Society. The skeletal remains were transferred to the University of Guelph in 1979. The site was located approximately 65 miles northeast of Toronto. It has a radiocarbon date of 1490 ± 80 A.D. (I-9865). Such a date does not make the site unequivocally prehistoric, but the date plus aspects of the ossuary's construction make a pre-contact date very likely. For example, there were virtually no grave-goods, a trait which typifies pre-historic ossuaries and distinguishes them from historic ossuaries rich in grave-goods (Cook, 1977). The Uxbridge Ossuary was located not far from historic Huronia.

The bone is in good condition, but most skeletal material from the site is fragmented. The skeletal material is divided into many stratigraphic units. The excavators tried to identify articulations in the field, and one individual discussed below was identified as a "bundle". Throughout the ossuary, material is very well mixed, with fragments of a single bone coming from widely dispersed stratigraphic units. Most pathological specimens are such isolated fragments of single bones.

The highest estimate of total population size comes from a count of the genial tubercles of the anterior mandible. The minimum sample size is 457, of which 32% are immature and 68% are mature individuals. Infants under two years of age make up 13.5% of the total (Pfeiffer 1983).

CONGENITAL ABNORMALITIES

Hereditary Multiple Exostoses (osteochondromatosis, diaphyseal aclasis

This condition is transmitted as an autosomal dominant with full penetrance (Solomon, 1964). The disorder affects the endochondral skeleton, usually during childhood or adolescence, and may result in deformities and/or interfere with growth (Steinbock, 1976; Zimmerman and Kelley, 1982). One or more bony projections (exostoses)

capped with cartilage appear in areas of active growth. These continue to grow until endochondral bone growth ceases. The most frequently affected area is around the knee, followed by the proximal humerus, distal tibia, metacarpals and phalanges of the hand (Ortner and Putschar, 1981). Other areas are less commonly affected. The projections are usually bilateral and typically symmetrical. As few as one, or as many as several hundred exostoses may occur. In a few cases (1-25%) chondrosarcoma, a malignant condition, develops from the benign exostoses.

The affected individual from Uxbridge is represented by a bundle burial including most of the long bones but none of the axial skeleton. All epiphyses are fused, indicating adult status. The long bones are relatively small and delicate.

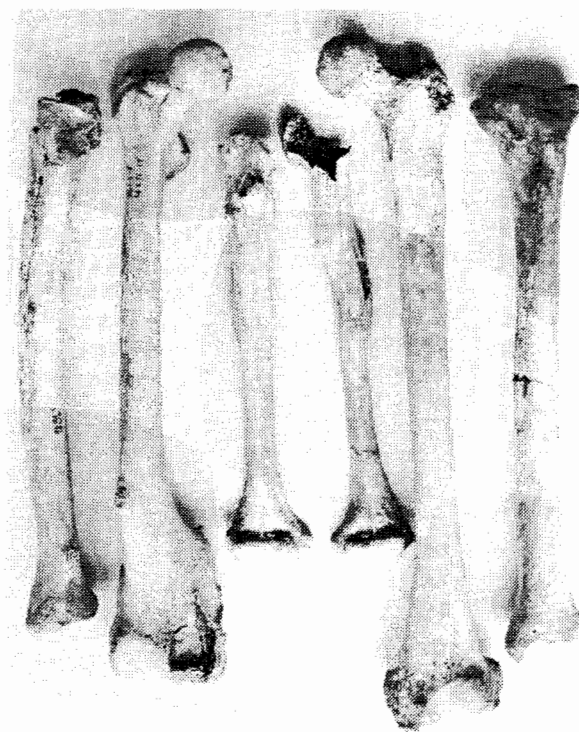


Fig. 1 Hereditary multiple exostoses. A bundle burial: the humeri, right femur and right tibia are most clearly affected.

Both humeri exhibit exostoses (Fig. 1). On the right humerus a large, rounded lesion is located along the greater tuberosity. On both humeri the deltoid tuberosity is abnormally expanded with an exaggerated crest. The medial side of the shaft, opposite the deltoid insertion is similarly expanded. A break along the enlarged region of the left humerus shows irregular structure of the underlying trabecular bone and radiographs show cortical thinning of this area.

The right radius appears to be normal with the exception of a small thin ridge of bone just proximal to the distal articulation with the ulna on the medial shaft. The



Fig. 2 Craniostenosis of the sagittal suture; age approximately six years.

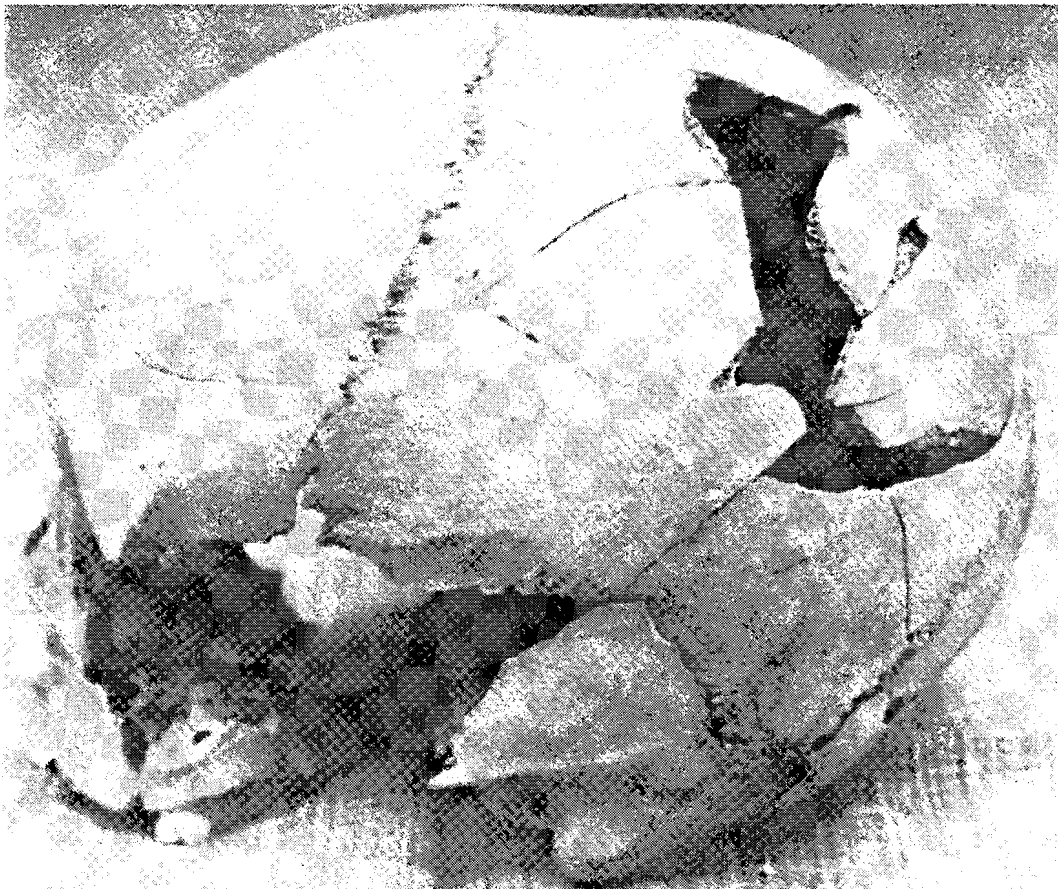


Fig. 3 Craniostenosis of the sagittal suture in a 9-11 year old. Note post-coronal constriction.

right and left ulnae are unaffected and the left radius is not present.

The right femur (Fig. 1) is the most severely affected element and it was this bone which first caused us to consider hereditary multiple exostoses as the cause of the lesions. Two small tubercles appear anteriorly and one posteriorly on the neck of the femur. On the anterior aspect of the shaft a large exostosis occurs in the midline. Distally, two large continuous lesions extend approximately 90mm to the condyles in such a way that the entire distal end is expanded. The protruding lesions are broken, exposing irregular trabeculae. The left femur is unaffected. Its maximum length of 431mm exceeds that of the right (affected) femur by 24mm.

The right tibia exhibits a large lesion on the posteromedial surface just distal to the medial condyle. Another lesion is found on the posteromedial surface just proximal to the distal end. Part of the exostosis has been broken off. The left tibia has a small tubercle just distal to the medial condyle on the posterior surface. Both tibiae are also characterized by a generalized periostitis including plaque formation and spongy porous bone medial to the anterior crest along the shaft.

On the right fibula there is a ridged lesion similar to the one on the radius. Here, it occurs just distal to the head on the lateral surface. A periosteal reaction is visible along the proximal half of the shaft. Just proximal to the distal articular surface there is another tubercle. The left fibula exhibits a generalized periosteal reaction. The right patella appears normal.

For differential diagnosis and further discussion of this case, see Katzenberg, Kelley and Pfeiffer (1983).

Craniosostenosis (premature suture fusion)

Three crania (of the approximately 125 extant crania) exhibit premature suture obliteration. Two of the three are very similar in pattern, extent, and age at death.

A six year old exhibits complete fusion of the sagittal suture, from bregma to a point of skull breakage just superior to lambda. Hence, at least two thirds of the suture was obliterated. The age of this individual is based on the intact deciduous dentition and incomplete root formation of the first permanent molars. No other cranial abnormalities are apparent, nor is there any notable modification in vault shape.

A second immature individual displaying sagittal fusion appears to have been approximately 9-11 years old at death. In this specimen, the vault is more complete. There is no trace of the sagittal suture from bregma to lambda. The mixed dentition includes a worn m^2 (the other anterior teeth were lost post-mortem). Both first permanent molars are fully erupted. The roots of the permanent central incisors are incomplete. Mild *cribra orbitalia* is present (unusual in this sample). The vault shows clear post-coronal constriction, and perhaps some anterior-posterior elongation.

The third example of craniosostenosis is an adult, probably female, showing premature fusion of the left half of

the coronal suture. A mid-adult age is probable, based on pre-mortem loss of the mandibular molars (the face, including the maxilla, is absent). Sex is assigned on the basis of several gracile cranial and mandibular features. The closure of the left half of the coronal suture is likely to have occurred long before this individual's death, since marked remodelling is apparent. The right parietal is bulbous in shape, while the left parietal is flat and notably smaller. The sagittal suture runs obliquely, tending leftward posteriorly. It is obliterated endocranially. Even the occipital region is asymmetrical, with the right side being more bulbous.

Although the face is absent, the glenoid fossae indicate malalignment of the mandible. The right fossa is shallow and flat. Both fossae show mild arthritic changes. The endocranial surface displays evidence of several Pacchionian depressions in the central parietal region. This female has red ochre staining of the forehead region, a cultural trait which is quite unusual for this site. The contemporary incidence of craniosostenosis is difficult to ascertain clinically, since in some cases it is asymptomatic, in other cases it may be part of a more complex disorder. An autosomal recessive pattern of inheritance is said to be most likely in cases where craniosostenosis alone occurs (Paulson and Allen, 1970).

Hemi-vertebrae (butterfly vertebrae)

Two adults display this rare developmental malformation of the vertebral body. The more complete specimen, from a young adult, is a partial vertebra column including lower thoracic and upper lumbar vertebrae. Of these, T12 is a true butterfly vertebra and is fused posteriorly to T11. The posterior fusion is complete, including both sets of intervertebral facets and the tips of the spinous processes. The bodies of T11 and T12, however, remain distinct. Of the two lumbar vertebrae present, one may be L1, and hence articulate with the hemi-vertebra, but it is uncertain. More likely, these units are L2 and L3. A separate thoracic vertebra, probably T8 or T9, shows abnormal modelling of the inferior body and left transverse process, very similar to that seen on T11. It is most simply explained by the presence of a second butterfly vertebra immediately inferior to it. There is no evidence of any scoliotic curvature of the spine.

The second example of a hemi-vertebra consists of one isolated hemi-vertebral body. Its color, size and texture indicate that it is adult, but probably not the same adult as previously described. Its size is consistent with that of a thoracic vertebra. It is not compressed medially, and so is likely to represent one half of another butterfly vertebra.

Scoliosis

A fused vertebral segment from an adult (> 25 years) displays the lateral torsion and rotation characteristic of scoliosis. Four thoracic vertebrae, probably T8 - T11, are completely fused anteriorly. The two most superior bodies are markedly wedged, showing the greatest compression

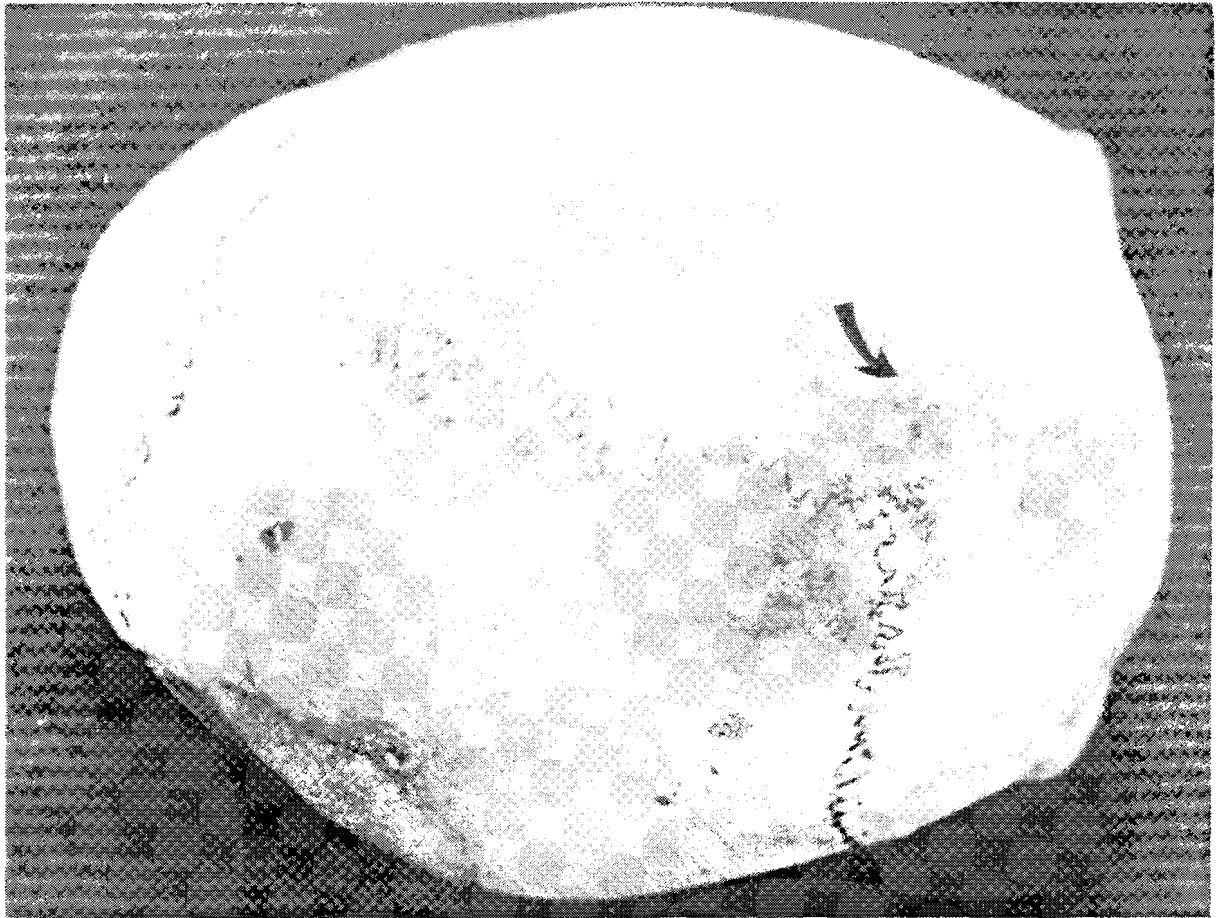


Fig. 4 Craniostenosis in a mature female, showing obliteration on the left half of the coronal suture (arrow) and resulting in considerable torsion.



Fig. 5 Fusion of T11 and T12, the latter being a butterfly vertebra.



Fig. 6 Same fused vertebrae, showing inferior view of butterfly vertebra.

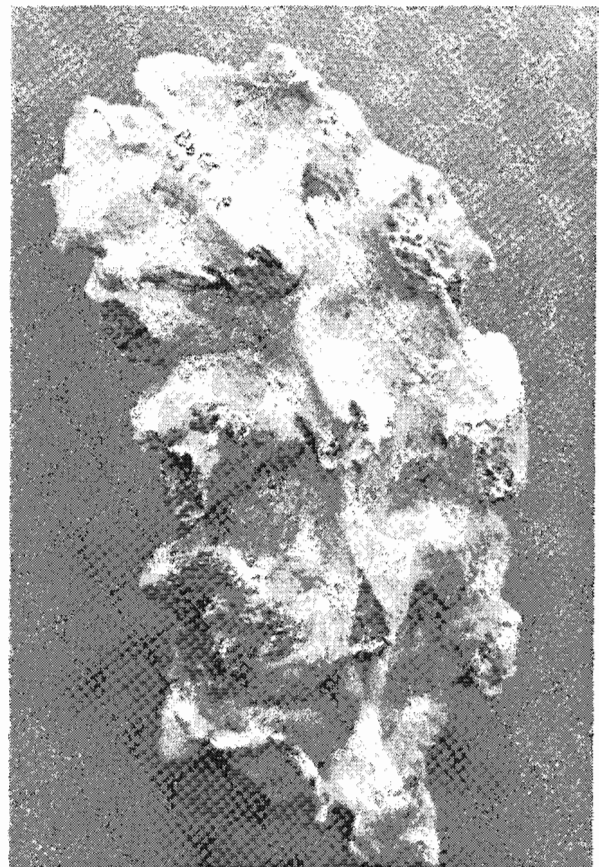


Fig. 7 Scoliotic spine, dorsal view.

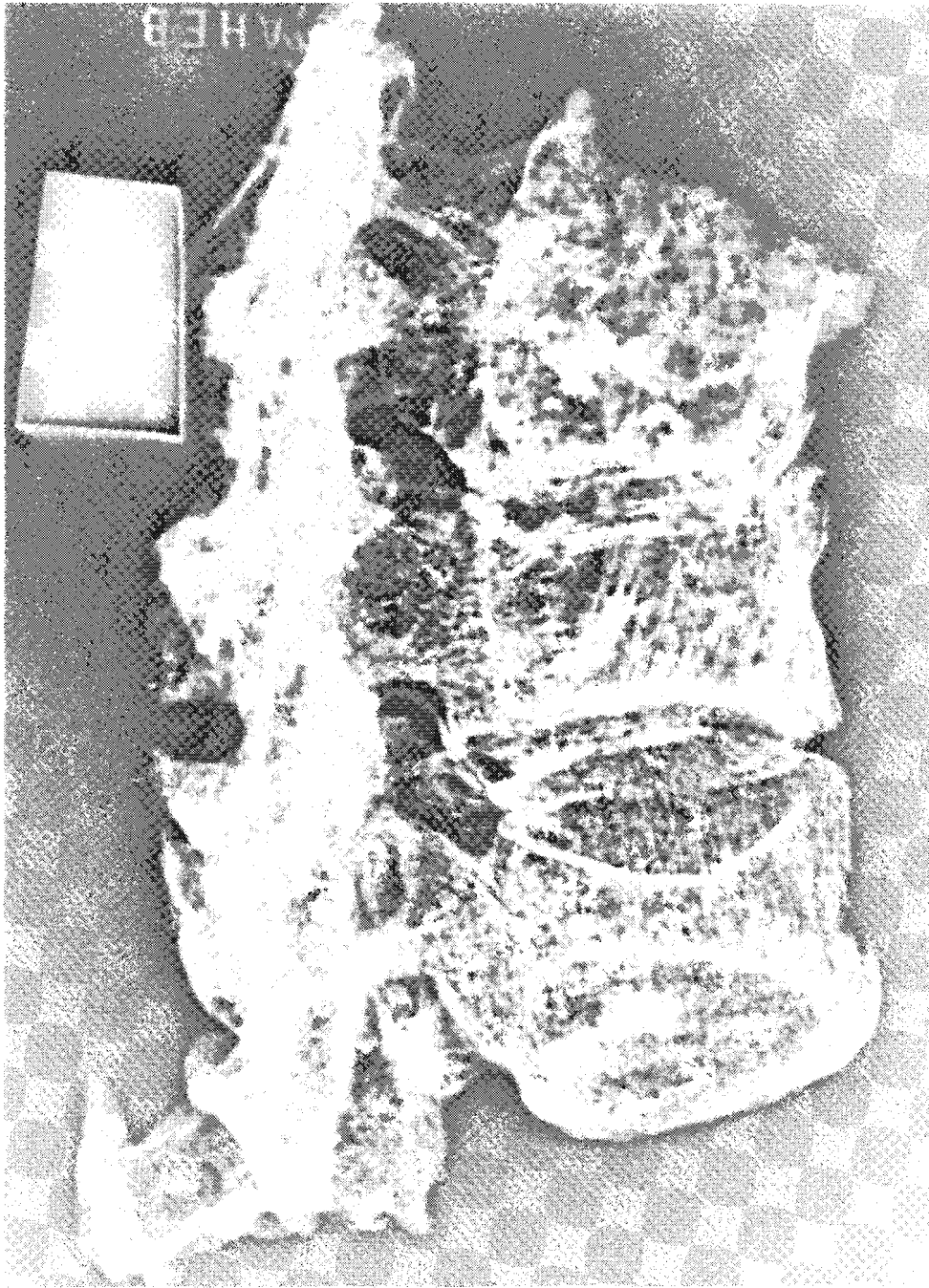


Fig. 8 Lateral Xerograph of scoliotic spine. Note twisted orientation of medial trabeculae.



Fig. 9 Three mandibles displaying Stafne defects, as indicated by arrows. Note the unerupted extra tooth in the top mandible.

in the left, anterior direction. The body of the vertebra immediately inferior to them is wedged slightly, and all three are fused along the left side. Trabeculae of the two inferior bodies show a twisted orientation. The vertebra immediately superior to the fused segment, probably T7, is similarly twisted. The left rib facets are atrophied. The right rib facets are normal, though porous in appearance. On the inferior aspect of the fused segment, the left intervertebral facet is expanded and arthritic in appearance, while the right intervertebral facet is absent. There is no evidence of any disorganized new bone growth, localized bony deterioration, infection or trauma. Hence, a diagnosis of congenital scoliosis is suggested.

Such cases appear to be rare in the paleopathological literature (cf. Ortner and Putschar, 1981:326). Contemporary clinical literature indicates an incidence of scoliosis requiring treatment (> 11 degrees) of 2.75/1000 (Rogala *et al.*, 1978). The exact mode of inheritance remains undetermined.

Stafne Defect

Four mandibles exhibit evidence of a cyst, referred to by Finnegan and Marcsik (1980) as a Stafne Defect. The defect is also referred to as a static or latent bone cyst, a developmental defect containing salivary gland tissue, most commonly of the submandibular gland (Gorlin and Vickers, 1977). All four defects occur on the right side and all are from adults. The first specimen (top of Figure 9) shows a defect located inferior to the right third molar. Just posterior to the relatively deep resorptive area is a smaller resorptive lesion. The second specimen, like the first, shows considerable attrition to the third molar. The defect is located more posteriorly than in the first case and is smaller and more shallow. It is just anterior to the gonial angle. Most teeth were lost antemortem in the third case. The defect is inferior to the position of the second molar. Of the four cases, this defect is largest and deepest. The fourth case is a partial mandible, broken at the left canine. The defect is circular, located inferior to the third molar area and inferior to the mylohyoid groove. All right molars were lost premortem.

Finnegan and Marcsik (1980, 1981) classify the Stafne Defect as an anomaly rather than a pathology. While certain types of mandibular bony cysts are recognized as heritable (McKusick, 1975), the etiology of the Stafne Defect is uncertain. There is consensus, however, that it is not traumatic in origin. It is unlikely that the cyst would have inconvenienced affected individuals. It is of interest here as a developmental defect represented in four individuals, or one percent of the ossuary sample. This level of incidence is the same as that cited by Finnegan and Marcsik (1980) for surveyed archaeological samples in which the defect is present. It is substantially higher than the clinically reported incidence of 1/10,000 to 1/3500.

DISCUSSION

Of the five conditions presented, all except Stafne's Defect may have imposed disadvantages upon the af-

ected individuals. Symptoms noted in cases of hereditary multiple exostoses include: localized pain, interference with movement, deformity, pregnancy complications and impinged nerves, including compression of the spinal cord. Premature suture closure may cause distortion in the growing skull, and in severe cases, may cause mental retardation and vision disorders (Kelley, 1980). (It is quite possible, however, that none of the cases described here caused any serious disability.) Hemi-vertebrae and scoliosis affect posture and increase the risk of spinal cord injury.

There is evidence from ethnographic and osteological sources that populations like Uxbridge could and did support individuals with disabilities. More interesting, for the purposes of this study, is the multiple occurrence of three of the five conditions. Approximately two percent of the intact crania show craniostenosis, one percent of adult mandibles show Stafne's Defect and two cases of hemi-vertebrae are present. Given its autosomal dominant mode of inheritance we are surprised at finding only one case of multiple exostoses. This is most likely explained by the fragmentary, mixed nature of the ossuary material. It was fortuitous that one affected individual was recovered as a partial bundle burial.

The incidences reported here cannot, unfortunately, be compared to "global" incidences for Iroquoian ossuary populations. It would be helpful to researchers working with such populations to have a check-list of rare congenital anomalies and/or pathologies for which to look. The unique ethnographically-documented origin of these samples gives us the opportunity to study genetic relatedness in ways which might be inappropriate if applied to other kinds of prehistoric skeletal samples. We believe that the occurrence of multiple cases of rare conditions is most easily explained by postulating a high coefficient of heritability for the Uxbridge sample. Further research with other samples from this region could substantiate or refute this proposal.

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INHERITANCE AND EVOLUTION: THE ROLE OF LAMARCKISM IN CONTEMPORARY BIOLOGY

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Abstract: Although many recent authors would like to see revisions of the synthetic theory of evolution, few of them have professed a return to a Lamarckian model of evolutionary change. It is difficult to define Lamarckism today since in the past it has meant many things to many people. Lamarck's own writings were greatly misconstrued and misinterpreted. A biological definition of Lamarckian inheritance today would embody two aspects: first, the occurrence of controlled or directed mutations which would mean that the creativity would lie with the process of variation itself rather than with natural selection and second, that passing of these directed variations across the Weismann barrier from soma to germ plasm over one generation. A number of recent observations within biology have shown that the Weismann barrier is not unsurpassable. However, if all acquired variation could pass from soma to germ cells we would still need some kind of selection process so that only certain outcomes of the random could endure in order to prevent genetic chaos. Much of past genetic research has been conducted to show that the production of variation is random and not directed. Recently though, some workers have even claimed the existence of directed mutations at the molecular level and others have argued that directed mutations must exist in such a teleologic looking world. The popularity of purpose or necessity as opposed to chance in evolution has broad philosophical underpinnings. However, for sexually-reproducing multicellular organisms the existence of somatic flexibility negates the need for a Lamarckian explanation of inheritance, a process which is tied too rigidly to genetic determinism.

Résumé: Bien que plusieurs auteurs récents aimeraient voir des révisions faites à la théorie synthétique de l'évolution, peu d'entre eux ont professé le retour au modèle lamarckien de la transformation évolutionnaire. Aujourd'hui, il est difficile de définir le lamarckisme puisqu'autrefois, cela signifiait plusieurs choses à beaucoup de gens. Les écrits mêmes de Lamarck étaient largement mal interprétés. De nos jours, une définition biologique de l'héritage comprendrait deux aspects: premièrement, l'occurrence des mutations contrôlées ou dirigées, ce qui voudrait dire que la créativité reposerait sur le processus de la variation elle-même plutôt que sur la sélection naturelle et, deuxièmement, le passage de ces variations dirigées à travers la barrière de Weismann, du soma au protoplasme du germe au-delà d'une génération. Un nombre d'observations récentes en biologie ont montré que la barrière de Weismann est sans pareille. Toutefois, si toute variation acquise pouvait passer de cellules de soma à celles de germe, on aurait toujours besoin d'un processus de sélection pour que seuls certains résultats du choix au hasard puissent durer afin de prévenir un chaos génétique. Les recherches génétiques se faisaient essentiellement pour montrer que la production de variation est au hasard et non dirigée. Mais récemment, quelques travailleurs ont même affirmé l'existence des mutations dirigées au niveau moléculaire et d'autres ont soutenu que les mutations dirigées existent dans un monde à l'air si téléologique. La popularité de but ou de nécessité opposée au hasard dans l'évolution a de larges étanconnements philosophiques. Néanmoins, pour les organismes multicellulaires se reproduisant sexuellement, l'existence de la flexibilité somatique nie le besoin d'une explication lamarckienne de l'héritage, un processus qui est trop rigide lié au déterminisme génétique.

Recent years have seen a plethora of published articles calling for a revision of evolutionary theory or the development of a new evolutionary synthesis (Ho and Saunders, 1979; Rosen and Buth, 1980; Tuomi, 1981; Plotkin and Odling-Smee, 1981; Gould, 1982; Van Waesberghe, 1982; Arnold and Fristrup, 1982). In this instance, I am not referring to the so-called creationist-evolutionist debates but to more detailed theoretical discussions led by biological scientists who accept as fact that all living organisms are part of a general process of "descent with modification".

The criticisms of the synthetic theory of evolution assert that it has broken down on some of its fundamental claims. As recorded in a recent book tracing the origins of the synthesis, the theory states that evolution occurs through two processes:

1. a gradual accumulation of small genetic changes by random mutations and genetic recombination and the ordering of this variation by natural selection.
2. all observed evolutionary phenomena, including macroevolution and speciation, can be explained in a man-

ner consistent with the known genetic mechanisms. The synthetic theory amalgamates Darwin's theory of natural selection, Mendel's theory of inheritance and our knowledge of the actions of genes in populations. (Mayr, 1980).

As Gould notes (1982) Darwin himself was a pluralist who saw the proposal of natural selection as his major accomplishment but who also emphasized the importance of the inheritance of the use and disuse of parts, and the direct action of external conditions on organisms and thus accepted the theory of acquired characteristics as being an important component of his general theory of evolution. After his death, history records a long period from the 1890's to the 1930's, sometimes known as the "eclipse of Darwinism", which was fraught with disputes between the Mendelians and biometricians who could not reconcile the level at which evolution operated and between strict selectionists and evolutionary pluralists who could not reconcile what the major forces of evolution were (Gould, 1982).

Present day critics of the synthetic theory also have difficulty with its essential claims or at least with some of the corollaries of these claims although for different reasons than early 20th century dissenters. For example, Gould (1982) is not opposed to natural selection per se but to its corollaries, gradualism and adaptation, arguing that gradual allelic substitution as a model for all evolutionary change is insufficient and that we have widespread evidence for large-scale trends and episodic change in the evolutionary process. In critiques of the adaptationist program various authors (Gould, 1982; Gould and Lewontin, 1979; Gould and Vrba, 1982) argue that nonadaptations or features of organic architecture and developmental pathways that have never been adaptations to anything but arose as by-products or incidental consequences of changes, are pervasive in evolution and far more numerous than the direct adaptations that engender them.¹ In addition, Gould (1980; 1982) and others (Arnold and Fristup, 1982; Stanley, 1979) have argued for a hierarchically based theory of evolution where "natural selection" operates at a variety of levels such as alleles, individuals and species, retreating from what they see as extreme reductionism embodied in the focus on organisms as units of selection. And there are those who have emphasized various forms of theoretical pluralism, describing their new models of evolution as dynamic, multi-level (Tuomi, 1981), multiple-level, multiple process (Plotkin and Odling-Smee, 1981) or cybernetic (Van Waesberghe, 1982).

None of these critics wishes to totally eliminate Darwinism from the theory. They still see natural selection as the most viable explanation for a *creative* mechanism of evolution, fulfilling the role of preserving fitter phenotypes from a pool of random variants. But others see these criticisms as erecting "straw man" arguments (Stebbins and Ayala, 1981) and the proposed new themes of evolution as part and parcel of the modern synthesis simply because the synthesis is all encompassing and can presumably incorporate diverse knowledge into its frame-

work. It may be worthwhile here to record Simon's (1981) comment "that a theory that purports to account for everything may turn out to account for nothing." However, of one thing everyone is certain, the modern synthetic theory of biological evolution does not accept a Lamarckian model of change.

It is common textbook practice to contrast Darwin's theory of natural selection with the theory of acquired characteristics, ascribed to Lamarck. Lamarck's failure and Darwin's triumph are caricatured through a series of cartoons depicting giraffes feeding on the leaves of trees. Darwin's giraffes become long-necked through natural selection. Some would inherit *random genetic variations* that produce a slightly longer neck and allow them to reach the leaves more easily. These giraffes survive and are 'selected' to pass on their variations to subsequent generations. Lamarck's giraffes, in contrast, stretch their necks willfully to reach higher leaves compelled by inner "wants" and "wishes". This gradual willful stretching becomes acquired by their first generation offspring and all subsequent generations.

Neither Darwin's nor Lamarck's theory, as formulated, was sufficient to explain the mechanism of the inheritance of characteristics; how does like produce like? Darwin, independent of natural selection theory, proposed pangenesis, a process by which circulating particles (gemules) pick up information from all parts of the body and inject it into the sex cells. This notion clearly implied that selection might act upon variation *within* individuals rather than between individuals.

Lamarck, writing at the turn of the 18th century, had nothing to say about the mechanisms of heredity. Referring to the "preservations of acquisitions" by "generations of new individuals" he simply presented a concept which was a widely held belief during his day and back into history (Mayr, 1972; Boesiger, 1974; Burkhardt, 1980), or as Nanney (1983) says an idea "embedded in ancient folklore". Through the ages people have observed that physical traits are transmitted from generation to generation. They have also seen that these traits can be modified by influences of the environment. It is therefore not unreasonable to assume that these modifications may also be inherited. Zirkle (1945) notes that records and accounts of the inheritance of acquired characters reached their peak in the eighteenth century; more than twenty of Lamarck's contemporaries described the concept before he used it to explain evolution. Medawar (1977), among many others, has commented on the political incentives for believing in the inheritance of acquired characters by French Revolutionaries and Soviet policy-makers alike because it allows for acquired capabilities to be passed on with progressive improvement over generations (be it for the French state or Soviet agricultural output) rather than the *laissez-faire* like conception of society under Darwinism which proclaims inborn inequality and lifelong competition.

Neither was pangenesis a new concept when Darwin proposed it in the mid-nineteenth century. As early as 400 B.C. Hippocrates wrote "the seed comes from all parts of

the body, healthy particles will come from healthy parts and unhealthy from unhealthy" (ref. Zirkle, 1945). Pangenesis was overthrown by Weismann's doctrine of the Continuity of the Germ Plasm in 1883 which stated that heredity is brought about by the generation to generation transfer of a substance, "germ plasm", that is set aside from the rest of the body or soma in the developing embryo. It is fundamental to Weismann's theory that the germ plasm be handed down unaltered, unmodifiable by the environment during the life of an individual. Thus, information from modified somatic cells does not get into the autonomous germ plasm, the site of the forming sex cells.

Of course, Weismann's doctrine ignores a certain class of reproduction, the mitotic division of unicellular organisms to produce clones of free-living daughter cells. It also forms the basis for the current emphasis on the *genetic* individual as the primary unit of selection. Weismann's doctrine was later altered by the chromosome theory of inheritance which states that the hereditary factors (genes) are located on chromosomes in the nucleus of the cell. During the production of sex cells, meiosis, the number of chromosomes is halved which then join again the contributions of each parent at fertilization. Thus the hereditary material is equally distributed to all nuclei of all somatic cells of the embryo. Recent experiments in nuclear transplantation and molecular biology support the idea that the nucleus of any differentiated cell contains all of the genes ever utilized by that organism, i.e. a complete genome. But genetic totipotency is not sufficient for developmental totipotency (Browder, 1980). It is thought that during differentiation a large fraction of the total genome is transcribed into nuclear RNA in the nucleus but only a small part of this resultant RNA is allowed to pass into the cytoplasm to be translated into protein (Davidson & Britten, 1979; Stein, 1982). Certain cell-specific molecules are thought to determine which gene products among the newly transcribed RNA will leave the nucleus. This model thus explains why the union of a highly differentiated sperm and egg cell can direct embryological development or why the differentiated tissues of many plants and animals have regenerative properties. Grant (1977) has also noted that the evolution of sexual reproduction in eukaryotes has channeled and ordered genetic exchange between lineages by producing a chromosomal gene headquarters in the nucleus that directs development.

The appearance of Weismann's "germ plasm" theory, subsequent discoveries about the role of the cell nucleus in the production of gametes, and rediscoveries of Mendel's laws, should have sounded the death knell for the theory of acquired characteristics. However, from the 1890's to the 1930's when the modern synthesis was formulated there existed a wide variety of theories of evolution incorporating a variety of concepts of inheritance.

There was a continued belief in what Mayr (1980) terms "soft inheritance", the possible change in the genetic material itself (either over one generation or several generations) due to *acquired effects* in the parent's body.

These effects could be of 3 types:

1. direct effects (injuries or mutilations)
2. functional effects (related to the use or disuse of parts)
3. effects related to the influence of the surrounding environment (such as climatic variations).

All of these came to be associated with the Lamarckian theory of acquired inheritance in the middle of this century despite the fact that Lamarck had categorically denied that *direct* modifications in shape and organization of animals could be transmitted to future generations (Elliot, 1914). He did say that important modifications of the conditions of life induce modifications in animals' "needs" (besoins) so that animals act necessarily in a different way. He saw the form of an organism as an analysable interaction between structure and environment.

Lamarck's writings have been mistranslated and misinterpreted ever since his death. Cuvier's eulogy to Lamarck was, in fact, a scathing attack in which the word "desire" was substituted for "needs" in describing the Lamarckian theory (Cannon, 1959; Burkhardt, 1977). Ever after Lamarck has been attributed with believing in some "metaphysical inner necessity" (Lasker & Tyzzer, 1980) that drives organisms to improve themselves, a form of vitalism.

Those scientists labelled as neo-Lamarckians at the turn of this century believed variously in vitalism and accepted assorted versions of acquired inheritance. Mayr (1980) has pointed out that these beliefs were prolonged for several reasons. First, there was the protracted debate over mutation and biometrics or discontinuous versus continuous variation. Most naturalists understood mutation only in the deVriesian sense as a drastic, disturbing event and they could not accept that small selective differences could be important in evolutionary change. Therefore they listed a number of phenomena that they believed were consistent with soft inheritance but inexplicable under Darwinian natural selection. In addition, Mayr emphasizes that most of these early 20th century thinkers were essentialists (typologists) who saw selection as a purely negative process that could only eliminate unfit deviations from the ideal type, not as a creative process acting upon copious variability. More recently even Weismann has been labelled a neo-Lamarckian because he allowed that influences of climate (the third type of acquired effect) may very possibly produce hereditary variations (Matsuda, 1982).

From a modern vantage point Lamarckian inheritance can be said to embody two aspects. First, it requires that the environment directly produce favorable mutations, that is, controlled mutations. Under this claim, organisms, their physiologies or even their molecules would "perceive" felt needs and adapt their bodies accordingly. This postulate places creativity within the process of variation itself rather than with selection (Gould, 1982). Second, Lamarckian inheritance calls for these directed variations to be capable of being passed on to first generation offspring by the transfer of information from changed

somatic cells into germ cells.

It is possible to recognize the existence of several phenomena that may qualify as examples of Lamarckian inheritance. Some of these are readily accepted by scientists and scholars and are outside the realm of general biology. Within biology, there are some examples that are accepted but discounted as of minor importance. As well, there are suggested examples of Lamarckian biological inheritance that only a very few heretical biologists presently favor. What are these phenomena and what significance do they have for the synthetic theory of evolution?

It has been popular for at least 20 years not only for anthropologists writing general text books of anthropology, but for other social scientists, biological scientists, and philosophers to emphasize exosomatic, psychosocial or cultural evolution² as that which makes humankind unique, successful and evolutionarily innovative (Medawar, 1977; Popper, 1972). This non-genetic transmission of learned, cultural behaviors is Lamarckian in *procedure* and is now being subjected to quantitative analysis and theoretical evaluation by biologists (Cavalli-Sforza and Feldman, 1981; Pulliam and Dunford, 1980; Lumsden Wilson, 1981; Boyd and Richerson, 1983). Dawkins (1976) has coined the term "memes" for those heritable units of taught/learned information. Changes or variations in memes can be directed or controlled with foresight or intention in human cultures according to the Lamarckian model but of course, exosomatic inheritance is so named because it is not Lamarckian in *mechanism* since we know of no acquired cultural variations that pass as physical elements from somatic cells to germ cells.

The stated purpose of quantitatively analysing cultural transmission is to be able to predict variability in behaviors much like geneticists predict Mendelian ratios. In addition, students of behavior have asked, what is it that makes cultural transmission an adaptive evolutionary strategy? It is suggested that cultural transmission of acquired, taught/learned information allows for rapid transmission of modified phenotypes. In this way populations can track environmental fluctuations with fewer selective deaths. Boyd and Richerson (1983) tested this argument by comparing models of cultural and strict genetic transmission with varying environmental conditions. As expected they found genetic transmission to be most adaptive in rigidly determined environments but cultural transmission of acquired variation was found to be beneficial under a moderately broad range of environmental conditions. Yet, except for humans, only a restricted range of traits in a few species are culturally transmitted. This prompted Boyd and Richerson to ask, why is cultural evolution not more widespread among living organisms? But in fact, we know that many living organisms are characterized by a wide range of somatic and behavioral flexibility which has a bearing on arguments for and against Lamarckian inheritance and which I will return to later in the paper.

Within biology, a recounting of certain historical incidents illustrates how curious, unusual, unexplained phenomena are often promptly summoned upon as support

for popular theories. As Nanney (1983) tells us, cytoplasmic inheritance was a challenge and a threat to genetic orthodoxy in the 1940's and 50's. It was one of the "hard cases" which stubbornly refused easy accommodation to the chromosomal theory of inheritance and nuclear supremacy because of its refusal to follow strict Mendelian patterns. The Lamarckians of this period often cited it as support for their cause. But by the 1950's the "chromosome theory" was converted into a "nucleic doctrine" and the importance of cytoplasmic inheritance was trivialized since it became irrelevant whether replicating nucleic templates were located in chromosomes, mitochondria, plastids or other cytoplasmic organelles. Thus these cytoplasmic organelles were not special, they contained the same basic genetic material as cell nuclei and there certainly was no evidence at that time that they cavorted about freely within multicellular organisms moving from somatic to germ cells. Finally, the developed "central dogma" of molecular genetics solidified the view that information flow was one-way from DNA to RNA to protein so that an altered protein could not transmit change back to its informational molecule.

The central dogma seemed to establish the destruction of the second postulate of Lamarckian inheritance (soma to germ information flow) at the molecular level. And as Nanney points out (1983), much of genetics research in the 1940's was conducted to disprove the first postulate, directed mutation; showing instead that genetic changes in bacteria and other organisms arise by chance and are only selected by the prevailing environment, not specifically induced by that environment.

Yet, one example which has been cited as evidence of Lamarckian inheritance (Fine, 1979) is the symbiotic-origin theory which proposes that extra-nuclear organelles such as mitochondria, flagella and other organelles have their own genetic autonomy that allowed their ancient ancestors to invade primitive cells millions of years ago (Margulis, 1970). Thus, the very crucial evolutionary transition from prokaryotic to eukaryotic life may have been by the inheritance of acquired material. Recent sequencing of nucleic acids and proteins lends further support to the theory since similar sequences in eukaryotes and prokaryotes are presumed to have been derived from cognate sequences carried in ancestral forms and conserved for billions of years (Mercer, 1981). However, this past historical event of symbiosis has no bearing on present evolutionary mechanisms found in multicellular forms such as humans and which we presume to be strictly Darwinian.

Recently some interesting suggestions have been made regarding bacterial evolution. Bacteriologists now accept as a normal event that living prokaryotic species do trade genetic material back and forth between different cells by transformation, transduction or conjugation via extrachromosomal genetic elements (ECE's) such as phages and plasmids. Investigations of the phenomenon of multiple drug resistance have shown that an explanation for its occurrence lies in the "infectious" cell-to-cell spread of transferable resistance plasmids rather than the simulta-

neous occurrence of spontaneous mutations which confer resistance (Davey and Reaney, 1980). Consequently, Reaney (1976) has proposed that prokaryote evolution may have proceeded largely through the cell-to-cell transfer of ECE's, rather than by the "classical" mode of evolution which is the accumulation of many random mutations, in bacterial species with their short generation times and large population sizes. Davey and Reaney (1980) have expanded upon this hypothesis seeing extra-chromosomal elements as the "experimental" DNA of bacterial evolution which are able to engage in a rapid and adventurous evolution while the more basic cellular life processes are somewhat preserved in the more *conservative* structure of the bacterial cellular chromosomes. In a practical application of this possibility molecular biologists now utilize artificial genetic engineering in the form of recombinant DNA techniques to transfer genetic material from the cells of one species to another in the laboratory.

If Davey and Reaney's assertions are correct then a form of "acquired inheritance" would take up a central role, at least in prokaryote evolution. It would fulfill the second postulate of Lamarckian inheritance by being a form of immediate transfer of acquired heritable traits. However, one may argue justifiably to set this aside as a special case since prokaryotes do not exist as collections of somatic and germinal cells separated from one another as is the case for multicellular forms. Indeed, Darryl and Reaney point out that "such DNA transfer (of ECE's) means that strains, species and even genera of bacteria, when living in a grouped ecology, need not evolve as genetically insulated units" (1980). Campbell (1983) relates that more than 20 years ago he was criticized when he referred to lysogenization by phage (a process whereby the single copy bacteriophage genome becomes part of the genetic content of the host cell either at a specific site or randomly depending on the type of phage and is stably transmitted from generation to generation) as an example of Lamarckian inheritance. It was argued that Lamarckism had already been disproved with respect to traits determined by real genes and what bacterial viruses might do to their hosts is irrelevant. However, in 1984 the picture has changed somewhat. Genetic rearrangement is not an attribute exclusive to viruses but pervasive in living organisms. Campbell (1983) suggests that even the first postulate of Lamarckian inheritance (induced or controlled mutations) may be conceived of at the molecular level because of specific rearrangements of the heritable material. An example might be supplied by the bacterial transposable element Tn 917, the erythromycin resistance transposon. Mobility of this genetic element is specifically induced by low concentrations of erythromycin and this mobility can promote both amplification and interbacterial transfer under circumstances in which both processes may be selectively advantageous (Campbell, 1983).

Because of the rapid progress allowed by recombinant DNA techniques in understanding gene structure it is now clear that parts of the nuclear DNA of eukaryote cells are also highly mobile, moving about in the nucleus

during cell differentiation. In addition, these rearrangement processes are highly regulated (Campbell, 1983). These *transposable elements* (examples include the copia sequences of *Drosophila*, V130 genes of mice, Alu sequences of primates and the generation of antibody diversity in mammals) belong to the category of moderately repetitive DNA, possessing DNA sequence repeats at their ends. It now looks as if the process of patchwork rearrangement of nuclear genes and parts of genes is a common one in cell nuclei. In addition, the evidence that DNA can jump back and forth from cytoplasmic organelles to the nucleus expands the possibilities for gene mobility (Lewin, 1982). The possibility of cell to cell transfer is established for bacteria and suggested for eukaryotes. Interestingly, transposable elements show notable homologies with retroviruses (RNA tumor viruses). Retroviruses are RNA-containing structures that can synthesize DNA copies of their RNA via the enzyme, reverse transcriptase, and insert or "infect" these copies into the nuclear DNA of a host cell, becoming part of the genetic complement of that cell. The discovery of reverse transcriptase by Temin modified the "central dogma" of molecular biology by allowing for reverse information flow from RNA back to DNA, (although not from proteins to RNA).

In 1971, Temin discussed in his proviral hypothesis the possibility that retroviruses may have evolved from ancestral transposable element-like genes by successive cycles of transcription, reverse transcription and reintegration. He also suggested that retroviruses may act to direct somatic cell-to-cell nucleic acid transfer within the individual organism so as to promote a specific and integrated programme of embryogenesis. Others like Reaney (1976) and Davey and Reaney (1980) have suggested the same idea; that somatic cell-to-cell transfers of genetic material could help to direct cell differentiation and development in metazoans. But this proposal can be taken even further. In 1979, Steele suggested that there can be a transfer of cloned somatic gene mutations of immunoglobulin genes to an endogenous retrovirus which "captures" the mutated gene in the form of mRNA. This RNA virus crosses the tissue barrier partitioning the gametes in the gonads, infects the ova or sperm (either in the chromosomes or travelling as ECE's) and synthesizes a copy of germline DNA via reverse transcription. This model fulfills the notion of acquired inheritance but Steele still allows for *randomly produced* variation (in the form of cloned somatic mutations of lymphocytes) within the individual to be selected and then transmitted across the Weissman barrier.

Steele subsequently developed support for his argument by conducting experiments with mice. Male mice were rendered immunologically tolerant to foreign antigens via massive foreign cell infusions at infancy. When adult, these males were then mated to normal females. Gorczynski and Steele (1980) observed foreign cell tolerance in certain proportions of first and second generation offspring from these matings indicating that acquired Mendelian inheritance had occurred. Steele argued that a

retrovirus was the somatic cell to germ cell vector for the acquired tolerance. Unfortunately his experimental results have not been confirmed by others³. But Steel is not totally alone in suggesting a central role for viruses in metazoan evolution principally because of the observed strong resemblance between transposable elements and retroviruses (Anderson, 1970; Ycas, 1982).

The genomes of *endogenous* retroviruses are found in multiple DNA copies in the chromosomes of many vertebrates (Jaenisch, 1983) and are transmitted vertically as Mendelian genes in contrast to exogenous retroviruses which are transmitted horizontally by infection. Numerous experiments have been designed to determine whether endogenous viruses have always coexisted with their host species as germline determinants. Early mouse embryos exposed to exogenous Moloney leukemia virus integrated the virus into the DNA of their germline cells and transmitted it endogenously over the next generation (Jaenisch, 1983). The question is, could endogenous retroviruses "pick up" and incorporate any other somatic genetic material into germline DNA? No one has demonstrated such a mechanism. However, one very interesting discovery is that of small nuclear RNA pseudogenes in human genomes which are very common and which have been inserted back from RNA to DNA by some mechanism of reverse transcription (Marx, 1983). No one knows exactly how they got there but it is suggested that retroviruses have "accidentally packaged" the cellular RNA and introduced the complimentary DNA into cells during infection.

Not only would these various phenomena allow for retroviruses as agents of "nonconjugational gene flow" (somatic to germ cell transfer of genetic material) but also for transfer between quite dissimilar plant and animal lineages, that is, genes jumping from species to species. Supportive evidence for interspecific gene flow is suggested by the very close homologies between certain genes in species that have been separated for millions of years (Hyldig-Nielsen, et al., 1982; Scheller, et al., 1981).

Following a slightly different path of enquiry, Buss (1983) has pointed out that Weismann's doctrine of the autonomy of the germ plasm lacks universality because the extent of developmental determinism of body cells varies enormously among multicellular taxa. To explain this he defines three broad categories of developmental mode in organisms: 1) *somatic embryogenesis* in which at least one cell lineage remains totipotent through the life cycle of the animal; 2) *genetic development* which only germ cells remain totipotent, but these remain undetermined until late in ontogeny; and 3) *preformistic* development, where only germ cells are totipotent, and these are sequestered very early in the embryo. Developmental modes 1 and 2 least closely approximate Weismann's doctrine. These modes characterize a diversity of organisms such as the fungi, plants, protists, molluscs, annelids and many arthropods and in their case the notion of genetic individuals is less distinct. That is, there is a greater opportunity for somatic variations arising in totipotent cell lineages to find their way into gametes or ramets (asexual

propagules) a description which would readily fit the second postulate of Lamarckian inheritance. Organisms characterized by preformistic development are actually rare in the living kingdom according to Buss's tally. They include mammals, nematodes and rotifers, but of course, being members of one of these orders probably partly accounts for humans' focus of interest on animals with preformistic development. Buss argues that the number of extant species in phyla with epigenetic or somatic embryogenic development is orders of magnitude higher than for phyla with the preformistic developmental mode. This is perhaps accounted for by a greater capacity to speciate in the abundant phyla because of the incorporation of somatic variations into subsequent generations. Conversely, the evolution of multicellularity also produced a new selection pressure, the necessity to control the proliferation of undesirable somatic variations and restrict their access to reproductive tissues. Thus mechanisms such as the architecture of cell walls, somatic tissue incompatibility systems, phagocytosis, etc. have probably evolved to prevent such incorporations occurring. In fact, such mechanisms have been argued to be the main prohibitors to Steele's model of retrovirus incorporation of somatic variants into the mouse or human genome. If such an incorporation could occur indiscriminately one asks, how would the gametic genomes select from the variety of desirable and undesirable somatic variants (Crow, 1980)?

Could a Lamarckian mode of inheritance utilizing the mechanisms described here operate on human populations? The most cogent argument against such an event is that detailed by Bateson (1979). Bateson argues that if Lamarckian inheritance were the rule the whole process of evolution would become tied up in the rigidities of genetic determination. His argument centers around the importance of somatic flexibility. Somatic change, says Bateson, is simply bodily change brought about during the lifetime of the individual. Somatic change is hierarchic in structure; it deals with immediate adjustments at the superficial (most concrete) level and more general adjustments at deeper (more abstract) levels. A man travelling from sea level to 12,000 feet experiences immediate somatic changes such as panting and tachycardia. An extended visit to the mountains results in long term acclimation such as respiratory changes, high hemoglobin levels, etc. Populations living in mountainous areas may perhaps pass on some of these characteristics to their offspring but a shift from somatic flexibility to genetic stability would only occur if environmental stresses are constant. Genetic change is the highest, most abstract component in the hierarchy of adaptive adjustment, and should therefore be the least reversible. Lamarckian inheritance without selection would eat up somatic flexibility because all acquired change would enter the genome. There is no doubt that the biological world looks like a product of Lamarckian evolution. And evolutionists have generally ignored the valid laments of some of the earlier Lamarckians and the more recent integrationists who point out that environmental change and organisms,

by their own life activities and because of somatic and behavioral flexibility, determine which aspects of the outer world make up their environment. The rigidity of a genetic change is avoided and delayed until environmental circumstances or stresses previously handled by the soma are themselves permanent.

I believe that much of the dissatisfaction with the neo-Darwinian synthesis and the attractiveness of Lamarckian models lies with the unwillingness to accept a random component in evolution (chance versus necessity). But as Gould (1982) and many others before him have noted, selection provides for the creative component of evolution, natural selection is not simply the destroyer or eliminator. Dobzhansky says (1974) "Mutation, sexual recombination and natural selection are linked together in a system which makes biological evolution a creative process. (Natural selection) is a cybernetic servomechanism that channels the flow of information from the environment to the gene pool." If endogenous retroviruses or some other extrachromosomal element could pick up induced somatic change and insert it into the germline DNA of multicellular forms (and there doesn't seem to be any fundamental barrier to such an activity based on what we are learning about cells, viruses and genetic molecules) such a mechanism would have to have a selection process so that only certain outcomes of the random could endure. However, if one could demonstrate the pervasive existence of the first postulate of Lamarckism, directed or controlled mutations, such as is suggested by the Tn917 transposition example, then natural selection would be unnecessary because creativity would lie with variation itself. Despite some recent proposals for the existence of such a phenomenon (Cook, 1977; Rosen and Buth, 1980) neither those following the mainstream of the evolutionary synthesis or the great majority of their critics accept such a notion.

NOTES

1. It is important to note that they are referring to phenotypic features. The neutral mutation theory can represent a justifiably separate process under the synthetic theory because neutral genetic changes are found only at the level of genes, being inviable to Darwinian processes of selection at the phenotypic level.
2. Though this last term has other misleading associations, particularly for anthropologists, in that it can be taken to mean an evolution of culture rather than an evolution of which culture was an agency.
3. Gorczynski et al. (1983) have since suggested a maternally derived origin for the transmission of tolerance to offspring of neonatally tolerant fathers based on further breeding experiments.

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A CRITICAL REAPPRAISAL OF THE ENIGMATIC "ZINJANTHROPUS" (OH5) PROFILE.

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Abstract: A careful reappraisal of the original OH5 racial reconstruction reveals that an excessive amount of reconstructive material appears to have been employed resulting in an overly orthognathic profile. It can be demonstrated that by carefully re-aligning a few fragments, the lower portion fits much more closely to the upper facial portion. The revised re-alignment results in a much more appropriate facial angle, a reduced facial height, and a greatly altered overall physiognomy, featuring considerably less robustness. This revised reconstruction could have significant implications in the assessment of Plio- Pleistocene hominid phylogenetic relationships and systematics.

Résumé: Une réexamination de la première reconstruction raciale de O.H.5, a relevé qu'une reconstruction excessive a donné un profile orthognatique exagéré. On peut démontrer que quand quelques fragments sont remaniés, la partie inférieure de la machoire s'aligne plus précisément avec la partie supérieure du visage. Avec la nouvelle reconstruction l'angle facial est beaucoup plus logique, l'hauteur du visage est réduit, la physionomie générale nettement changée, se montrant en conséquence beaucoup moins robuste. Cette nouvelle reconstruction de O.H.5. pourrait tenir un rôle capital dans la ré-évaluation des relations phylogénétiques des hominidés de l'époque du plio-pléistocène.

Key Words: Zinjanthropus, Reconstruction, Plio-Pleistocene Hominids, Systematics.

INTRODUCTION

Ever since Mary Leakey's discovery of Olduvai Hominid 5, this fossil has been the center of controversy. Originally Louis Leakey suggested that OH-5 represented an early member of the human lineage, the fabricator of the Oldowan tool tradition, and finally that it warranted a new taxon, "*Zinjanthropus boisei*" (Leakey, 1959). Robinson (1960, 1962) suggested that the fossil was an excellent example of *Paranthropus robustus*. If Robinson's insightfulness had prevailed, much of the current phyletic, as well as taxonomic confusion surrounding Plio-Pleistocene hominids would have been alleviated.

When Jonathan Leakey found OH-7 in 1960, Louis Leakey became convinced that the 1959 specimen, OH-5, was no longer a likely candidate for early human ancestry. With the publication of *Homo habilis* in 1964, "*Zinjanthropus*" was relegated to a position of phyletic insignificance. Louis Leakey developed a theory which posited multiple, contemporaneous lineages in East and South Africa, this is illustrated as scheme A in Fig. 1 (Leakey, 1966). This view was to be challenged in the late sixties by the rise of the "Single-Species Hypothesis", a by-product of the overworked inductive reasoning of an American school of thought spear-headed by C.L. Brace and M. Wolpoff (Fig. 1, Scheme B, Brace, 1972; Wolpoff, 1968), which assumed that the two lineages of Plio-Pleistocene hominids represented males and females of the only known mammalian species with qualitatively dimorphic dentitions. This idea, to a much greater extent than Leakey's, has done more to hamper understanding in

this critical area of human origins than anything since the "Piltdown hoax" and until the arrival of "*Australopithecus afarensis*", the latest *nomen nudum* to have a significant obfuscating effect on naive students and laypersons (Tobias, 1980).

Among the major difficulties in attempting to perceive our origins are the stumbling blocks resulting from erroneous fossil reconstructions. In some cases these unfortunate attempts can result in decades of misunderstanding. A classic case in point: when Franz Weidenreich and Lucille Swann attempted to reconstruct the skull of "Peking Man" in the 1930's, the total lack of any reasonably complete face for *Homo erectus*, anywhere in the world, combined with the dissociated nature of the Choukoutien material made it virtually inconceivable that a reasonably accurate reconstruction could result. Weidenreich and Swann obviously made a gallant effort, but recent discoveries of *Homo erectus* skulls of a fairly complete nature such as the Petralona skull from Greece (Hemmer, 1972) and ER-3733 from Kenya (Leakey and Walker, 1976), coupled with the suggestion that the mandible employed by Weidenreich and Swann was from a considerably smaller individual than the cranium (F.C. Howell, personal communication, 1976) suggest that the resulting reconstruction underestimated the relative facial size. The general underestimation of *H. erectus* faces, which derived from the "Peking Man" reconstruction, has resulted in significant confusion regarding the phyletic relationships of *H. erectus* and later Neandertal populations

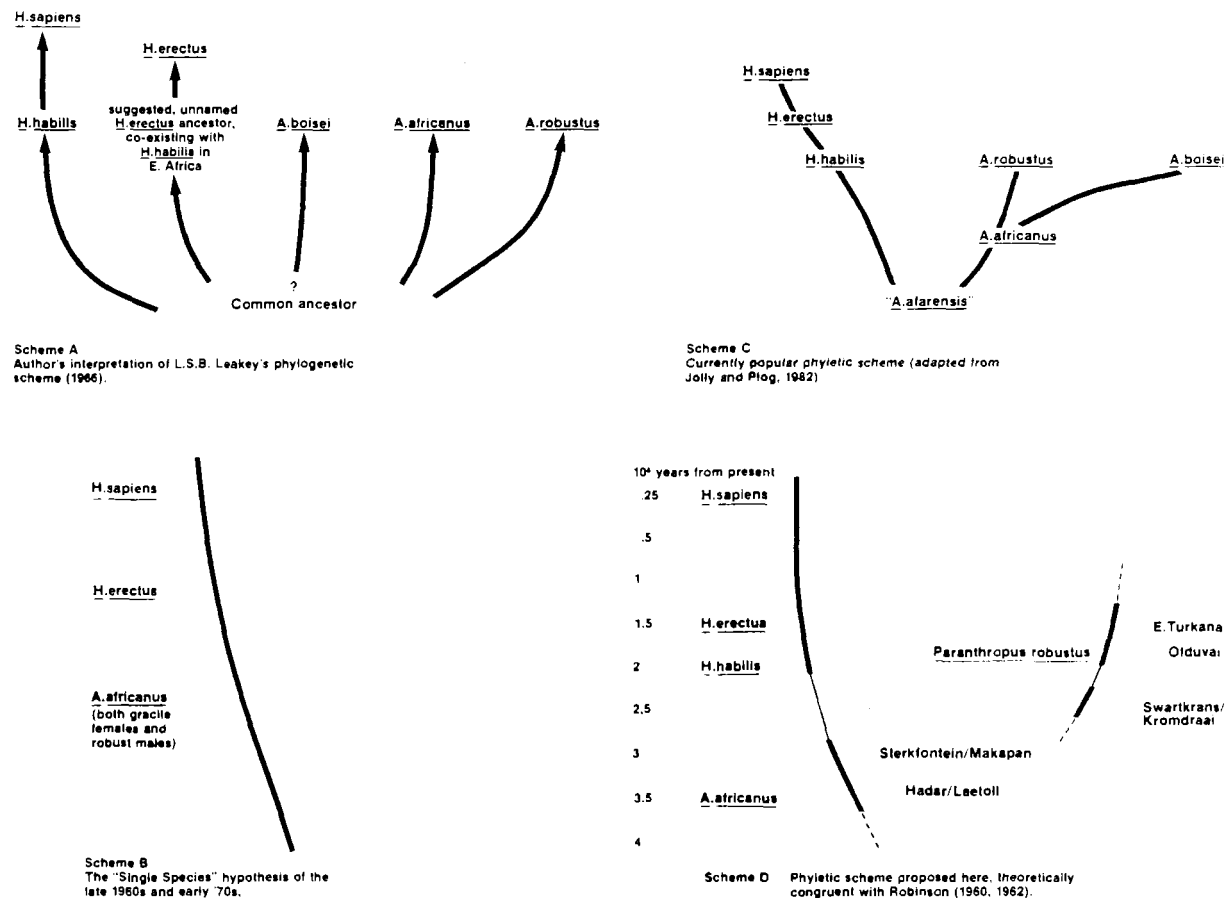


Fig. 1 Alternative Plio-Pleistocene hominid phylogenetic schemes discussed in text.

over the past several decades. Recently, the existence of *Homo erectus* in Europe has been questioned (Stringer, Howell and Meleutis, 1979) reflecting this continuing confusion.

A more recent example of probable misrepresentation of fossil morphology, though deriving from totally different causes, is the modeling of the "*A. afarensis*" cranium. While Weidenreich relied on his consummate knowledge of modern human anatomy in rendering the face of *H. erectus* from China, and thus created the error, Johanson and White, not wishing to run such risks, used a palate (AL 200) and many tiny, dissociated cranial fragments, and relied on the Hammon-Todd collection of chimpanzee skulls to guide their judgement in producing their version of their species.

THE OH5 RECONSTRUCTION

The subject of this discussion is yet another reconstruction. Mary Leakey's 1959 discovery of Olduvai Hominid 5 represented the culmination of years of arduous toil in Olduvai Gorge which, while archaeologically rewarding, had been particularly frustrating in terms of the dearth of meaningful hominid fossils unearthed. The Leakey's enthusiasm over their exciting new discovery is

understandable and was fully justified. They had found the most complete robust australopithecine cranium known up to that time; the first Plio-Pleistocene hominid to be absolutely datable; and the first hominid remains to be found in undoubted association with Oldowan stone tools. Unfortunately, this enthusiasm resulted in the conclusion that the fossil *must* represent not only the fabricator of the Oldowan tools but might also be representative of a totally new and previously unrecognized hominid lineage warranting a new taxonomic appellation.

The fossil was named "*Zinjanthropus boisei*" by Louis Leakey (1959) while Mary Leakey undertook to piece together the fragmented, though remarkably complete, facial portion of the cranium (Tobias, 1967; R.E.F. Leakey, personal communication, 1971). I suggest that the desire to see this 1.75 million year old hominid as our direct ancestor led Mary Leakey to model too orthognathic a facial angle, which resulted in an awkward occlusal plane relative to the Frankfort Horizontal and gave an over pneumatized appearance to the face in general. This, in turn, has lead many workers to refer to "Zinj" as hyper-robust and justifies, to a large extent, the original contention of a third australopithecine lineage (Leakey 1959; Tobias, 1967). For some time I had perceived that the fragments of the face could be assembled in a much

more compact fit. It appears that an excessive amount of modelling material was used in the original reconstruction.

Prior to the 1959 discovery of OH-15, the most complete *Paranthropus* cranium available was Sk-48 from Swartkrans. This specimen had suffered considerable damage during fossilization and subsequent recovery, and hence is not the best paradigm of *Paranthropus* skull morphology. After Richard Leakey discovered the magnificently preserved ER-406 cranium in 1969, he acknowledged (personal communication, 1971) that the OH-5 face, as rendered, was probably too flat.

Figures 2 through 7 compare the frontal and lateral views of both the original OH-5 reconstruction and the revised reconstruction with KNM-ER 406, probably the best preserved *Paranthropus* skull known to date. The reduced facial height and slightly smaller cranial size are apparent.

PHYLETIC AFFINITIES

The original "Zinj" reconstruction and its eventual descriptive monograph, (Tobias 1967) appeared during a time of refreshingly divergent theoretical leanings in paleoanthropology, quite unlike the current conservative atmosphere, almost single-minded in its theoretical approach. The once popular "single-species hypothesis" based on certain interpretations of South African data, led to a major controversy fueled by the suggestion of a third lineage in East Africa. This confusion ultimately resulted in the currently popular, unsatisfactory situation where all of the australopithecines are typically regarded as a single genus with three or four species presently being recognized (see Fig. 1, scheme C).

Much of this confusion would evaporate if we recognize (as Robinson did in 1960) that OH-5 is a large, fairly complete skull of *Paranthropus*, not significantly different from material previously recovered at Kromdraai and Swartkrans.

The phyletic affinities of the *H. habilis* and "*A. africanus*" hypodigms are almost certainly with the material previously recognized at Sterkfontein and Makapansgat. Since the workers in East Africa have demonstrated the coexistence of both lineages (Leakey, Tobias and Napier, 1964; Leakey and Walker 1976) and since developing awareness of the nature and degree of the variation in Plio-Pleistocene hominids has virtually resolved the question of generic separation (Leakey and Harris, 1975), it is time to overhaul the artificial, unwieldy and recent, taxonomic muddle.

This new reconstruction of the OH-5 cranium, accomplished by the realignment of fragments, without the loss of any major pieces, demonstrates a profile much more congruent with known South African *Paranthropus* fossils such as SK-48. Together with ER-406 and a number of other fossils, particularly mandibles such as Natron (Leakey and Leakey, 1964), SH-7A-125 from Omo (Howell, 1969) and ER-729 (Leakey, 1970), it clearly demonstrates the presence of *Paranthropus robustus* in

East Africa. Hopefully, it will help to diminish the idea of a separate (hyper-robust), phyletically distinct lineage in East Africa.

CONCLUSION

We are able to recognize two (and only two) lineages of Plio-Pleistocene hominids, separated at the generic level (Fig. 1, scheme D). The OH-5 cranium, like ER-406 and the rest of the robust specimens from East Africa, should be assigned to *Paranthropus robustus* (Broom, 1938). *Australopithecus africanus* (Dart, 1925) has obvious taxonomic priority for our lineage, but recent doubts have arisen as the result of attempts to thrust the Hadar material into the lime-light as the earliest representatives of human ancestry, and warranting recognition as a new species, (Johanson, White and Coppens, 1978). Whether the Hadar fossils represent our earliest ancestors, or not, is an issue for the geochronologists to resolve, but does not, apparently, warrant any restructuring of hominid systematics (Tobias, 1980).

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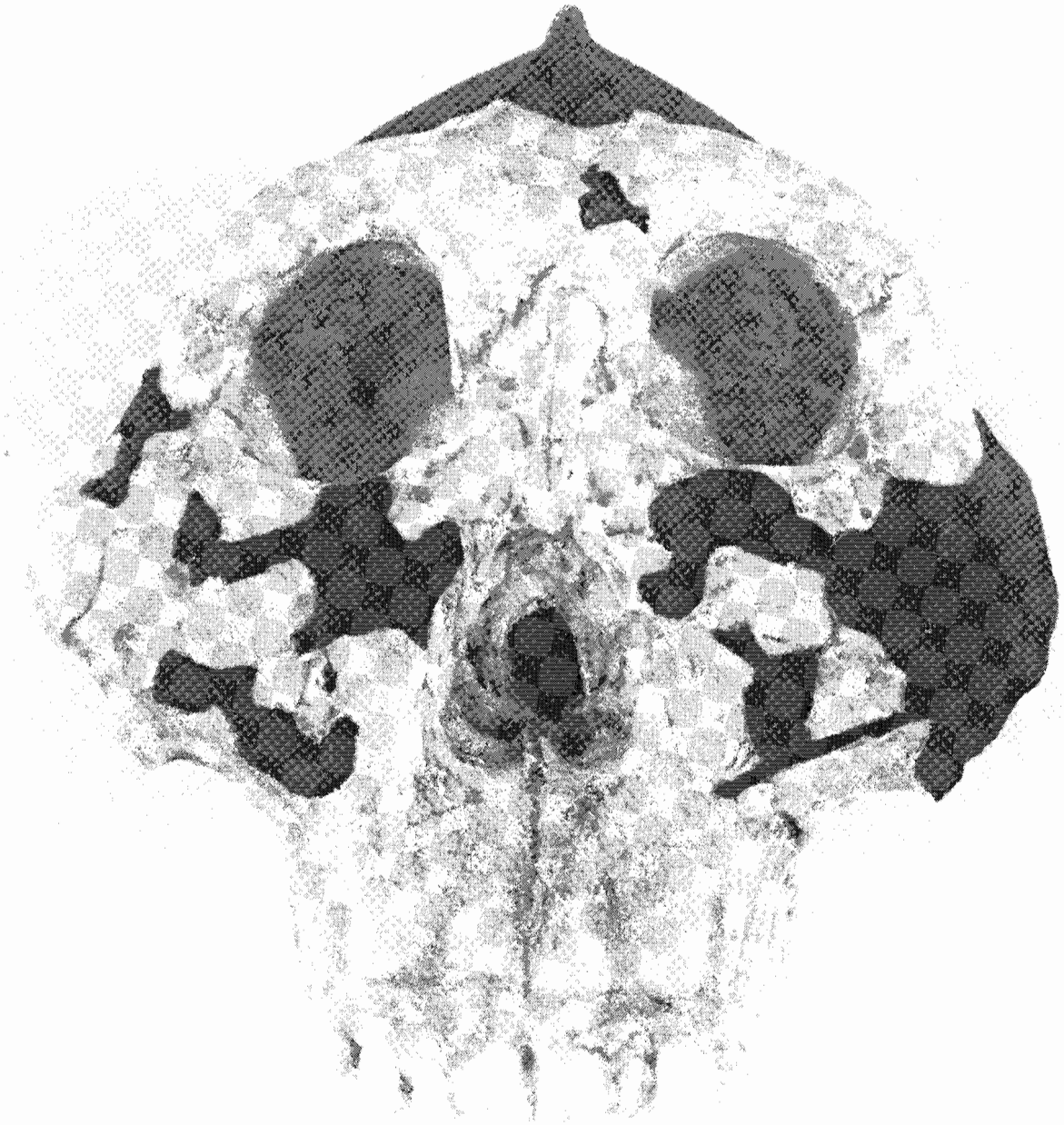


Fig. 2 Original Leakey/Tobias OH5 reconstruction (*Norma frontalis*).



Fig. 3 Revised OH5 reconstruction (*Norma frontalis*).

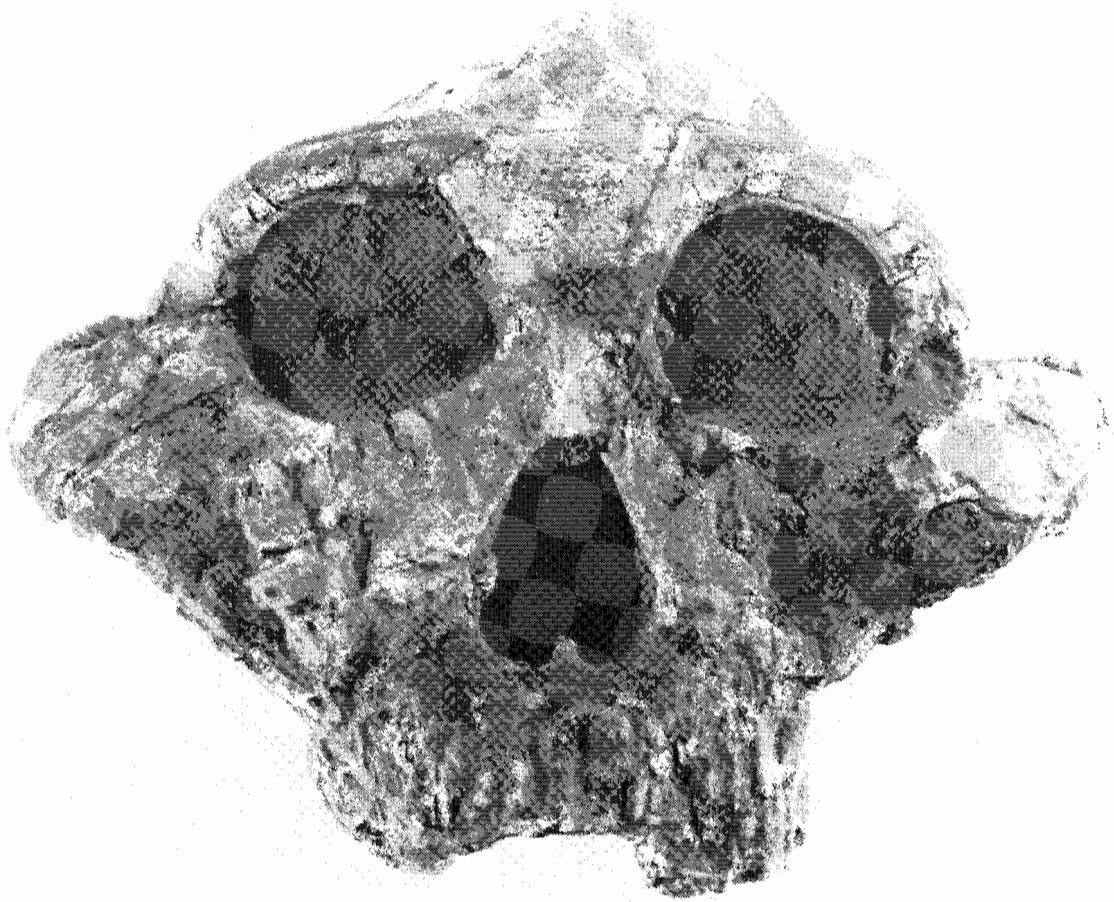


Fig. 4 KNM-ER406 cast (*Norma frontalis*).

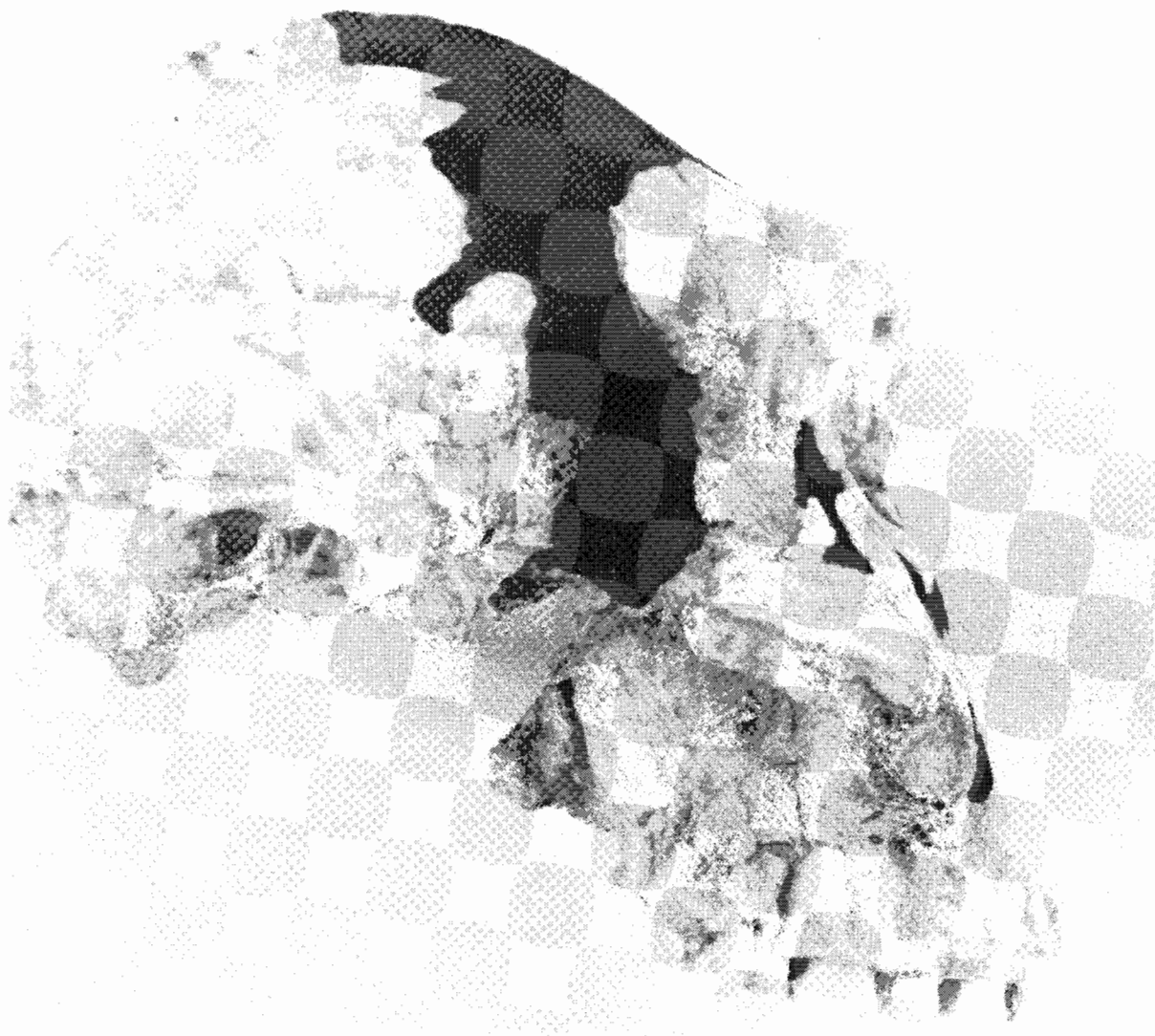


Fig. 5 Original Leakey/Tobias OH5 reconstruction (*Norma lateralis*).

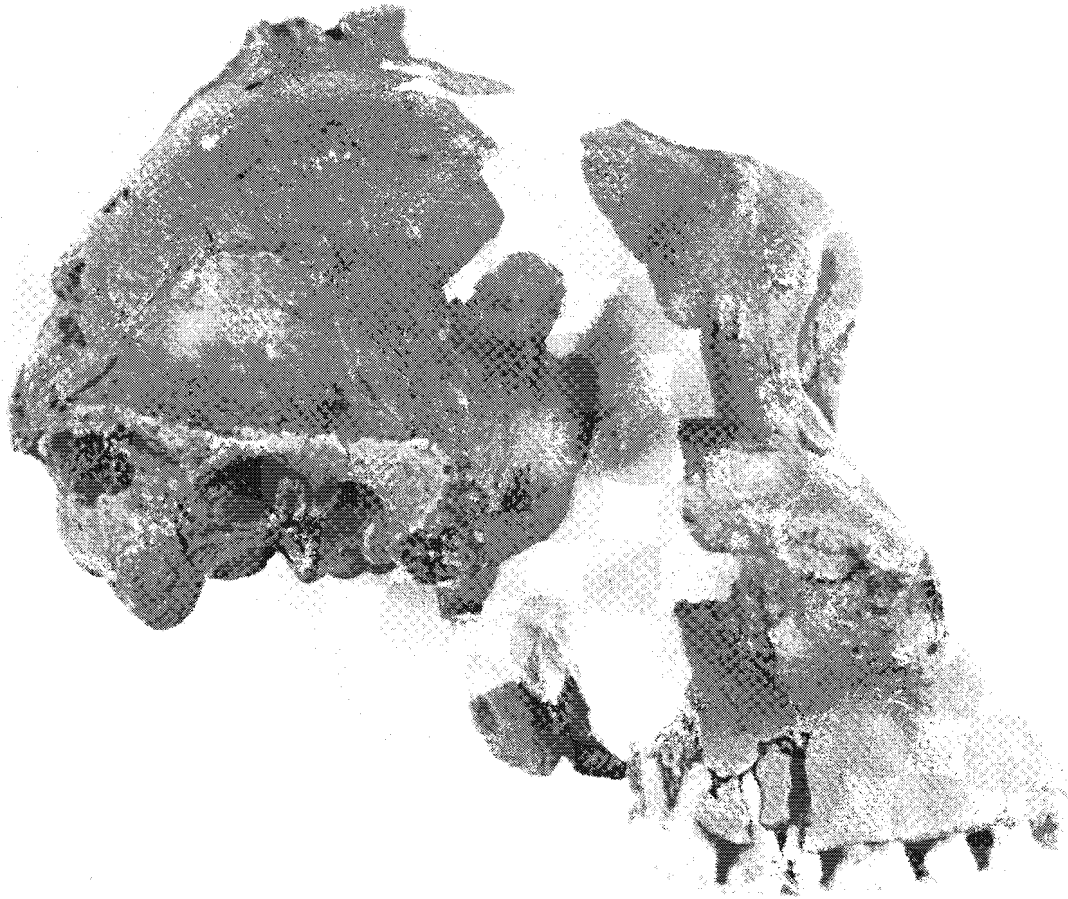


Fig. 6 Revised OH5 reconstruction (*Norma lateralis*).



Fig. 7. KNM-ER406 cast (*Norma lateralis*).

NOTES TO CONTRIBUTORS

MANUSCRIPTS

Please submit three copies. These must be typewritten and double-spaced throughout (text, quotations, tables, legends, notes and references) on one side only of 22 x 28 cm (8.5 x 11) paper with 2.5 cm (1 in) margins. Tables should be placed on separate pages at the end of the manuscript. All pages should be numbered consecutively beginning with the title page. The title page should include the title, author(s) and address(es).

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FIGURES

These must be submitted as either original drawings in black ink or as glossy prints. If possible, lettering should be a sans-serif type face (e.g., Univers Medium which is available on transfer sheets) or produced by Leroy lettering guides. Typewritten legends within a figure are not acceptable. Please allow for up to 50% reduction if figures are not submitted at the following camera-ready sizes: full page (including legend and title), 15 x 23 cm (6 x 9); half page, 15 x 11.5 cm (6 x 4.5); single column, no wider than 8 cm (3 in). Colour photographs and fold-out figures cannot be accepted unless financed by the author. Figures which do not conform to acceptable standards will be returned to the author for representation. Marginal notations on the manuscript should indicate where figures and tables are to appear.

NOTES

These are to follow the text and precede the list of references. They should be numbered consecutively. Footnotes for tables should be indicated within the table by lower case letters (a, b, etc.) and appear below the table.

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Canadian Journal of Anthropology

Revue Canadien d'Anthropologie

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